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ZOOPLANKTON PRODUCTION AND ENERGY FLOW- TOWARDS A BIOLOGICAL MODEL OF SOUTHAMPTON WATER.

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ABSTRACT

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ZOOPLANKTON PRODUCTION AND ENERGY FLOW -TOWARDS A BIOLOGICAL MODEL OF SOUTHAMPTON WATER.

by Andrew Garwood Hirst

Growth rates, production and the ecology of calanoid copepods, together with abundance of meroplankton, were examined within Southampton Water, U.K. Estimated biomass values of calanoid copepods are greater in the inner estuary (ie. total range found was between 0.0206 and 17.844mgCm^{-3} at Cracknore), and lower at the mouth of the estuary (ie. between 0.0006 and 15.175mgCm^{-3} at Calshot). Estimated annual calanoid copepod production rates were typically <290mgCm^{-3}yr^{-1} at the estuary mouth, while mid-estuary rates averaged ~530mgCm^{-3}yr^{-1}. Estimates of other pelagic and benthic components were also derived to allow a box model of annual carbon production rates of the dominant compartments to be established. Calanoid copepod annual production rates represent around 0.5% of total annual primary production, while estimates of ciliate annual production were 6.2 to 9.3 times greater than the copepod rates. This study therefore confirms the dominance of the microbial community in this area with regard to carbon ingestion and production.

Calanoid copepod weight-specific growth rates were found to vary between 0.008 to 0.378d^{-1} when measured in situ at Calshot. Biomass of calanoid copepods was very low in comparison to many other temperate areas, which may be the result of high flushing rates and the relatively lower growth rates. The calanoid production rates are lower than in most other estuarine and neritic areas previously studied. Gelatinous predators within the estuary appear to have strong impacts upon mesozooplankton numbers at times, even though their apparent production and ingestion demands are much less than in many other neritic areas. These impacts are pronounced as a result of the low biomass and production rates of calanoids. Annual gelatinous production rates were higher in the upper estuary, where they reach 27.5mgCm^{-3}yr^{-1} at Cracknore, with annual ingestion demands at the same site reaching 77.2mgCm^{-3}yr^{-1}. As the mouth of the estuary gelatinous production ingestion demands are little over 1.6mgCm^{-3}yr^{-1}. The gelatinous predators may prey heavily upon meroplanktonic larvae in addition to copepods, the initial weight of such meroplankton is highlighted as a potentially important source for these predators, and as a benthic-pelagic energy-matter pathway.

Weight-specific growth rates of marine copepods are shown to be dependent upon body size using compiled data from many sources from the poles to the tropics. From the compiled results a new empirical model of copepod growth, dependent upon temperature and individual body size, is produced. Preliminary examinations appears to show that the equation may be more appropriate for net zooplankton production rate predictions than contemporary models.

The production limits to a species population are described, highlighting the importance of recycling of production in pelagic systems. The consequences of compartmentalization, with particular regard to energy-matter flux and recycling are examined, and shown to be of fundamental importance.

'Alexander is said to have wept because there were no more worlds left to conquer. Plankton ecologists have nothing to cry about.'

-Turner and Roff (1993)

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CHAPTER 1

AN INTRODUCTION TO ZOOPLANKTON PRODUCTION AND NERITIC ENERGY FLOW MODELS.

1.1 INTRODUCTION

Production has become a widespread measure in terrestrial and marine ecology as a means of quantification of the processing rates of species, and as a tool to examine biological interactions. It is also used as a major way of examining energy flow and the pathways which energy, matter and nutrients take. Determination of growth rates and secondary production estimation are currently important foci of zooplankton ecology. Zooplankton secondary production has been increasingly quantified and examined in recent years, it being important with regard to the understanding and the effective management of resources in the marine environment. Growth is also of interest as an indication of a populations physiological and nutritional state. The many reviews on production in fresh and marine waters is a testament to the interest it generates among scientists (eg. Mullin, 1969; Edmondson and Winberg, 1971; Winberg, 1971; Winberg *et al.*, 1971; Greze, 1978; Conover, 1979; Downing and Rigler, 1984). The purpose of the present investigation is to develop the topic of zooplankton growth and production, to investigate the ecology and population dynamics of zooplankton populations in Southampton Water, and to develop a box model of carbon production and flow within this area.

The production of a population over a specific period of time is defined as the sum of growth increments of the individuals existing at the beginning of the period and born during this period (Winberg, 1968). This includes not only the growth increments of the individuals surviving to the end of the period, but also the increments of the individuals which do not survive to the end of the period owing to mortality, predation, etc. Accordingly the production of a population can be divided into:

1. Growth increment of individuals existing at the beginning and surviving through the time interval.

2. Growth increment of individuals existing at the beginning of the period but dying before its end.

3. Growth increment of individuals born during the period and surviving to the end.

4. Growth increments of individuals born during the period and dying before its end.

5. The initial weight of all individuals born throughout the interval.

Hence production (P) for a given volume or area can be defined simply by the equation:

$$P = B_t - B_o + B_e \qquad (1)$$

Where B_t is the population biomass at the end of the period

B_o is the population biomass at the beginning of the period

and B_e is the total biomass of individuals eliminated during the period.

The earliest published record of an estimate of secondary production conducted in the aquatic environment was that produced by Boysen-Jensen (1919). The introduction of a conceptually correct method is also attributed to this work, equation 1 being equivalent to the formula of Boysen-Jensen. Production estimates have previously also been divided into the sum of growth increments 'somatic production', and the initial biomass of new-born individuals 'germinated production' (Zaika, 1972). Thus total production is the sum of both of these terms, indeed equation 1 incorporating them both. The growth of individuals involves not only somatic cells, but the growth of gametes, exuviae, and other separable parts of the body. Production is thus the formation of new biomass within an interval of time, regardless of whether that biomass survives to the end of the time interval (Ricker, 1946; Allen, 1951; Winberg, 1971). While its definition is precise, its accurate determination may however be extremely problematic for many zooplankton groups (see for example Huntley and Lopez, 1992).

There are many difficulties associated with working in nearshore and estuarine regions, although as a result of their accessibility, and the relatively lower effort needed for their study in comparison to offshore areas, they have been more extensively studied. The marine environment can be divided into two broad categories, namely the benthic environment and the pelagic environment. The pelagic environment is defined as the water column whereas the benthic environment is defined as the surface and underlying volume below the water column. These two 'volumes' or regions are very different even though organisms may live across these boundaries. Planktonic organisms are those which live in the water column, while benthic organisms are those which live in, or on the bottom. In the present investigation it is the planktonic community which is to be studied with most effort, although in attempting to appreciate energy-matter fluxes within Southampton Water, the benthic environment has been included.

Plankton is typically difficult to quantify in terms of abundance, biomass and distribution, particularly in comparison to the benthos, because of its fast turnover rate and great temporal and spatial variability. A major problem associated with investigating the ecology of pelagic organisms in nearshore areas, particular estuaries, is the problem of tidal fluxes and the effects these may have upon the abundance and distribution of planktonic organisms. Estuarine areas are subject to marked changes in the numbers, types and biomass of pelagic organisms, as well as in physical and chemical properties, over very short time periods. These fluctuations are the result of vertical and horizontal movements of the water environment, in addition to active changes in positioning by the zooplankton themselves. Since production estimates and other measures of the processing rates of zooplankton usually rely upon measurements of abundance and biomass, then accurately describing such rates are made doubly difficult in an environment where the rate per individual is variable with time and place, and the location of individuals is variable. Neritic and estuarine areas are typically not 'closed', rather they are remarkably 'open', ie. they are systems which have a large amount of exchange with other external areas. Since the production defining equation given above is strictly a measure of production in a closed system the equation has to be altered to allow for measurements of production in a non-closed system, this is undertaken in conjunction with an examination of the sources of energy-matter to predators in a non-closed system in Chapter 6.

To date there have been relatively few detailed models combining measures of energy and/or matter flux through a multitude of organisms in nearshore communities, and most published studies examine single components of such systems. Those which assess more than one or two trophic levels typically rely heavily upon many assumptions in construction and in the estimates themselves. Some are so heavily dependent upon untested assumptions that they must be regarded as little more than 'guesstimates' (see Mills, 1980). Assumptions made in the construction of food webs may typically include those relating to the 'design' of the food web (and pathways of energy-matter), as well as in the compartmentalization of the system. Some of the ways in which compartmentalization may change the interpretation of food webs, and also cause erroneous measurements of energy-matter flow, are covered in Chapter 7. Researchers are limited by time and effort, and as such most examinations of energy-matter flux and production through marine systems are limited to small parts of the community, or must draw upon many different pieces of individual work ie. they are compilatory in nature. 'Compilation' energy-matter networks have been described as often little more than 'exercises in fitting and reconstruction' (Roff *et al.*, 1990). Listed in Table 1.1.1 are a number of energy-matter networks which have been constructed for nearshore planktonic/benthic communities.

COMMUNITY TYPE REGION	NUMBER OF COMPARTMENTS	NUMBER OF TROPHIC LINKS	SOURCE
Neritic Community (benthic and partial pelagic) Temperate, Bay of Morlaix, France (Average depth 20m)	12	26	Chardy and Dauvin, 1992
Neritic Community (pelagic) Temperate, Southampton Water, U.K. (Average depth 15m)	5	4	Leakey *et al.*, 1992
Neritic Community (pelagic) Tropical, Kingston Jamaica (Average depth 20m, Station depth 30m)	26	96	Roff *et al.*, 1990
Neritic Community (pelagic) Temperate, Gulf of Maine, U.S.A. (Average depth 25m)	4	4	Montagnes *et al.*, 1988
Shelf Community (pelagic) Temperate, English Channel	7	19	Vézina and Platt, 1988
Shelf Community (pelagic) Temperate, Celtic Sea	7	20	Vézina and Platt, 1988
Shelf Community (pelagic and benthic) Temperate, S.E. Nova Scotia (Average depth 90m)	11	17	Mills, 1980
Slope Community (pelagic and benthic) Temperate, S.E. Nova Scotia (Average depth 320m)	12	19	Mills, 1980

TABLE 1.1.1 A summary of some contemporary energy-flow models for neritic and shelf areas which include production estimates for the pelagic and in some cases also the benthic biotas.

Construction of box models of energy-matter flux are continually improving as more information is gathered, both specific and general, and will continue to improve as more is understood about trophic relationships, feeding and processing in natural communities. The complexity of the energy-matter models published varies dramatically. Some of these contemporary models (see Table 1.1.1) incorporate 5 or fewer separately defined compartments (eg. Montagnes *et al.*, 1988), while others have greater than 25 (eg. Roff *et al.*, 1990). The complexity of these models depends upon the specific aims of individual investigators, and the amount of information available to them, as well as the effort expended. The number of links (pathways of energy-matter flow) also varies dramatically between studies, some show a very small number of links, and may grossly over-simplify flow complexity (eg. Leakey *et al.*, 1992). Others may include more realistic energy-matter recycling processes (eg. Chardy and Dauvin, 1990). The more effort expended on examining structure and functioning of systems, then the greater the understanding, and generally the increasing described complexity of the system (Pimm *et al.*, 1991). Presumably however, laws of diminishing returns apply, and a time when extra effort will lead to little or no further understanding of system functioning will come about.

1.2 MESOZOOPLANKTON PRODUCTION

Over the last century many efforts have been made to estimate productivity in marine systems. Studies have been carried out successfully on phytoplankton, macrobenthos and fish, however, far less success has been achieved for zooplankton (Tranter, 1976). The progress made in measuring phytoplankton productivity can be attributed to the relative ease by which measurements can be made, and the precision and accuracy of the results. Primary production measures predominantly utilize release or the uptake of gases or ions, no such simple direct methods exist for measurements of secondary production (Mullin, 1969). Additionally, as primary production is described in one trophic level, whereas secondary production occurs across many, then a single measurement may be applicable, whereas for secondary production many measurements may be needed to understand flow. Although certain biochemical procedures are being developed, which may allow fast, accurate estimations of secondary production, and a new radiochemical method for crustaceans has recently been introduced (Roff *et al.*, 1994b), most methods of measuring production are time consuming, and may often only be used to examine specific groups of organisms. Estimates of secondary production have therefore lagged far behind the measures of primary production; indeed there are now broad global perspectives of primary production rates (Koblentz-Mishke *et al.*, 1970), and yet apparently not for zooplankton (Roff *et al.*, 1994b). The application of theoretical models to animals which have diverse and complex life histories is difficult and is partly responsible for the slower development of secondary

productivity estimating techniques. The determination of secondary production is also made more difficult as a result of the diversity of secondary producers.

Since most ecosystems have a 'plethora' of species, some biologists have been led to examine ecosystems where communities comprise fewer species and are more amenable to study (ie. Rigler *et al.*, 1974). Examinations of energy-matter flows through 'whole' ecosystems almost without exception have previously been compartmentalized at a coarse level, for example at a supra-species level or often much greater eg. herbivores, carnivores etc. (see Roff *et al.*, 1990). This may potentially lead to major analysis problems. Flow analysis and production recycling are major topics associated with the assessment and determination of energy-matter flux; new problems of marrying such theory with real measurements are examined in Chapter 7. From this work, important questions arise with regard to current recycling measuring techniques in the analysis of real systems.

Natural populations usually behave in such a complex way that to be able to measure or describe their functioning perfectly is currently impossible. Simplifications in describing the functioning of the populations must therefore be made. Indeed the mathematical formulations used in estimating production involve some simplifying assumptions. It is evident that the degree of agreement between an estimated production value and the real one relies not only upon the ability to obtain accurate measurements of the populations but also the correctness of the assumptions made regarding the natural situation. Thus when examining the secondary production of zooplankton in Southampton Water, the assumptions made are as minimal as is possible within the constraints of this study, and hopefully reflect the natural situation as closely as possibly. The effects of hidden or unstated assumptions on the calculated production values are scrutinized when appropriate.

The importance of metazoan zooplankton as a principle food source for fish, and other higher predators of economic importance, are a driving force to work which aids more effective understanding and management of resources. However, little quantitative data have been produced on the biology of individual species inhabiting estuarine regions around the world, and data on zooplankton species production and trophic interactions in these areas are greatly lacking, although less so than offshore. Metazoan zooplankton have been described and regarded by some as important in estuarine food webs (Jerling and Wooldridge, 1991) and by others as being a minor and unimportant herbivorous link (Williams *et al.*, 1968).

In macro-benthos and fish the comparatively slow turn-over rates allow cohorts to be

distinguished and their growth and mortality to be measured relatively straightforwardly. Most zooplankton species however, are not so enduring, and populations turn over many times annually, and often cohorts cannot be distinguished, which complicates *in situ* measurement. Studies estimating the production of neritic and estuarine copepods have increased in recent years as a result of methodological as well as theoretical developments and improvements. Improvements on earlier methods used for identifying natural cohorts (eg. Marshall, 1949; Digby, 1950), and for determining growth and development rates *in situ*, have been made (Evans, 1977; McLaren, 1978) and applied (Evans, 1977; McLaren, 1978; Uye, 1982a). Growth rate methods which require *in situ* incubation of artificially generated cohorts have also been developed, which allow finer temporal and spatial resolution of production. These types of experiment have broadly been separated into those where adult growth has been measured (ie. egg production rates), and those in which juvenile growth has been measured. Food-saturated laboratory growth rates, measured at temperatures relevant to the natural environment have most commonly been conducted. As more evidence accumulates that growth rates in nature may commonly be food-limited, developments of *in situ* incubation techniques have taken place, particularly in growth estimation of non-adults (eg. Burkill and Kendall, 1982; Kimmerer and McKinnon, 1987; Peterson *et al.*, 1991; Hutchings *et al.*, 1995). Theoretical improvements and concept clarifications have been made with regard to zooplankton growth measurments and application (Kimmerer, 1987).

Obviously the sorting and analysis of species, particularly small zooplankton, makes examination less appealing and more time consuming. The lack of taxonomy skills or capabilities may further intensify these problems (Bradford-Grieve, *in press*.). Various models of copepod and zooplankton growth, which do not require detailed taxonomic knowledge or time consuming microscopy, have been constructed. These include methods for the estimation of growth and production from; biomass and temperature data (Huntley and Lopez, 1992); biomass size distribution and temperature (Ikeda and Motoda, 1978); and biomass, temperature and chlorophyll concentrations (Huntley and Boyd, 1984). Methods which allow estimation of production without the need to measure development or growth rates may be made instantaneously and may be much easier to utilize; they may however be less accurate. In Chapter 4 contemporary models which allow copepod growth estimation are compared, with particular emphasis being placed upon determining whether copepod weight-specific growth is body weight dependent. A new empirical model is also derived, and its predictive abilities compared to other methods.

While the ecosystem concept is an important tool for organizing data, it is still invaluable to have extensive studies of individual species. We cannot understand the whole if we do not

know how the parts work. In this investigation production estimates are species-specific when this is possible. More frequent than ecosystem productivity studies are those on the productivity of single species, often involving laboratory measures to aid as supplements to the field data produced. However, problems arise in attempting to relate the production of individual species to the ecosystem production as a whole.

An important part of the planktonic system, in nearshore areas in particular, is the meroplankton. Although there has been an increase in the data produced on the growth rates of many zooplankton species, there is still almost no information on growth rates and production of the short-stay mero-planktonic organisms. The importance of these organisms in the pelagic food web probably declines in an offshore gradient. In shallow areas with a large standing stock of benthic organisms and high output of sexual products, including eggs and young into the water column, these organisms may provide food for other mero-planktonic organisms, holo-planktonic organisms or alternatively feed on other mero-planktonic organisms or holo-planktonic organisms. The dependence of the benthic system upon the pelagic system is relatively well understood; however, other benthic-pelagic energy-matter links are often ignored. These links are examined in Chapters 5 and 6, where it is hypothesized that pelagic organisms are dependent upon the meroplankton production and benthic reproductive production. Some sources of energy-matter available to pelagic organisms appear to have been ignored in many studies.

The main aim of this work is therefore the construction of a box model of carbon flux through the biological population of Southampton Water. Within this aim previous work within Southampton Water is explored and utilised as deemed appropriate. As the mesozooplankton population is the least well described group, this is examined in the most detail, thus allowing a filling of the apparent 'gaps' in understanding this area. Copepod biology and production are examined most extensively, although meroplankton are also enumerated and an attempt made to assess their importance. The impact of gelatinous organisms previously assessed by Lucas (1993) is re-examined and modified. There are potentially many ways to estimate the movement of energy or matter through a community. The method chosen in the present study is based broadly upon the assessment of production of trophic compartments and ingestion demands, that is, the amount of matter required to provide the given production. These assessments are made for a variety of groups and brought together in the final chapter as box models describing energy-flow at different sites within Southampton Water. A brief introduction to the topic of production and zooplankton has been completed here, more detailed introductions are given at the beginning of each chapter.

1.3 A DESCRIPTION OF SOUTHAMPTON WATER

The site of study is Southampton Water, an industrialised estuary on the South Coast of England. Southampton Water is a drowned river valley, which runs North West to South East in direction. At its southern end it opens into the Solent, at its Northern end it is fed by the rivers Test and Itchen, which converge at Dock Head. The Test and Itchen account for approximately 45% of the total freshwater inflow into the Solent (Webber, 1980). Discharges from the Test are estimated as $25m^3s^{-1}$ in mid-winter, and $6m^3s^{-1}$ in summer, discharges from the Itchen being about half those from the Test (Webber, 1980). A third smaller river flows into the estuary on its eastern side, the river Hamble. The estuary itself is a shallow, partially mixed coastal plain estuary approximately 16 km long and 2.5 km at its widest point (Dyer, 1973; 1982). The estuary is characterised by an unusual tidal regime consisting of a double high water, some two hours apart, followed by a short ebb tide, when surface currents may reach 0.5-1.0m s^{-1} (Dyer, 1973), therefore the ebb is faster than the flood. The tidal range varies between approximately 1.5 and 5 metres. Surface salinities rarely fall below $25^{o}/_{oo}$ at its head and $30^{o}/_{oo}$ at the mouth. Since it is predominantly marine in character Southampton Water has previously been aptly described by Raymont (1972) as an 'arm of the sea'. The estuary bed is mainly mud and sandy mud, most of which is supplied from the sea. There are also extensive mudflats exposed at low waters. The estuary is dredged to a depth of approximately 12 metres in the central channel.

CHAPTER 2

CALANOID COPEPOD AND MESOZOOPLANKTON BIOLOGY AND ECOLOGY IN SOUTHAMPTON WATER.

2.1 INTRODUCTION

Copepods and meroplankton are the major constituents of mesozooplankton in neritic and estuarine regions. Such areas show marked seasonal changes in species composition, abundance, biomass and production. Retention of endemic species populations depends on the reproductive rates of the organisms and their rates of loss (Perkins, 1974). Non-endemic species are dependent upon rates of movement into and out of a system, in addition to their reproduction within that area. Salinity and temperature and their variation, turbidity and flush-out rates can each have pronounced effects upon zooplankton distribution and abundance in estuaries. Zooplankton abundance and biomass are both important determinants in the rates of production and the nature of food webs and trophic transformations. Quantifying and understanding processes controlling abundance and production of zooplankton is therefore a major objective of biological oceanography.

Surveys of the mesozooplankton of Southampton Water have been undertaken by several workers over many years. Unfortunately many different methods of collection have been used, often dictated by the primary aims of the worker, and there has been no continuous or standardized collection. The zooplankton of Southampton Water was examined most recently by Lucas (1993) and Zinger (1989). However, both of these investigations only determined the dominant copepods at the level of harpacticoid, calanoid or cyclopoid, and in the more recent of these studies mesh size was generally inadequate to sample much of the meroplankton and copepod population. Taxonomically more detailed, and stage specific studies of the calanoid copepods and meroplankton components have been undertaken, namely by Conover (1957), Lance and Raymont (1964) and Raymont and Carrie (1964). These studies however, are now more than 30 years old, and would appear from preliminary comparisons to be unrepresentative of the present situation (see Zinger, 1989). It was therefore decided that an initial investigation should take place on the copepods and meroplankton, with the aim of describing the population at a single site over a 14 month period, and to examine physical and chemical factors of potential influence upon density and production.

2.2 METHODS

Samples were collected at two depths (5 and 10 metres) from 5 permanent sites marked by fixed shipping buoys within Southampton Water. These sampling sites are shown in Figure 2.2.1. The names and grid locations of these 'permanent' sites are given below:

(1). Calshot Spit	(50°48.33'N, 1°17.52'W)
(2). Hamble	(50°50.89'N, 1°19.53'W)
(3). N.W. Netley	(50°52.28'N, 1°22.64'W)
(4). Cracknore	(50°53.93'N, 1°25.12'W)
(5). Bury Buoy - Swinging Ground No.10	(50°54.27'N, 1°27.40'W)

Each of the sites were sampled on the same day, as close to spring tides as boat facilities would allow, over a period of 14 months. On each occasion the first sample was taken at Calshot then moving in sequence between sites from the mouth to the head, the final sample being taken at Bury Buoy. The period over which samples were collected spanned the high water stand, which lasted for 2 to 3 hours, and which had previously been shown to be the tidal phase associated with greatest daytime densities (Raymont and Carrie, 1964). Sampling times were also regulated in order to attempt to sample the 'same' body of water, and to standardize tidal influence. In similar investigations of zooplankton density and production in dynamic areas, samples have also been taken on the same point in the tidal cycle (eg. Jerling and Wooldridge, 1991; low water spring tides). Figure 2.2.2 demonstrates the heights of first and second high water and low water within Southampton Water (as predicted by ABP Tidal Charts), whilst Figure 2.2.3 shows differences in tidal height between high and low waters. The times during this period when sampling took place for both the 14 month preliminary investigation, and also the subsequent growth rate programme as detailed in Chapter 3, are also shown.

Plankton samples were collected from the appropriate depth using a 118μm mesh cod-end plankton net (mouth opening diameter 50cm, length approximately 125cm). This mesh size was chosen to allow collection of copepods, predominantly the copepodites (defined as all post nauplii stages), and other meso- and macrozooplankton, whilst ensuring reductions in filtering efficiencies during phytoplankton blooms were kept to a minimum. Tows were of a double-oblique nature (to 5 and 10 metres), with the towing speed around 2 knots. A lead weight was attached to the point where the bridles join the tow rope, helping to ensure the appropriate sampling depth could be maintained. The flushing time for each sample varied depending upon environmental conditions, but was generally less than 4 minutes in duration.

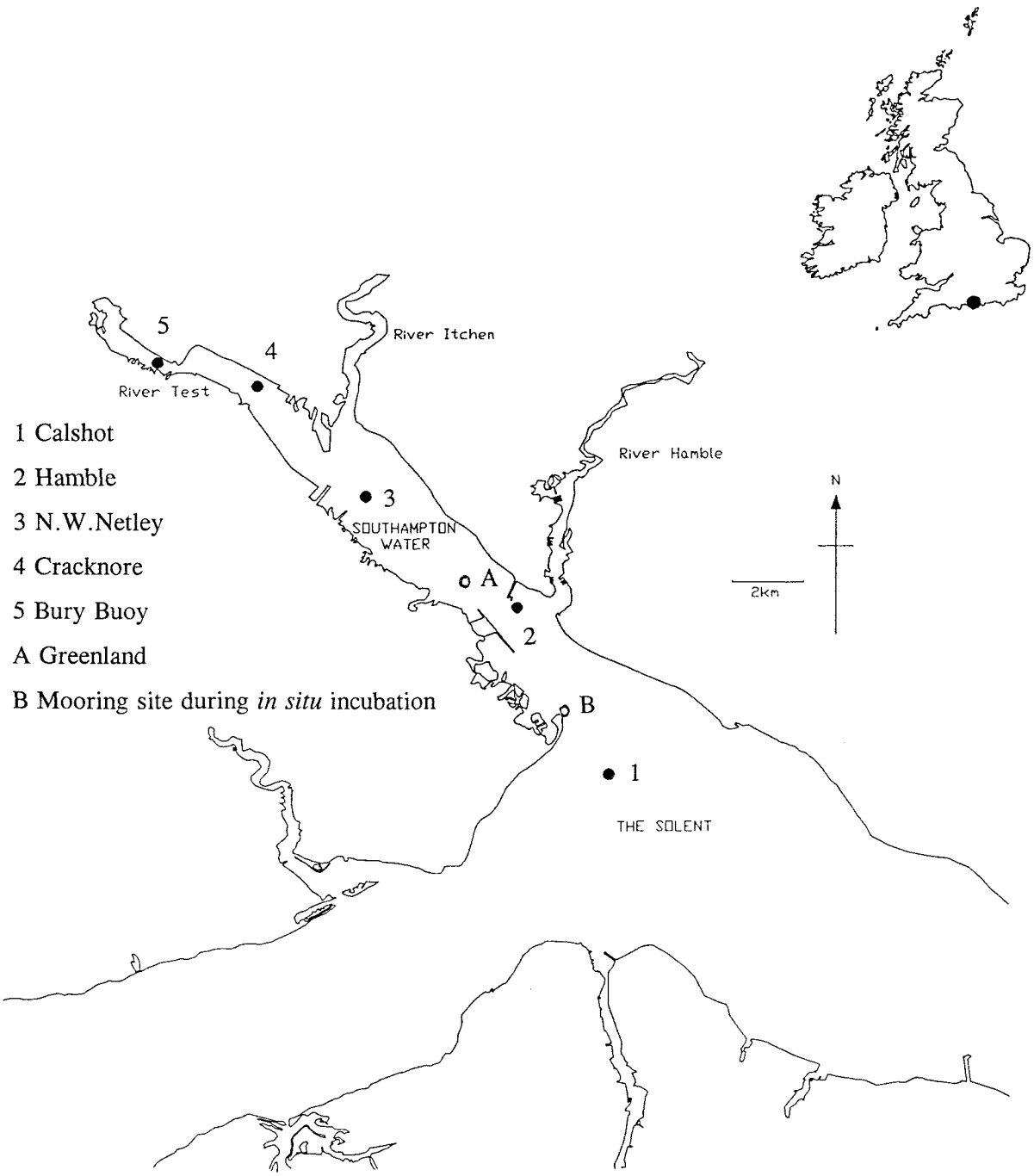


FIGURE 2.2.1 A map of Southampton Water with the location of the sampling sites during the initial 14 month investigation marked. The site of container mooring during the *in situ* growth rate work (Chapter 3), and those relevant to this work also indicated.

Since there was no opening or closing device fitted to the net, material could enter the mouth of the net as it was being deployed and retrieved. A calibrated T.S Flowmeter (Tsurumi-Seiki Co. Ltd.) was fixed in the mouth of the net so that the volume of water filtered could be determined. The flow meter was positioned in the net face, at a distance half the radius from the centre. On 2 occasions (12/3/93 and 26/3/93) the usual net was unavailable and a 200μm mesh net was used for zooplankton sampling. After each tow the net was rinsed from the outside using a hose with sea-water, with material being collected in a litre cod-end-container. The collected material was then transferred to a suitable glass container, and killed immediately by the addition of approximately 10ml of 4% formaldehyde-seawater solution. This ensured there could be no predation effects (UNESCO Handbook, 1976). On return to the laboratory the samples were part-preserved by the addition of 25ml of 40% formaldehyde solution to the sample. This ensured that the biological material would not deteriorate but that shrinkage in the gelatinous fraction would be minimal. Within 36 hours the Schyphomedusae and Ctenophora were separated from the remaining sample and preserved separately in sea-water containing a very low concentration of formaldehyde (ie. ~0.5%), this ensured that shrinkage would be minimal for these delicate taxa. Enough 40% formaldehyde was then added to the remaining samples to ensure the final preservative concentration was 4% formaldehyde-seawater solution. The zooplankton samples could later be decanted into suitably sized containers, ensuring that the material in the sample made up no more than 1 part plankton to 9 parts fixative by volume (UNESCO Handbook, 1976).

Sub-samples were produced from the entire samples after each had been made up to a volume of 500ml with 4% seawater-formaldehyde. Samples were vigorously but randomly agitated, and 2.5ml extracted using a fixed volume Stempel pipette. This process was repeated 4 times and the Stempel pipette samples pooled for each defined 'sub-sample' (ie. 10ml volume). This sub-sample represented a 2% fraction of the original sample, a fraction commonly used in zooplankton work of this nature (eg. Heinle, 1966 examined 1 to 7% of original sample volume; McLaren and Corkett, 1981 examined 2% of the sample; Ryan *et al.*, 1986 examined 0.2% to 10% of the original sample). All sub-samples were then examined using a Bogorov S-shaped tray with all zooplankton being picked carefully from the very large quantity of detrital material using fine forceps. All individuals collected were identified to the lowest taxonomic level possible using a Wild M8 (Leica) binocular microscope, and counted. All copepodites were identified to species level, staged and sexed when this was possible, although in the case of *Acartia*, non-adult copepodites were not determined to species level. Copepodites were separated into the groups; C1, C2, C3, C4 (sexed when possible), C5 (♀), C5 (♂), C6 (♀) and C6 (♂).

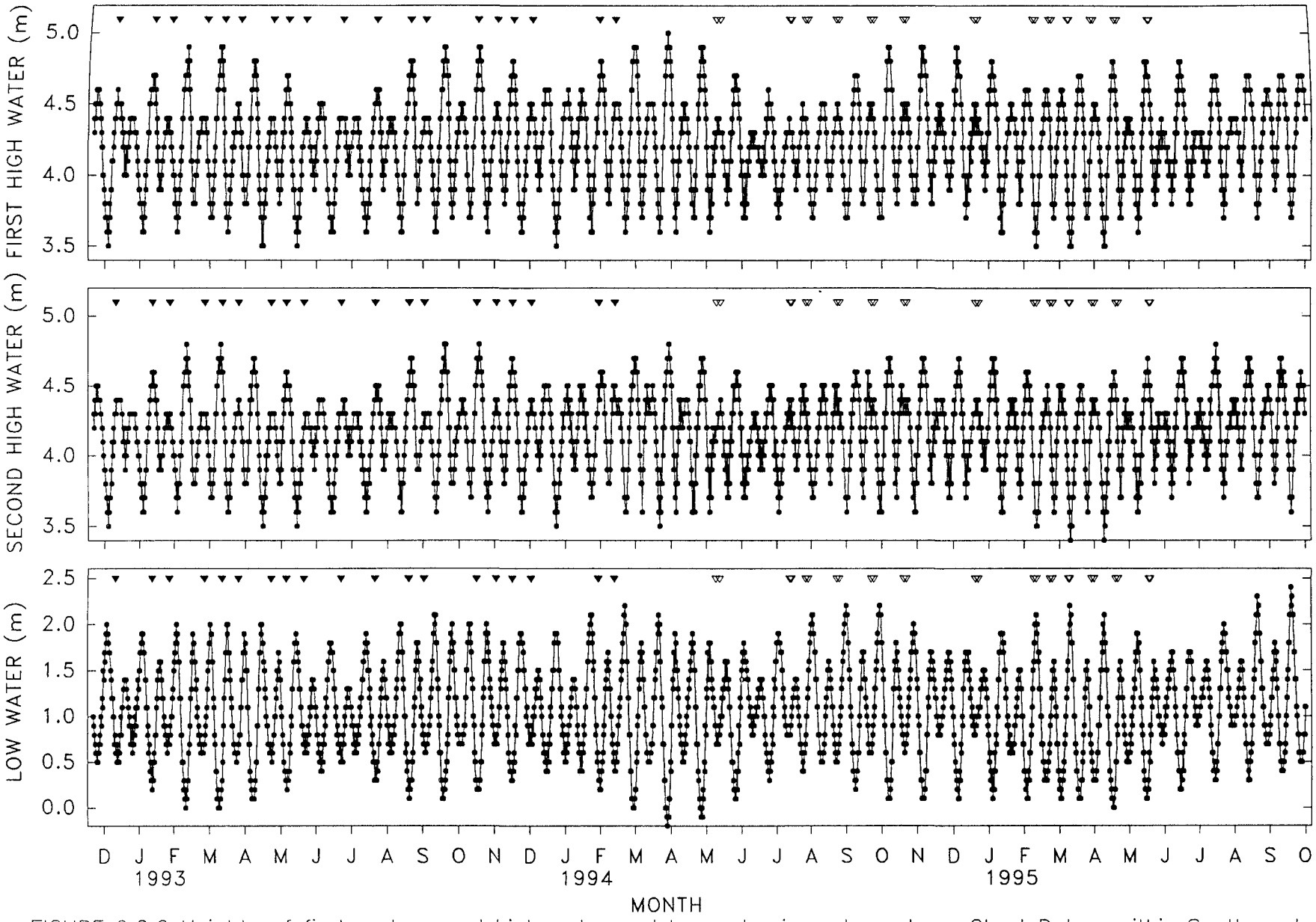


FIGURE 2.2.2 Heights of first and second high water and low water in metres above Chart Datum within Southampton Water, as predicted by ABP Tidal Charts. ▾ Abundance program ▿ Development program.

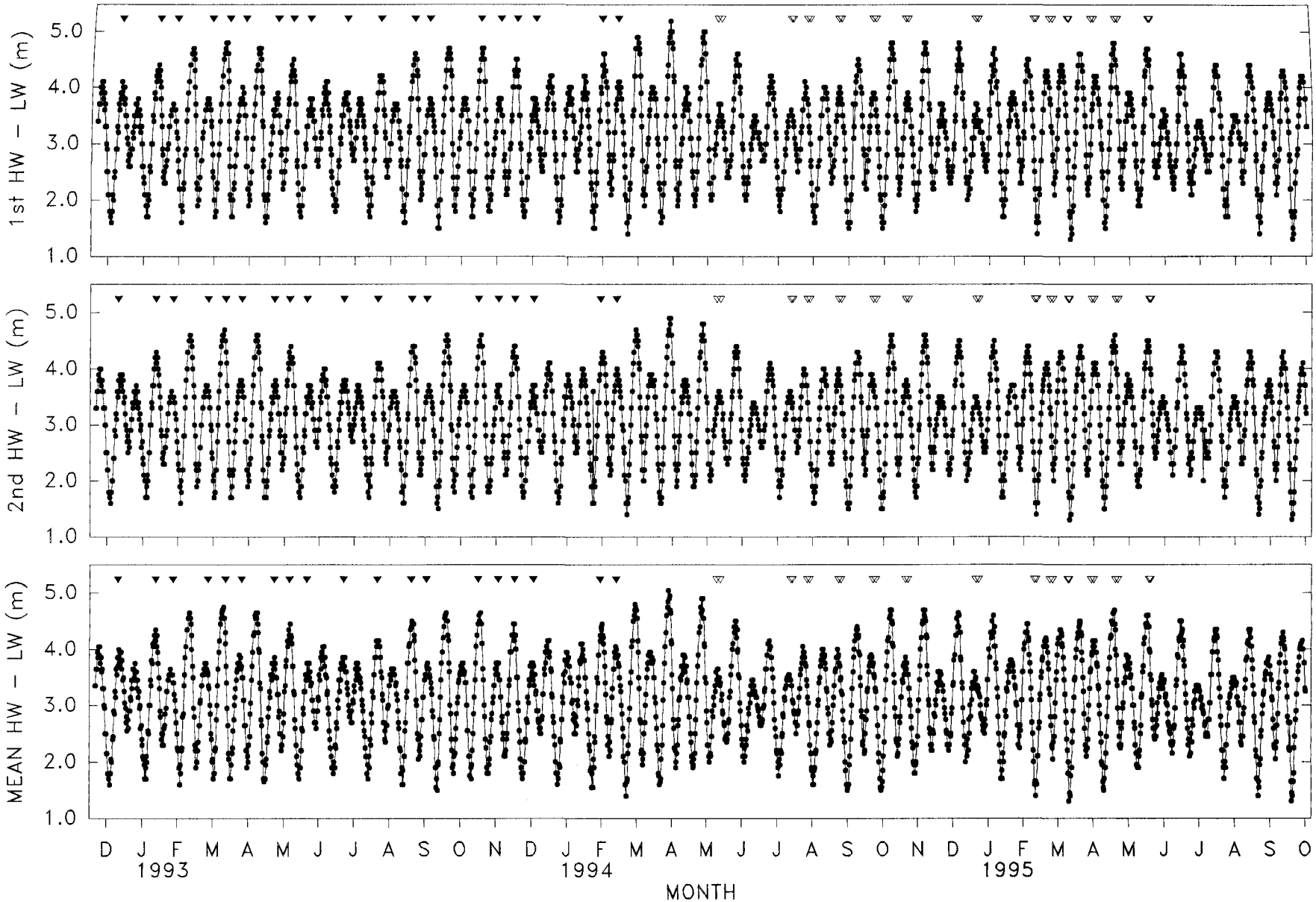


FIGURE 2.2.3 Differences in tidal heights of high and low waters within Southampton Water, as predicted from ABP Tidal Charts.
▼ Abundance program ▽ Development program.

Acartia species are separable in the non-adult forms; for example it is possible to distinguish *A.bifilosa* at least to copepodite III by the presence of rostral filaments (Raymont and Carrie, 1964), and sometimes to stage II (*personal observation*), however, such identification proved too time consuming in the present investigation. The number of spermatophores attached to adult female calanoid copepods was also noted. The nauplii stages were not identified to species level but were counted.

Measurements of the prosome length and greatest prosome width were made after at least 6 months storage in 4% sea-water formaldehyde. Prosome length, and greatest width measurements were made on each individual copepod in the sub-sample. Measurements were made using a calibrated eye-piece micrometer (100 subdivisions, one division being equal to 8.91μm), at a standard magnification of 100x. No correction was made to these prosome length measurements to allow for preservation, although there is some conflict as to changes as a result of preservation. Durbin and Durbin (1978) found no changes in prosome length of *Acartia hudsonica* with preservation, while Landry (1978) found there was a very small reduction (average reduction 8.5%) in *Acartia clausi* (*hudsonica*?) length. Uncorrected prosome lengths were used to estimate individual carbon weights, using prosome-length regressions adapted from the literature. The length-weight regressions compiled for the dominant calanoid copepods within Southampton Water (where regressions exist) are compared in Figures 2.2.4 to 2.2.6, while the equations themselves (in uncorrected and corrected formats) are given in Table 2.2.2. In the compilation of these regressions all have been converted to carbon. When the original study quoted dry weight this was converted to carbon assuming carbon to be 40% of dry weight (Omori and Ikeda, 1984; Båmstedt, 1986). When units were given as ash-free dry weight, these were converted to dry weight by assuming that ash represented 10.4% of the dry weight in *Temora longicornis*, 8.9% in *Acartia* sp. 8.5%, in *Pseudocalanus/Paracalanus* and 4.1% in *Centropages hamatus* (Laurence, 1976).

Studies on planktonic animals have demonstrated that fixation with formaldehyde can result in a considerable leaching of body substance. Table 2.2.1 is a compilation of weight loss of calanoid copepods during preservation (adapted from Giguère *et al.*, 1989). A mean weight loss of 31.6% was estimated from these works, and used to correct the literature length-weight equations where preservation had taken place. All measurements of length compiled were for the prosome (=cephalothorax) and therefore did not need any form of manipulation. Adult *Acartia* weights were determined using the appropriate species specific equation. For non-adult copepodites the length-weight equation from the dominant *Acartia* species was utilised.

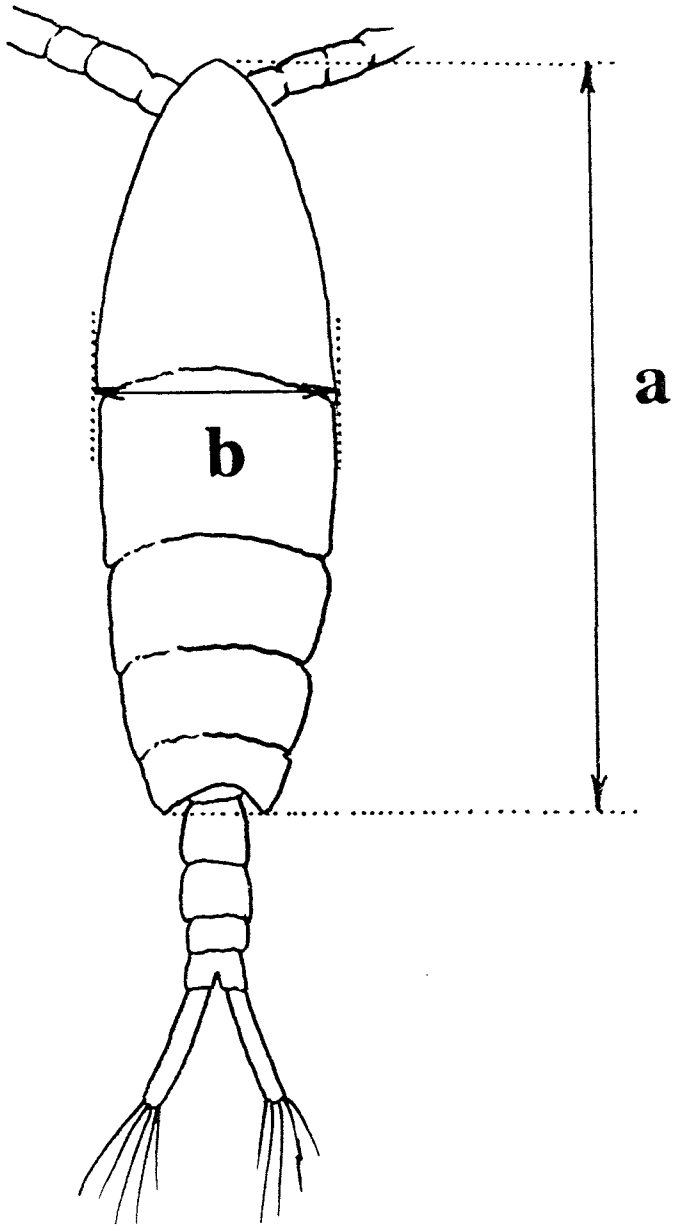


FIGURE 2.2.4 The copepod body dimensions measured were; (**a**). Prosome length and (**b**). Greatest prosome width.

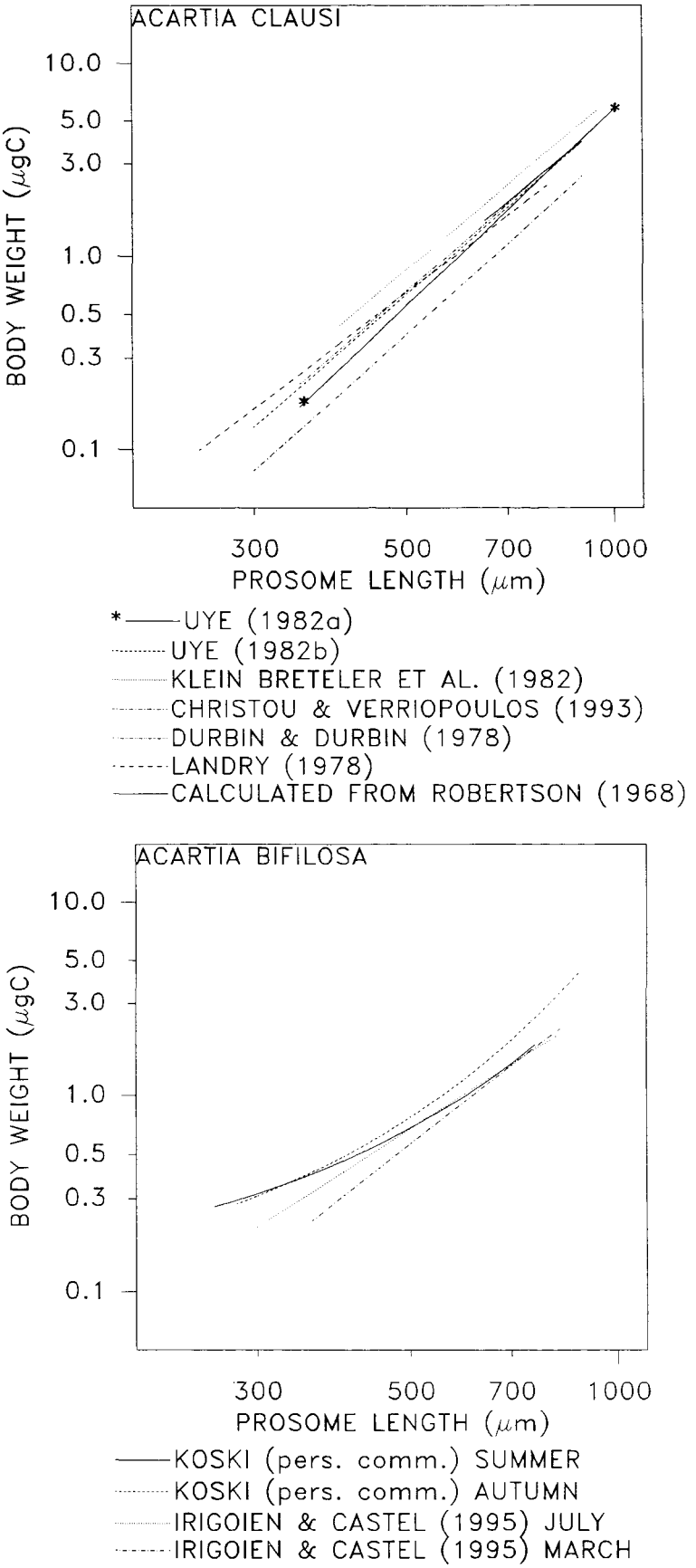
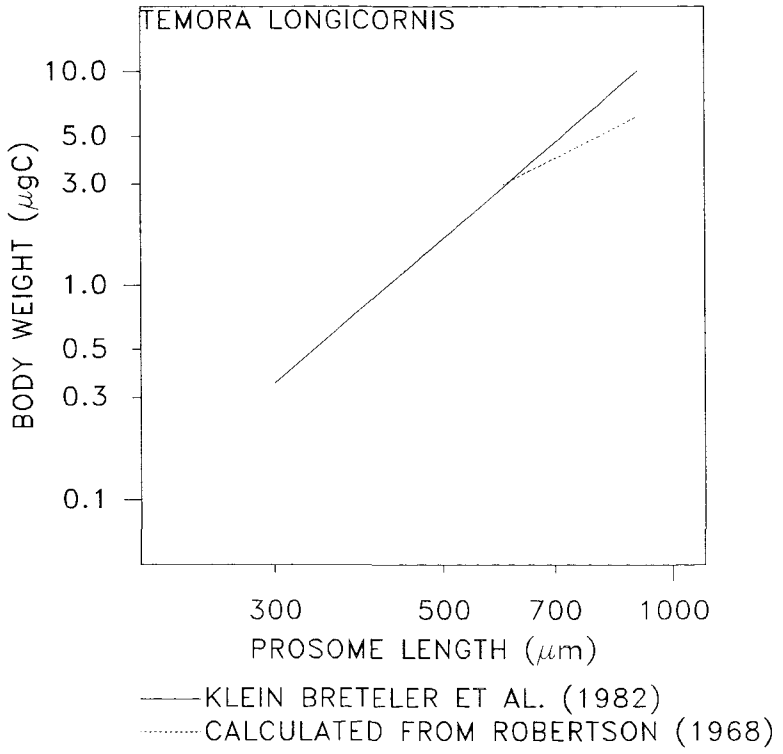


FIGURE 2.2.5 Relationships between carbon weight and prosome length for the species Acartia clausi and Acartia bifilosa collected from the literature. Appropriate conversions applied to allow for preservation and to convert to similar weight units ie. carbon.



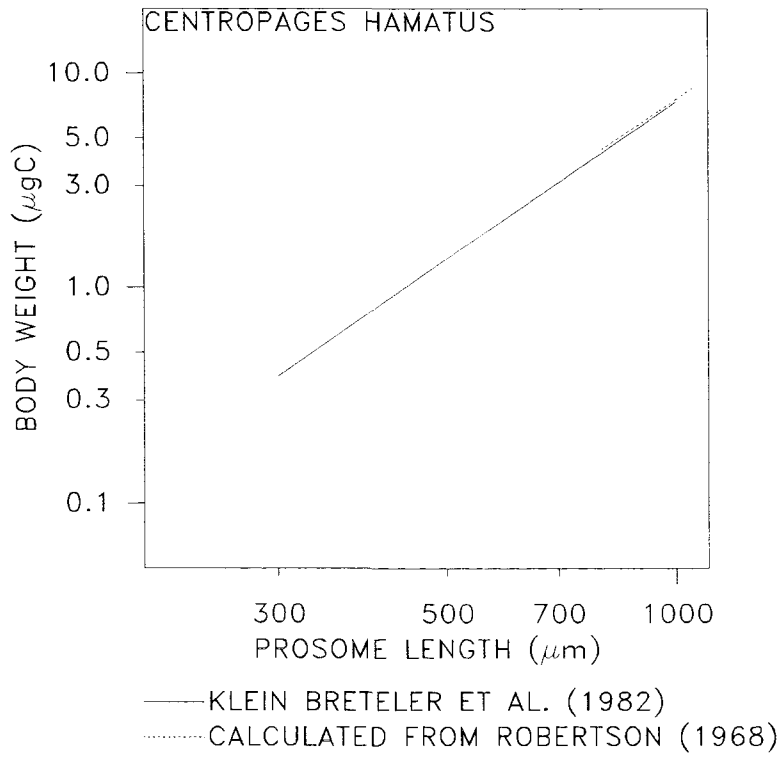


FIGURE 2.2.6 Relationships between carbon weight and prosome length for the species Temora longicornis and Centropages hamatus collected from the literature. Appropriate conversions applied to allow for preservation and to convert to similar weight units ie. carbon.

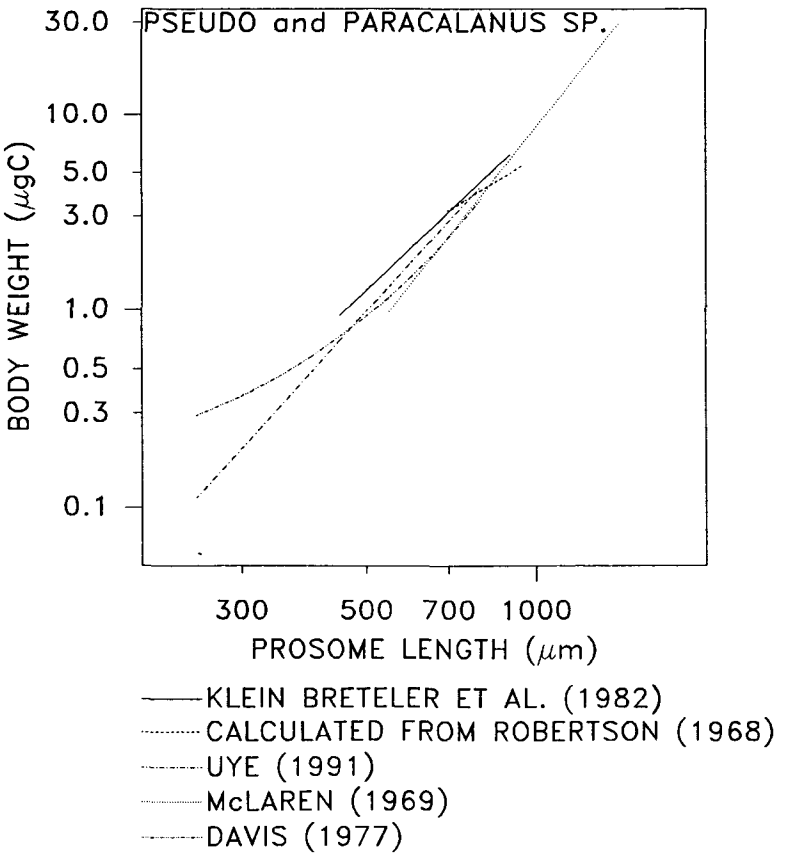


FIGURE 2.2.7 Relationships betweeen carbon weight and prosome length for the species Pseudocalanus and Paracalanus sp. collected from the literature. Appropriate conversions applied to allow for preservation and to convert to similar weight units ie. carbon.

Marine copepod species	Formaldehyde (%)	Duration (d)	Dry weight loss (%)	Source
Acartia clausi	6^{*h}	227-340	29.5	Durbin and Durbin, 1978
Acartia clausi	weak	?	37.0	Landry, 1978a
Pontella Mediterranea	$5^{\dagger b}$	2-31	22.5	Champalbert and Kerambrun, 1979
Calanus helgolandicus	4^{*b}	153	63.8	Williams and Robins, 1982
Calanus helgolandicus	4^{*b}	153	38.4	Williams and Robins, 1982
Calanus helgolandicus	4^{*b}	153	18.6	Williams and Robins, 1982
Calanus helgolandicus	4^{*b}	153	23.5	Williams and Robins, 1982
Calanus helgolandicus	4^{*b}	153	23.5	Williams and Robins, 1982
Calanus cristatus	10^{*h}	30	30.9	Omori, 1970
Calanus cristatus	10^{*h}	30	34.1	Omori, 1970
	10^{*h}	30	18.3	
Eurytemora affinis	$4^{\dagger h}$	549	30.1	Böttger and Schnack, 1986
	$4^{\dagger h}$	549	35.0	
Calanus sinicus	4^{*bh}	0-180	31.0	Omori, 1978
AVERAGE	5.6	180.2	31.6	
S.D.	2.7	180.0	11.4	

TABLE 2.2.1 Compilation of weight losses for calanoid copepods after preservation in formaldehyde solutions of various concentrations and with various additional constituents. Adapted from Giguère *et al.* (1989).* With seawater, †With freshwater, h With hexamine, b With borax.

Species	Original equation (L=Prosome length in µm) (Weight in µg)	Weights after preservation?	Carbon to length relationship after conversion	Author
Acartia clausi[1]	$logDW=2.86log(L/100)-1.74$	No	$C=10^{2.86log(L/100)-1.74}*0.4$	Robertson, 1968
Acartia clausi[1,2]	$DW=9.523*(L/1000)^{3.0778}$	Yes	$C=(L/1000)^{3.0778}*5.569$	Durbin and Durbin, 1978
Acartia clausi[1,2]	$logC=2.71logL-7.50$	No	$C=10^{2.71logL-7.50}$	Landry, 1978
Acartia clausi[1,2]	$logDW=3.36logL-9.09$	Yes	$C=10^{3.36logL-9.09}*0.585$	Uye, 1982a
Acartia clausi[2]	$logC=3.08*logL-8.51$	No	$C=10^{3.08*logL-8.51}$	Uye, 1982b
**Acartia clausi*[1]	$logAFDW=2.9672logL-7.7188$	No	$C=10^{(2.9672logL-7.7188)}*0.439$	Klein Breteler *et al.*, 1982
Acartia clausi[1]	$DW=8.995*(L/1000)^{3.185}$	No	$C=(L/1000)^{3.185}*3.598$	Christou and Verriopoulos, 1993a
**Acartia bifilosa*	$C=e^{-2.285+(0.003793L)}$	?	$C=e^{-2.285+(0.003793L)}$	M.Koski *pers. comm.* (summer)
Acartia bifilosa	$C=e^{-2.538+(0.004552L)}$	?	$C=e^{-2.538+(0.004552L)}$	M.Koski *pers. comm.* (autumn)
Acartia bifilosa[1]	$DW=6.88*10^{-8}L^{2.71}$	No[3]	$C=2.752*10^{-8}L^{2.71}$	Irigoien and Castel, 1995 (March)[4]
Acartia bifilosa[1]	$DW=1.52*10^{-6}L^{2.24}$	No[3]	$C=6.08*10^{-7}L^{2.24}$	Irigoien and Castel, 1995 (July)[4]
Acartia bifilosa[1]	$C=5.42(L/1000)^{3.02}$	No[5]	$C=5.42(L/1000)^{3.02}$	Tanskanen, 1994 (6 Nov. 1990)
Acartia bifilosa[1]	$C=4.54(L/1000)^{2.99}$	No[5]	$C=4.54(L/1000)^{2.99}$	Tanskanen, 1994 (3 Dec. 1990)
Acartia bifilosa[1]	$C=3.73(L/1000)^{2.71}$	No[5]	$C=3.73(L/1000)^{2.71}$	Tanskanen, 1994 (5 Feb. 1991)
Acartia bifilosa[1]	$C=2.51(L/1000)^{2.09}$	No[5]	$C=2.51(L/1000)^{2.09}$	Tanskanen, 1994 (11 Apr. 1991)
Acartia bifilosa[1]	$C=5.87(L/1000)^{2.93}$	No[5]	$C=5.87(L/1000)^{2.93}$	Tanskanen, 1994 (15 May 1991)
Acartia bifilosa[1]	$C=4.42(L/1000)^{2.51}$	No[5]	$C=4.42(L/1000)^{2.51}$	Tanskanen, 1994 (13 Jun. 1991)
Acartia bifilosa[1]	$C=5.71(L/1000)^{2.92}$	No[5]	$C=5.71(L/1000)^{2.92}$	Tanskanen, 1994 (17 Jul. 1991)
Acartia bifilosa[1]	$C=3.81(L/1000)^{2.64}$	No[5]	$C=3.81(L/1000)^{2.64}$	Tanskanen, 1994 (11 Aug. 1991)
Acartia bifilosa[1]	$C=2.91(L/1000)^{2.65}$	No[5]	$C=2.91(L/1000)^{2.65}$	Tanskanen, 1994 (5 Sep. 1991)
Acartia bifilosa[1]	$C=3.76(L/1000)^{2.64}$	No[5]	$C=3.76(L/1000)^{2.64}$	Tanskanen, 1994 (4 Oct. 1991)
Acartia bifilosa	$C=4.696(L/1000)^{2.868}$	No[5]	$C=4.696(L/1000)^{2.868}$	Tanskanen, 1994 (Combined results)

**Centropages hamatus*[1]	logAFDW=2.4492logL-6.0984	No	$C=10^{(2.4492logL-6.0984)}*0.417$	Klein Breteler *et al.*, 1982
Temora longicornis[1]	logDW=1.79log(L/100)-0.51	No	$C=10^{1.79log(L/100)-0.51}*0.4$	Robertson, 1968
**Temora longicornis*[1]	logAFDW=3.0640logL-7.6958	No	$C=10^{(3.0640logL-7.6958)}*0.446$	Klein Breteler *et al.*, 1982
Pseudo and *Paracalanus*[1]	logDW=2.39log(L/100)-1.13	No	$C=10^{2.39log(L/100)-1.13}*0.4$	Robertson, 1968
**Pseudocalanus* sp.[1]	logAFDW=2.7302logL-6.9121	No	$C=10^{(2.7302logL-6.9121)}*0.437$	Klein Breteler *et al.*, 1982
Pseudocalanus minutus[1]	$C=5.89(L/1000)^{3.64}$	Yes	$C=8.611(L/1000)^{3.64}$	McLaren, 1969
Pseudocalanus minutus	$DW=(e^{4.6097(L/1000)-8.7551})*1000$	Yes	$C=(e^{4.6097(L/1000)-8.7551})*585$	Davis, 1977 MS: as reported in Cohen and Lough, 1981
Paracalanus sp.[1]	logC=3.128logL-8.451	No	$C=10^{3.128logL-8.451}$	Uye, 1991

TABLE 2.2.2 Literature compilation of length-weight relationships for dominant calanoid copepods found in Southampton Water. Relationships of prosome length to carbon determined using factors given in text. Those with an asterisk applied in the present investigation.

1 Regression known not to include nauplii. NB. All the regressions of Robertson (1968) have been recomputed, prior to inclusion here, using the original data supplied in paper. 2 Original names given, although as these specimens were collected from the western Atlantic and Japanese coastal waters they are probably the similar species *A.hudsonica* and *A.omorii* and possibly others (see Bradford, 1976; Uye, 1982a; Ueda, 1986a;1986b). 3 Fixed in gluteraldehyde rather than formaldehyde therefore no correction for preservation made (see Kimmerer and McKinnon, 1986). 4 Equations of Irigoien and Castel (1995) given in incorrect format in original text, adjusted to allow for mistake. 5 Fixed in 4% unbuffered formaldehyde and frozen, in original text described as giving a final carbon content equivalent to that of unpreserved material, thus uncorrected.

As there was no equation available for *Acartia discaudata* and *Acartia margalefi*, the equations for *Acartia bifilosa* and *Acartia clausi* were applied respectively. The equation chosen to determine *A.bifilosa* weights was that supplied by M.Koski (*pers. comm.*), determined from specimens collected in the Baltic. The equations given by Klein Breteler *et al.* (1982) for southern North Sea populations were utilised (after appropriate conversion) to estimate the carbon weights of *A.clausi*, *Centropages hamatus* and *Temora longicornis*, while their equation for *Pseudocalanus* sp. was used to estimate weights of *Paracalanus parvus* and *Pseudocalanus elongatus*.

Physical and chemical parameters were measured at the same time and sites as the zooplankton samples were taken. The parameters chosen for measurement had previously been correlated with the abundance and productivity of zooplankton, although their full importance may be poorly understood. Other influential parameters were later measured during the field development rate investigations (see Chapter 3). The methodology used in measuring each of the parameters are given below.

(1). & (2).Temperature and Salinity

Temperature and salinity measures were made at each of the stations concurrently with the collection of zooplankton samples. A digital field salinometer (in house built) connected to a salinity-temperature probe was used to make these measurements. The sensitivity of the instrument is 0.1°C for temperature and $0.1^{o}/_{oo}$ for salinity.

(3).Chlorophyll a and Phaeo-pigment Concentrations

Samples of water were collected from 5 and 10 metres depth at the permanent sampling sites using a 5 litre Nisken water bottle. The collected water samples were stored in darkened glass bottles, and kept in a dark cool box. Upon return the samples were shaken and 50ml samples were taken and filtered through Whatman (GF/C) 2.5cm glass microfibre filters (pore diameter 1.2 μm) using a syringe with a filter holder attachment. Each of the filter papers were then folded in half and wrapped separately in foil and sealed in plastic bags. They could then be stored in a deep freeze (-20°C) until analysis could proceed. The maximum storage time for these filtered samples before analysis was usually less than 3 months, storage for periods greater than this is believed to be detrimental (D.Purdie, *pers. comm.*).

The fluorometric method was used to analyze chlorophyll a and phaeo-pigment

concentrations, this method is generally 5 to 10 times more sensitive than the spectrophotometric method, but it may be less accurate (Parsons *et al.*, 1989). Acetone extracts of the pigments were made as follows. Each filter was placed initially in an homogenizing tube to which a spatula measure of finely powdered magnesium carbonate ($MgCO_3$) was added, this was to ensure non-acid conditions. 3ml of 90% acetone was then added and the filter ground manually using a glass rod and then homogenized with an electric grinder. During this process the homogenizing tube was kept cool in a beaker of cold water. Homogenation continued until the filter was ground into a fine white slurry. The homogenized filtrate was then emptied into a centrifuge tube. The homogenizing tube was rinsed carefully with a further 3ml of 90% acetone, which was once again emptied into the centrifuge tube, the rinsing procedure ensured that no homogenate was lost. The centrifuge tube was then covered with parafilm and centrifuged at room temperature for 5 minutes at 2000rpm. After centrifugation the supernatant was decanted into a cuvette and its fluorescence measured before and after acidification using an Aminco® fluorometer. The fluorometer having been zeroed with 90% acetone on the most sensitive setting (0.1). The fluorescence of the sample before and after acidification was measured for each supernatant. Acidification was achieved by adding 2 drops of 10% HCl and then mixed by inverting the fluorometer cuvette several times following the addition of the acid. The concentration of chlorophyll a was calculated as follows:

$$Chlorophyll\ a\ (\mu g\ l^{-1}) = F_D \times \frac{(R_{BS} / R_{AS})}{(R_{BS} / R_{AS})-1} \times (R_B - R_A) \times \frac{v_e}{V_f} \qquad (1)$$

While the amount of phaeo-pigments was calculated from the equation:

$$Phaeo\text{-}pigments\ (\mu g\ l^{-1}) = F_D \times \frac{(R_{BS} / R_{AS})}{(R_{BS} / R_{AS})-1} \times ((\frac{R_{BS}}{R_{AS}} \times R_A) - R_B) \times \frac{v_e}{V_f} \qquad (2)$$

Where v_e is the volume of acetone (in millilitres)

V_f is the volume of water filtered (in litres)

R_B is the fluorescence reading of the sample before the addition of acid

R_A is the fluorescence reading of the sample after the addition of acid

R_{BS} is the fluorescence reading of the standard solution before the addition of acid

R_{AS} is the fluorescence reading of the standard solution after the addition of acid

It is necessary for a calibration to be undertaken using a solution with a known concentration of chlorophyll a. The concentration of this calibrating solution was determined using the spectrophotometric method. F_D is the calibration factor and is calculated as follows:

$$F_D = \frac{C_a}{R} \qquad (3)$$

Where R is the fluorometer reading for the standard

and C_a is the concentration of chlorophyll a in the standard calibrating sample (as determined using the spectrophotometric method (see below).

Spectrophotometric Method:

The concentration of chlorophyll a ($\mu g.l^{-1}$) in a calibrating solution obtained from Sigma Chemicals was measured spectrophotometrically as follows. The extinction of the chlorophyll a solution (90% acetone solution) was measured at the wavelengths 664nm and 750nm. The sample was then acidified by the addition of 2 drops of 10% HCl. The cuvette was inverted several times to ensure its complete acidification. After this acidification process the extinction of the solution is measured at the wavelengths 667nm and 750nm. On all occasions the samples were zeroed against a solution of 90% acetone. The chlorophyll a in the calibrating solution may then be calculated:

$$\textit{Chlorophyll } \underline{a} \ (\mu g \ l^{-1}) = \left(\frac{26.7(E_{664b} - E_{667a}) \times v_e}{V_f \times L}\right) \qquad (4)$$

Where E_{664b} is the extinction at 664nm before acidification

E_{667a} is the extinction at 667nm after acidification

L is the light path of the cuvette (1cm)

V_f and v_e are as defined previously

Since the concentration of chlorophyll a in this calibrating solution is known it may then be diluted in such a way so that values of known chlorophyll a concentrations may be compared against fluorometric readings (on all the scales used). This allows the fluorometer readings for the samples to be converted to real chlorophyll a and phaeo-pigment concentration values.

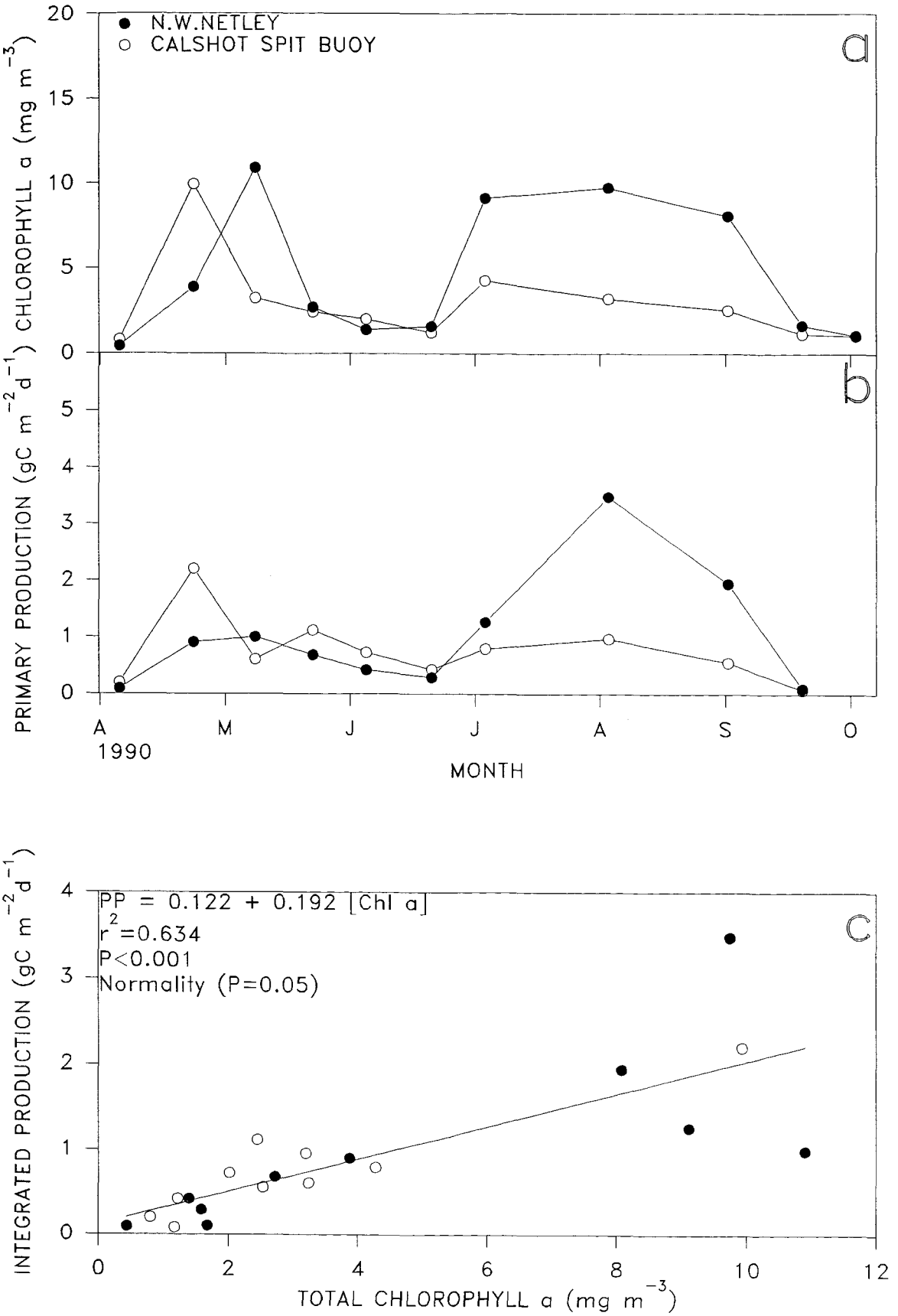


FIGURE 2.2.8 a. Unfractionated chlorophyll a concentration and b. Depth integrated primary production estimates, at N.W.Netley and Calshot during 1990. c. Least squares linear regression through combined data from both sites. (All data from Iriarte, 1991, and Kifle, 1992).

(4).Rate of Primary Production

Primary production measurements have been extensively undertaken in the estuary, furthermore regressions of chlorophyll a versus primary production have been completed (Bryan, 1979; Kifle, 1992), and utilised in the literature (Leakey *et al.*, 1992). In the present investigation primary production and chlorophyll a data given in Kifle (1992) and Iriarte (1990), for both the sites Calshot and N.W.Netley, were combined and a single relationship between primary production and chlorophyll a concentration derived (see Figure 2.2.8). The relationship deduced being:

$$\textit{Rate of Primary Production} = 0.122 + 0.192\ [\textit{Chl a}] \qquad (5)$$

Where Rate of Primary Production is in units of $gC.m^{-2}.d^{-1}$
and Chl a is the chlorophyll a concentration in units of $mg.m^{-3}$ (in application this concentration was depth averaged)

This equation was used to estimate estuarine wide primary production from chlorophyll a measurements derived herein.

(5).The Secchi Disk Depth

Water transparency was measured from the shaded side of the boat (Olsson and Ölundh, 1974), with a 25 cm diameter Secchi disk. The depth at which the Secchi disk became no longer visible (SZ in metres) was determined to the nearest 20 cm at each sampling station. From this value an extinction coefficient value and also the depth of the euphotic zone were calculated. The Secchi disk depth was converted to an extinction coefficient value (K_e) as follows:

$$K_e = \frac{1.44}{SZ} \qquad (6)$$

The euphotic zone depth, or 1% surface radiation (Parson *et al.*, 1984), was calculated by multiplying the Secchi disk depth by 3.5, as derived for turbid waters (SZ< 5m) by Holmes (1970).

(6).Dissolved Oxygen Concentration

Samples of water were collected using the Nisken water bottle so that oxygen concentration could be determined. Stoppered glass oxygen bottles were used to store the water samples. Immediately after collection of water samples, 1.0ml of manganous sulphate followed by 1.0ml of alkaline iodide were added. The bottles were then stoppered, shaken and stored under water until analysis could take place. When ready to be analyzed 2.0ml of concentrated H_2SO_4 was added to each sample bottle and the stoppers immediately replaced. The contents were shaken and left to stand for 20 minutes. Once all the precipitate had dissolved and the solution had turned a straw colour titrations could be completed. 25ml of the solution was removed and titrated against sodium thiosulphate of a known normality. Titration were repeated 3 times for each bottled sample, the average of these values being used in the final calculation. The oxygen concentration was calculated as follows:

$$mg\text{-}at\ O_2\ l^{-1} = \frac{A \times N \times V \times 1000}{B \times (V - 2) \times 2} \qquad (7)$$

Where A is the volume of thiosulphate titrated (mls)

N is normality of thiosulphate

V is the volume of sample bottle (mls)

B is the volume of sample titrated (mls)

The values obtained were converted to mg-O_2l^{-1} by multiplying by 16, or to ml-O_2l^{-1} by multiplying by 11.2. The percentage of oxygen saturation could also be calculated (Weiss, 1970) using the equation:

$$\ln C = A_1 + A_2\left(\frac{100}{T}\right) + A_3\ln\left(\frac{T}{100}\right) + A_4\left(\frac{T}{100}\right) + S[B_1 + B_2\left(\frac{T}{100}\right) + B_3\left(\frac{T}{100}\right)^2] \qquad (8)$$

Where C is the solubility of oxygen in ml (STP)/l from water saturated air at a total pressure of one atmosphere

S is the salinity in parts per thousand

A and B values are constants (A_1= -173.4292, A_2= 249.6339, A_3= 143.3483, A_4= -21.8492, B_1= -0.033096, B_2= 0.014259, B_3= -0.0017000)

C thus gives a value which is equivalent to 100% saturation, this can be compared to the value

measured to give a value for the percentage oxygen saturation.

2.3 RESULTS

The dates and times of sampling, together with meteorological conditions, are given in Appendix 1. Plankton abundance and environmental measurements made are given in Appendix 2. The abundance of each calanoid copepod species and stage (although the very rare species have not been included in this work), at the Calshot 5 metre site over the 14 month investigation, is shown in Figures 2.3.1 to 2.3.5. There are clear abundance changes throughout the year for each of the species. *Acartia* spp. are the dominant calanoid genus throughout much of the year, with peaks in numbers during both April-May and July-August. The peak in *Acartia* adult numbers is during April, this peak being predominantly *Acartia bifilosa* (see Figure 2.3.2). At the same point there is apparently no simultaneous pronounced peaks in copepodite numbers. The apparent lack of copepodites could be the result of them being missed to some degree in the March samples because of the 200μm mesh net used during this period. Figure 2.3.2 demonstrates that *Acartia bifilosa* was the dominant *Acartia* adult species during the first 6 months of the year, *A.discaudata* and *A.clausi* dominating from July until December-January. *Acartia bifilosa* adults also reached the greatest abundance of any single copepod adult, at almost 600 ind. m^{-3}. After the rapid decline of *Acartia bifilosa* adults in May-June, the numbers of *A.discaudata* and *A.clausi* adults appeared to increase rapidly. *A.clausi* reached a maximum of 140 ind. m^{-3} in July, while *A.discaudata* adults reached a maximum of 166 ind. m^{-3} in August. *A.margalefi* was rare or absent throughout most of the year, although it was found in May and August-September, though with maximum abundances never exceeding 18 ind. m^{-3}.

Centropages hamatus copepodites were found throughout much of the year, being abundant from April through until November, and rare or absent only during the late winter and spring period (see Figure 2.3.3). Adult numbers peaked in July at 53 ind. m^{-3}. Numbers of all stages appear to fall rapidly after August, although there was a second late abundance peak for C3 and C4's in November.

Temora longicornis were most abundant from April through to August, and generally absent during the winter months of October through to February (see Figure 2.3.4). Adults showed an initial peak in numbers during April, with a decline in early May, and then increase once again.

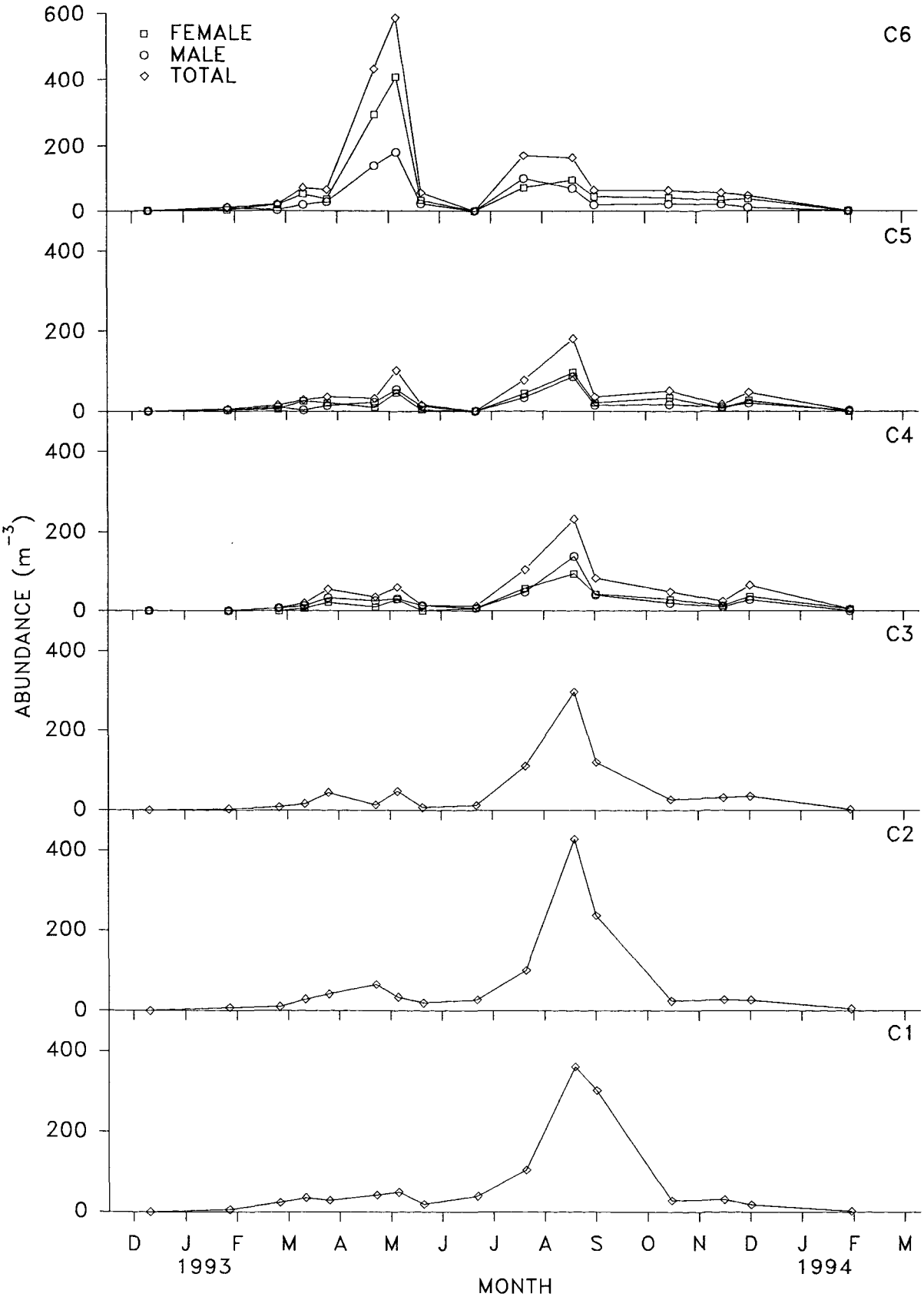


FIGURE 2.3.1 The abundance of the various stages and sexes of Acartia spp. during the period of the 14 month investigation. Samples from the Calshot 5 metre site. (Note Scale Change).

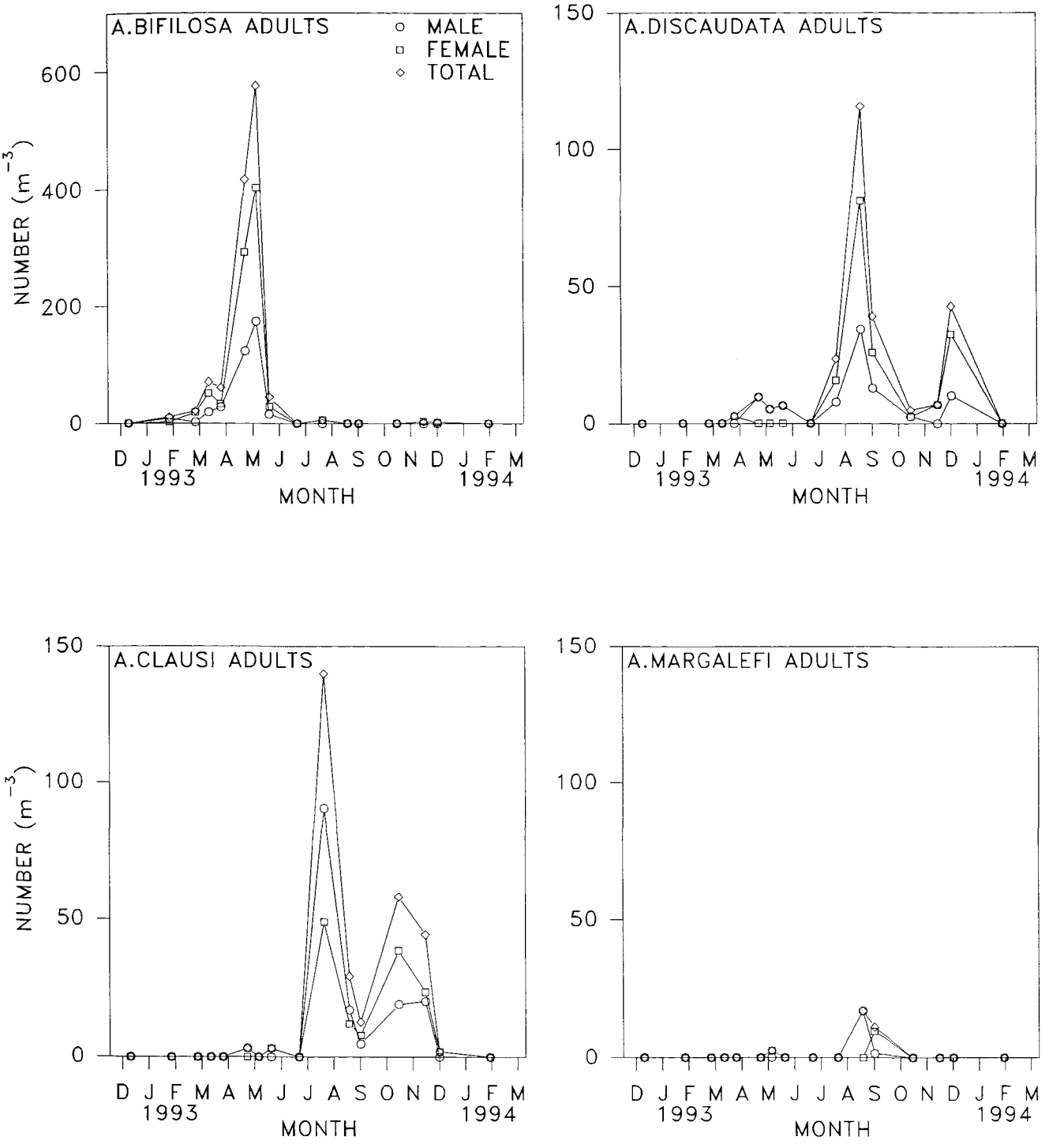


FIGURE 2.3.2 The abundance of adult Acartia (separated by species and sex) during the period of the 14 month investigation. Samples from the Calshot 5 metre site. (Note Scale Change).

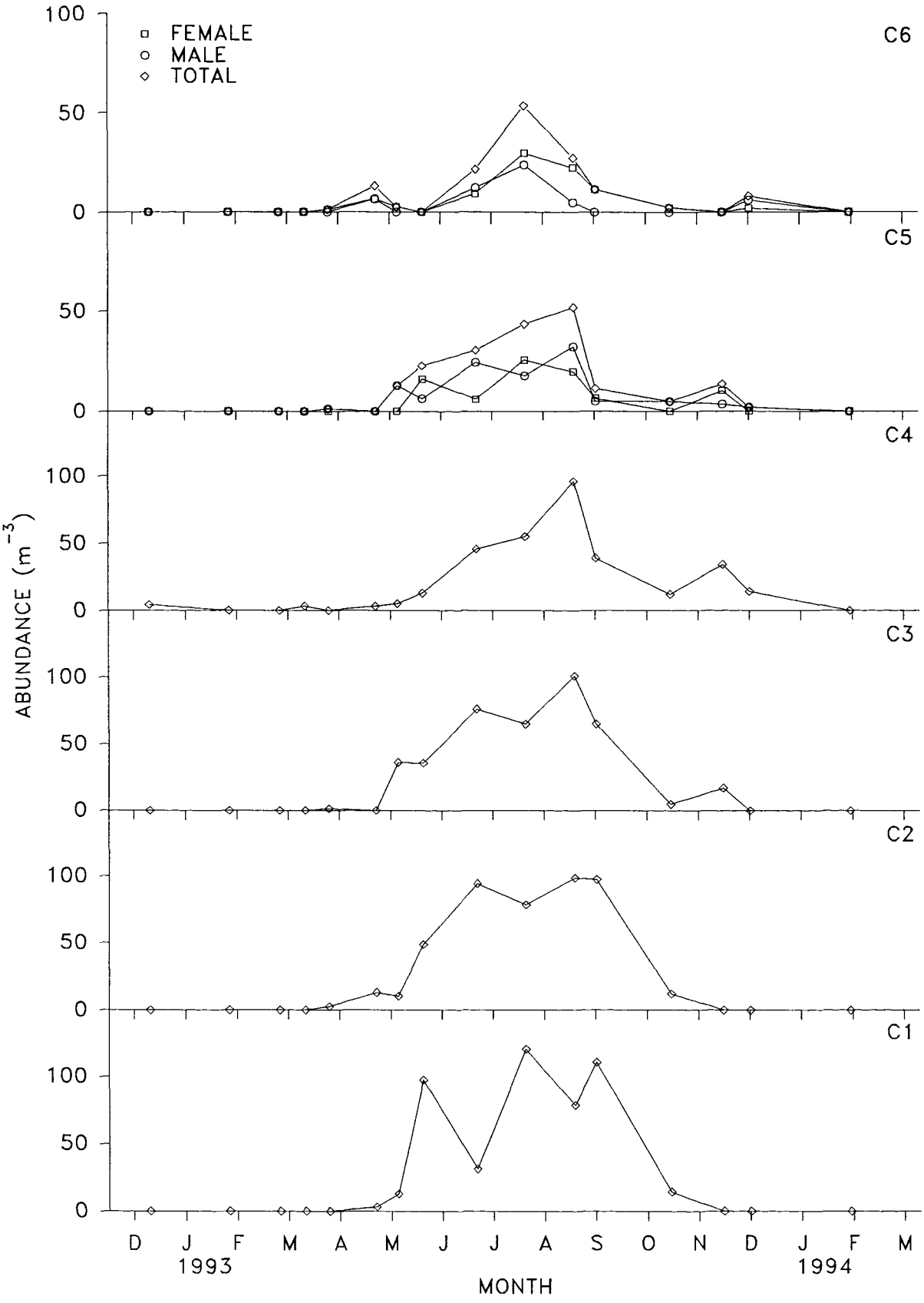


FIGURE 2.3.3 The abundance of the various stages and sexes of Centropages hamatus during the period of the 14 month investigation. Samples from the Calshot 5 metre site. (Note Scale Change).

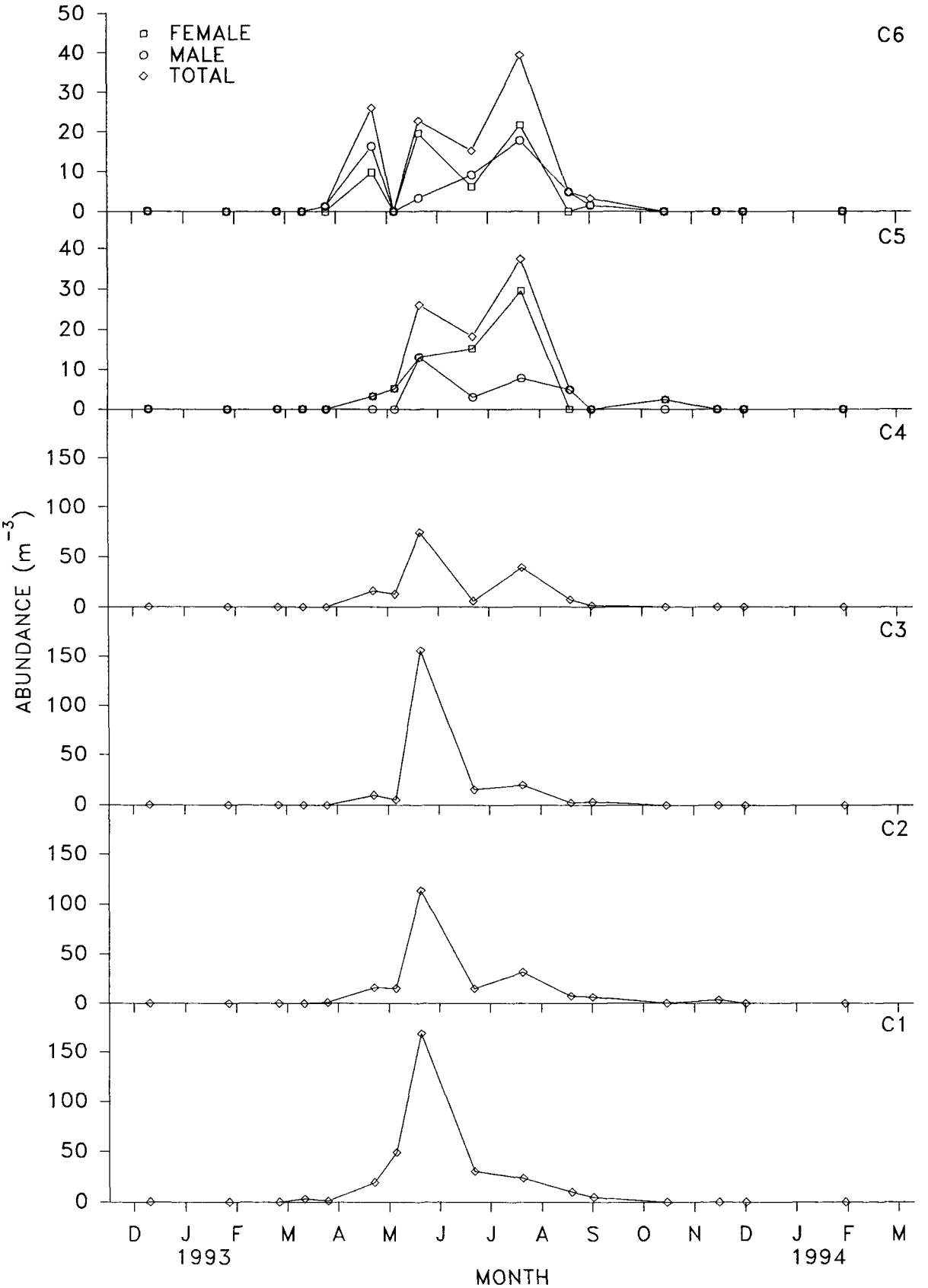


FIGURE 2.3.4 The abundance of the various stages and sexes of Temora longicornis during the period of the 14 month investigation. Samples from the Calshot 5 metre site. (Note Scale Change).

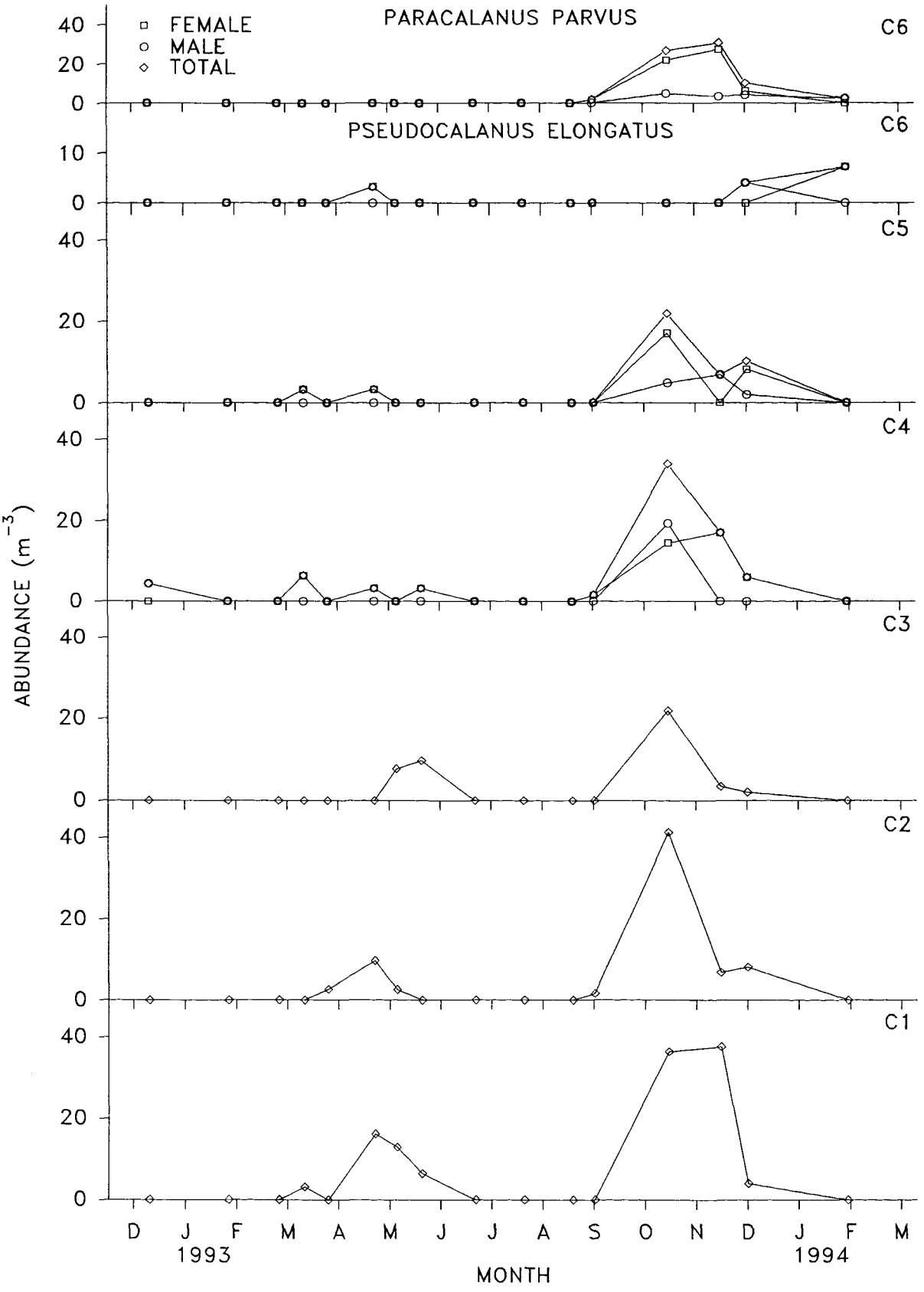


FIGURE 2.3.5 The abundance of the various stages and sexes of Para-Pseudocalanus during the period of the 14 month investigation. Samples from the Calshot 5 metre site. (Note Scale Change).

Maximum adult numbers were found in July, when they reached 39 ind. m^{-3}, C5 stages also peaked at this point, although the densities of earlier stage copepodites peaked in May.

As *Pseudocalanus elongatus* and *Paracalanus parvus* were generally rare, for the purpose of this analysis they have been combined into a single group (*Para-Pseudocalanus*) in the non-adult stages (see Figure 2.3.5). *Paracalanus parvus* adults were most abundant during November, when they reached 34 ind. m^{-3}. *Pseudocalanus elongatus* adults were much rarer than *Paracalanus parvus*, and were found in November to January, and in April. Maximum adult abundance of *Pseudocalanus elongatus* being only 10 ind. m^{-3} in January. Pre-adult stages were most common in October, when they reached 138 ind. m^{-3}, and these individuals were totally *Paracalanus parvus*.

In addition to estimates of calanoid copepod densities, many other groups were counted in the samples. Data from some of the more dominant groups are presented in the discussion section, together with density estimates derived from the most recent studies by Zinger (1989) and Lucas (1993).

Changes in the prosome lengths of each calanoid copepod species and copepodite stages are presented in Figures 2.3.6 to 2.3.10. It is generally recommended that an equal number of individuals are studied, and that this number should be fairly large (eg. 30 individuals of each stage as in Durbin and Durbin, 1978; McLaren and Corkett, 1981; Burkill and Kendall, 1982; see Bird and Prairie, 1985; Christou and Verriopoulos, 1993a). In the present study so much time was needed to separate copepods from detritus, time did not allow such numbers to be examined. Similarly standard, large numbers of individuals per stage have not always been examined by other workers. Chisholm and Roff (1990a) for example examined a total of 30 individuals for each species in their study of size changes in tropical copepods, while Digby (1950) and Marshall (1949) simply sorted a sub-sample with no specific number of individuals. In the present investigation the number of individuals measured are indicated on the figures demonstrating the results. Depending upon species, numbers per stage were commonly greater than 20, and in many cases greater than 40. However, numbers were also often relatively small, but given that a 2% sub-sample was examined, then almost all the sample would of had to have been examined to allow the measuring of 30 individuals, and certainly in many cases there would still not of been enough individuals. For each individual prosome measurement on each date, the number of individuals are given on the figures themselves.

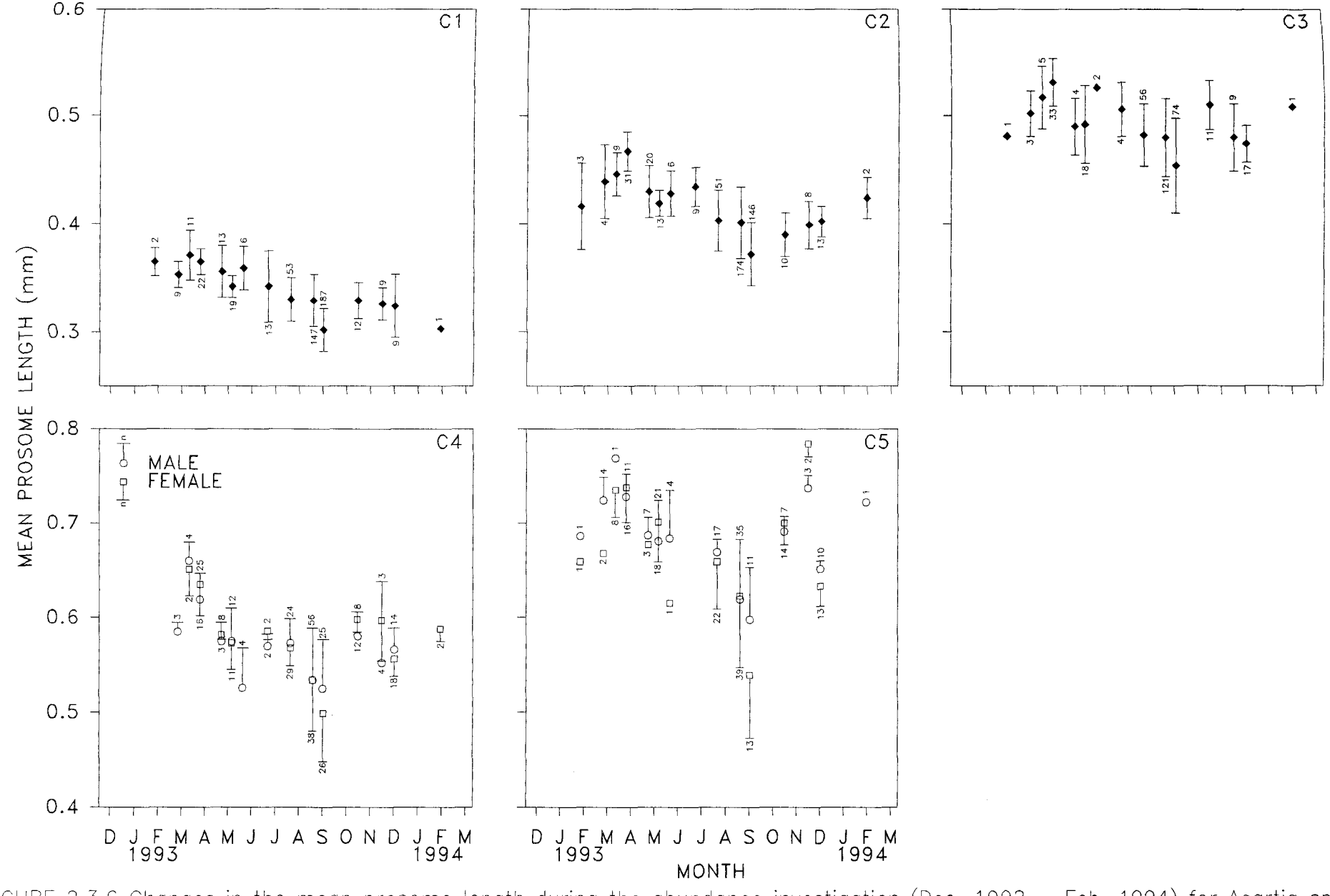


FIGURE 2.3.6 Changes in the mean prosome length during the abundance investigation (Dec. 1992 – Feb. 1994) for Acartia spp. stages C1 to C5 at the Calshot site. Error Bars give Standard Deviations of prosome lengths.

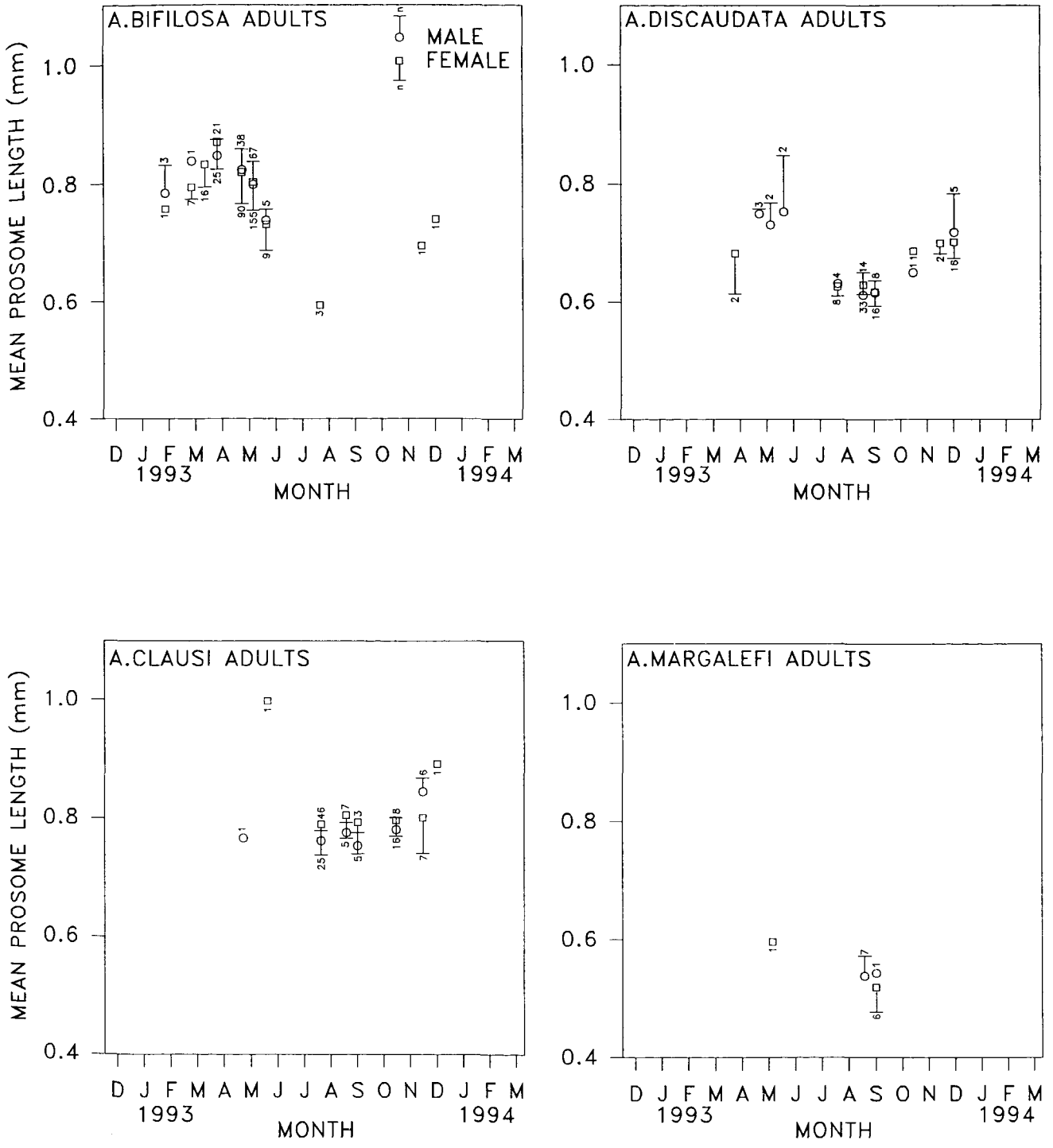


FIGURE 2.3.7 Changes in the mean prosome lengths of Acartia at the Calshot site during the abundance investigation (Dec. 1992 – Feb. 1994). Error bars give Standard Deviations of prosome lengths.

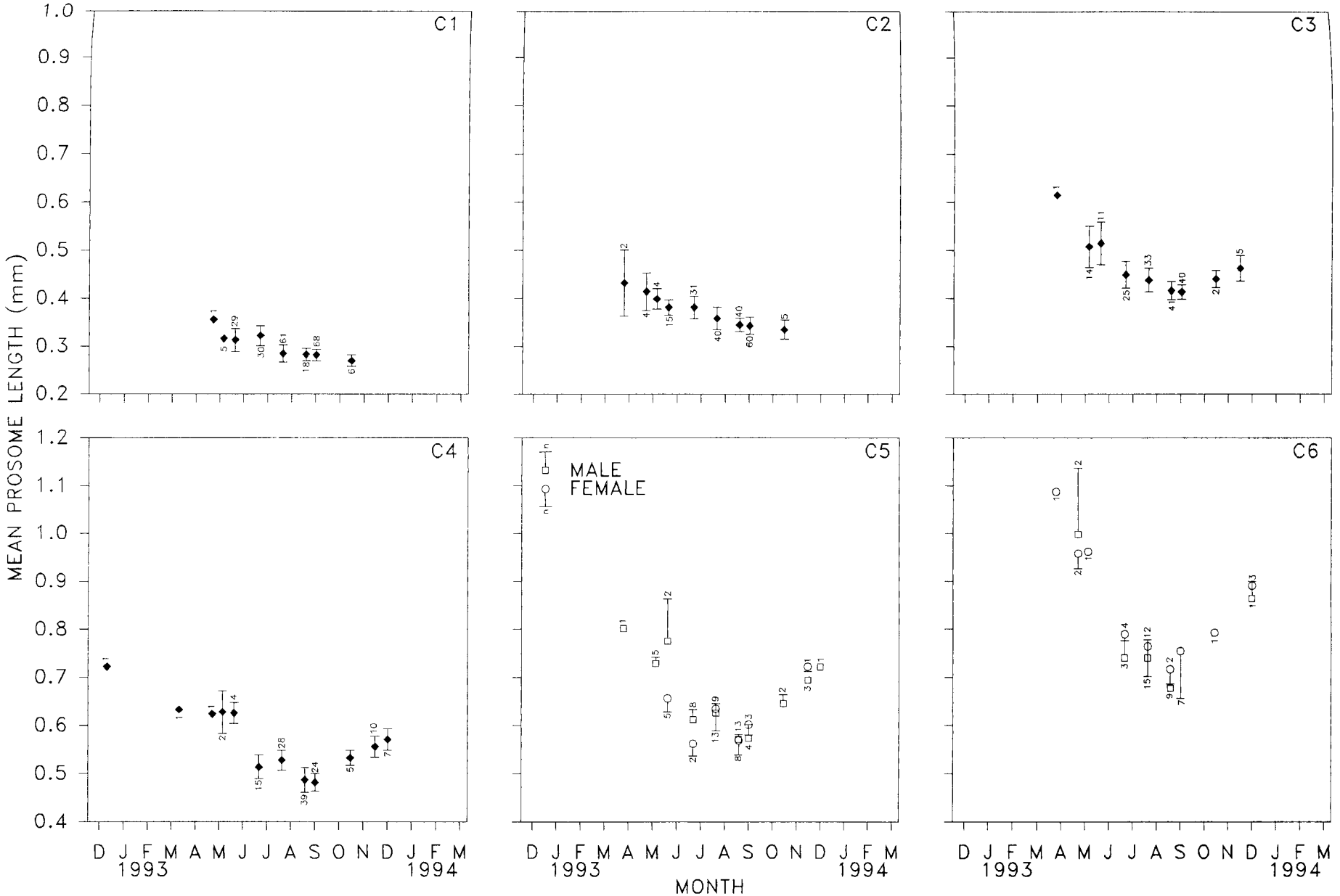


FIGURE 2.3.8 Changes in the mean prosome length during the abundance investigation (Dec. 1992 – Feb. 1994) for Centropages hamatus at the Calshot site. Error Bars give Standard Deviations of prosome lengths.

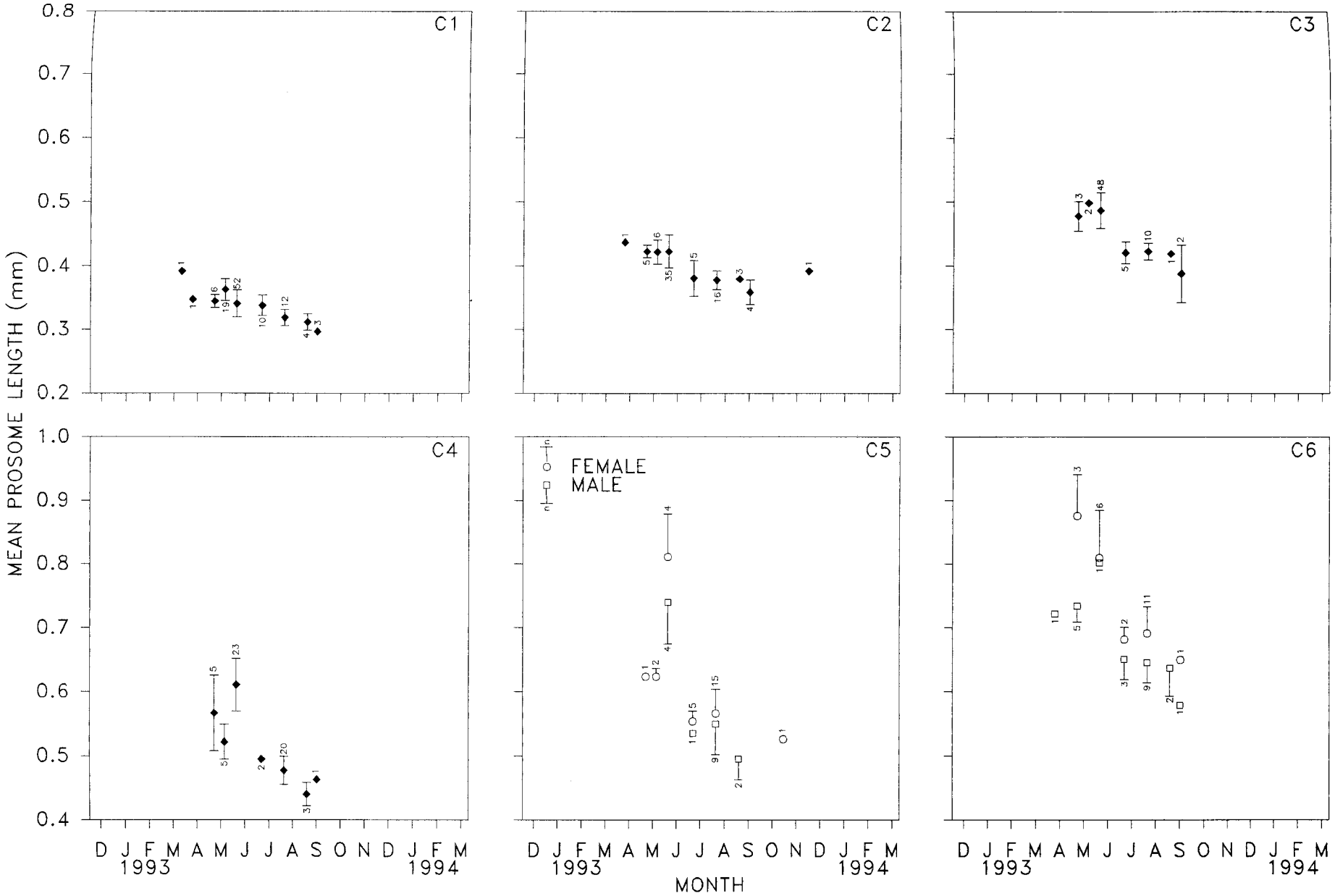


FIGURE 2.3.9 Changes in the mean prosome length during the abundance investigation (Dec. 1992 – Feb. 1994) for Temora longicornis at the Calshot site. Error Bars give Standard Deviations of prosome lengths.

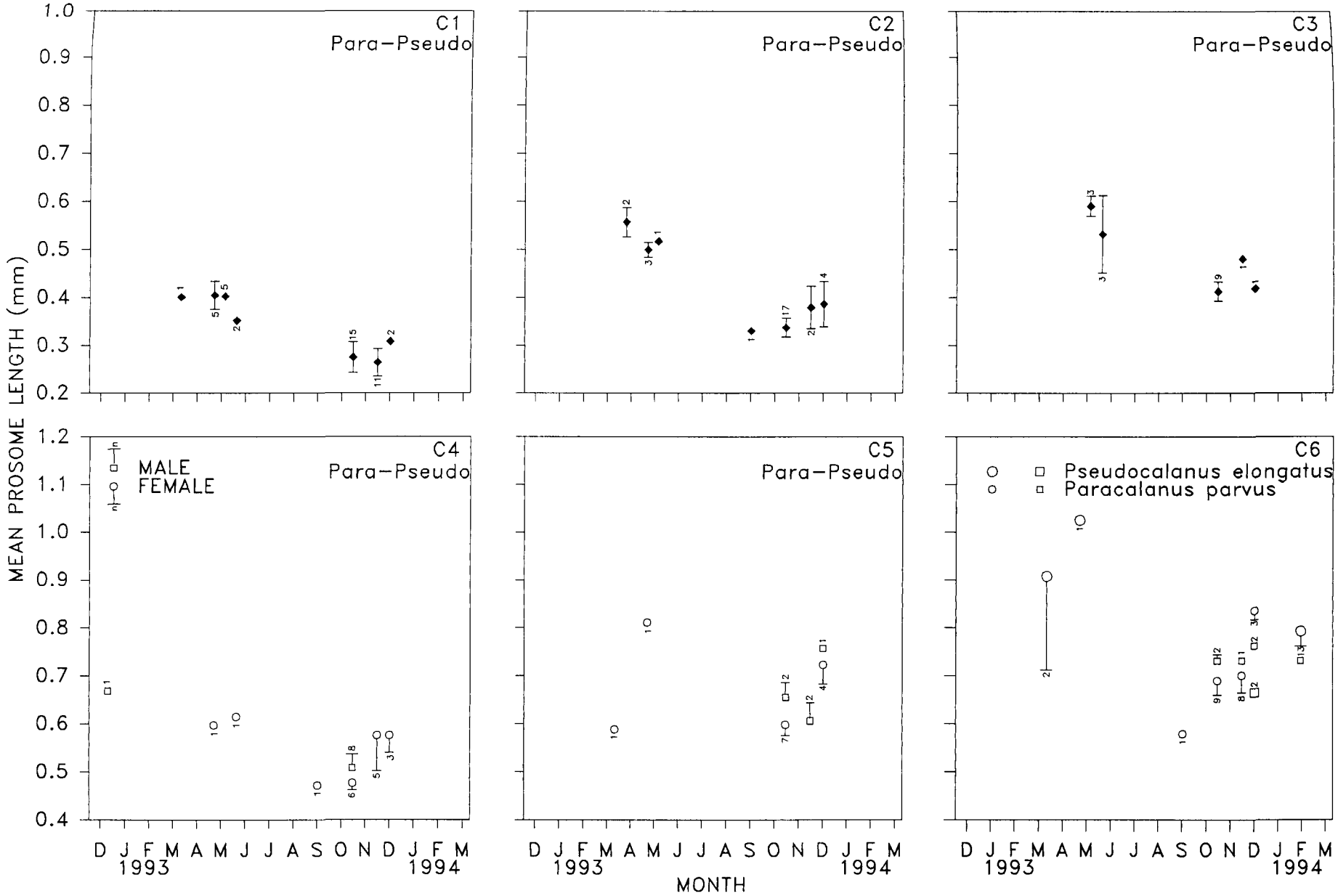


FIGURE 2.3.10 Changes in the mean prosome length during the abundance investigation (Dec. 1992 – Feb. 1994) for Paracalanus parvus and Pseudocalanus elongatus at the Calshot site. Error Bars give Standard Deviations of prosome lengths.

Acartia spp. non-adults were not separated into species because of the time that this would take, stages C1-C5 prosome lengths are presented in Figure 2.3.6, while adult lengths for each species and sex are presented in Figure 2.3.7. Copepodite stages C1 to C5 show clear changes in mean prosome length. There is a general pattern of increasing size from their first appearance in January-February until February-March. After this peak in size they generally decline until August when for most stages the minimum prosome length is found. Subsequently mean prosome lengths increase until the end of the study in January. The amount of absolute size variation during the year also varies between *Acartia* stages. Absolute changes are greater in the later stage individuals, indeed the adults show the greatest absolute change, although this is confused by the succession of species (see Figure 2.3.7). Copepodite stage 1's mean prosome lengths vary by size range of 0.069mm (mean size ranging from 0.302 to 0.371mm), while C5♂ show a size range of 0.171mm (mean size ranging from 0.598 to 0.769mm). In terms of the percentage of the range makes up of the largest size, the differences are fairly similar ie. 19% in C1's and 22% in C5♂.

Acartia bifilosa adults demonstrate a clear change in their mean prosome length. Sizes increase from January to March, when they reach their annual maximum. Adult males reaching their maximum at the same point as adult females, at 0.847mm and 0.870mm respectively. After this prosome lengths decline month on month until July, when recorded sizes are smallest (although unfortunately densities were so low, that no males were measured). There are no recordings of *A.bifilosa* adults after this size minimum until November and December, when sizes have increased once more to values similar to those recorded in the previous winter.

Acartia discaudata adult prosome lengths increase from March to May, when the males were the longest recorded, with a mean prosome length of 0.701mm. When individuals reappeared in July and August size had declined dramatically, reaching a minimum of 0.617mm in females and 0.612mm in males. After this low, mean prosome length increased until December.

Scatter in the mean prosome lengths of adult *Acartia clausi* adult is great, although the number of individuals on which these sizes have been determined are low at times. The maximum mean size found was in May, when a female was found at 0.998mm in length. Size was fairly constant from July to October, males ranging from 0.790 to 0.805mm, while females varied between 0.754 and 0.781mm. Following this period of fairly stable size, the size increased into winter.

The sporadic appearance and scarcity of *Acartia margalefi* adults makes the description

of seasonal trends virtually impossible. This species always had the smallest mean prosome length. Size never exceeds 0.60mm in this species, and fell as low as 0.52mm in females and 0.539mm in males during September. As *A.margalefi* is so similar to *Acartia clausi*, (indeed *A.margalefi* was only first recognised as different from *A.clausi* in 1976), it seems probable that it is very closely related. When both these species occurred together at Calshot *A.margalefi* always had a mean prosome length which was between 66% and 72% of that of *A.clausi.*

Figure 2.3.8 displays the mean prosome lengths for copepodites stages in *Centropages hamatus*. Sizes appeared to decline in all stages of this species from a winter or spring maximum to a minimum in June to August, after which the sizes increased once more in the older stages, but not in all the youngest stages. Again absolute size changes were greatest in the older stages as compared to those younger. Adult female mean prosome lengths were maximally 1.087mm and minimally 0.717mm, while adult males varied between 0.998 and 0.677mm. Smallest lengths were therefore remarkably only 67% (for both sexes) of the largest length. Adult females were almost always larger than adult males at the same sampling point.

Prosome lengths of *Temora longicornis* individuals are presented in Figure 2.3.9. The pattern of change in size of *Temora longicornis* was very similar to that for *Centropages hamatus*, with a decline from winter into summer, and sizes were least in the months of August to September. A few individuals were found after these months, and these indicate that size increased once more later in the year. There was however a general absence of this species after September. Once again the older stages showed relatively greater size changes than the younger stages, an apparently common feature across all species examined.

Although *Paracalanus parvus* and *Pseudocalanus elongatus* were separated in all copepodite stages, since they were so rare, and in most studies combined in non-adults, then the two have been combined in all the non-adult stages in the present analysis. Figure 2.3.10 demonstrates that prosome sizes decline from early in the year to lowest values in the summer, with a subsequent increase in to the winter. In fact the early group found from December 1992 to May 1993 are *Pseudocalanus elongatus* individuals, whilst those from September are almost all *Paracalanus parvus* (as observable in the C6 groups and, although not divided here, this is also true for younger stages).

Temperature and salinity measurements recorded over the 14 month initial investigation are presented in Figures 2.3.11 and 2.3.12. Temperature shows a cyclical annual pattern with the highest temperatures recorded at all of the estuarine sites in mid-August (maximum date average

18.6°C, on the 19th August 1993), and the minimum values recorded at the beginning of December (minimum date average 6.0°C, on the 1st December 1994). On each sampling date the temperatures recorded at the 5 stations and 2 depths were very similar, with the greatest temperature range on one sampling date being only 0.8°C. There would however, appear to be a slight temperature gradient within the estuary with the more seaward stations showing lower temperatures than the sites towards the head.

Salinity shows a clear gradient along the estuary, with the highest salinities towards the estuary mouth and the lowest salinities at the Cracknore and Bury Buoy sites (see Figure 2.3.12), the greatest variation between all sites and depths being 6.5°/$_{oo}$ in the month of April, while the least being 1.7°/$_{oo}$ in May. Salinity values throughout the year are variable, although the lower values are during the winter months and the highest values are during the summer. The lowest salinities recorded were on the 15th of October 1993. The minimum salinity value found was 27.3°/$_{oo}$, at Cracknore and Bury Buoy during October 1993. The highest value was 34.5°/$_{oo}$, recorded at the Calshot site in July of the same year. The data clearly demonstrate that salinity was significantly reduced in October 1993, sampling on this occasion shortly following a periods of intense local rainfall and flooding, and increased freshwater inputs (as shown from river flow data supplied by the NRA). Salinity is indicative of flushing rates, low salinity values represent high rates of flushing and high salinities represent low rates of freshwater input and lower flushing.

Chlorophyll a concentrations measured during the 14 month sampling program are shown in Figure 2.3.13. Chlorophyll a concentrations varied from 0.39µg.l^{-1} at Bury in May 1993, to 58.90µg.l^{-1} in late July 1993; once again at Bury. Chlorophyll peaks at most sites during July to August. There was a peak in early March at around 5µg.l^{-1}, and a more prolonged peak during May to September. These second peaks in chlorophyll a were earlier in their timing at the more seaward sites. Thus at Calshot a second peak of >10µg.l^{-1} was found in May, but at the same point in time chlorophyll a at Bury Buoy was <1µg.l^{-1}. Maximum chlorophyll a values were found during July at Bury Buoy and Cracknore and N.W.Netley. Concentrations of phaeo-pigments during this investigation are given in Figure 2.3.14. Maximum values occur generally during the chlorophyll a blooms, ie. early in the year during March, and through the months May to October. Values were also high during the winter months December to February. Values were also found to be generally greater at 10 metres than at 5 metres.

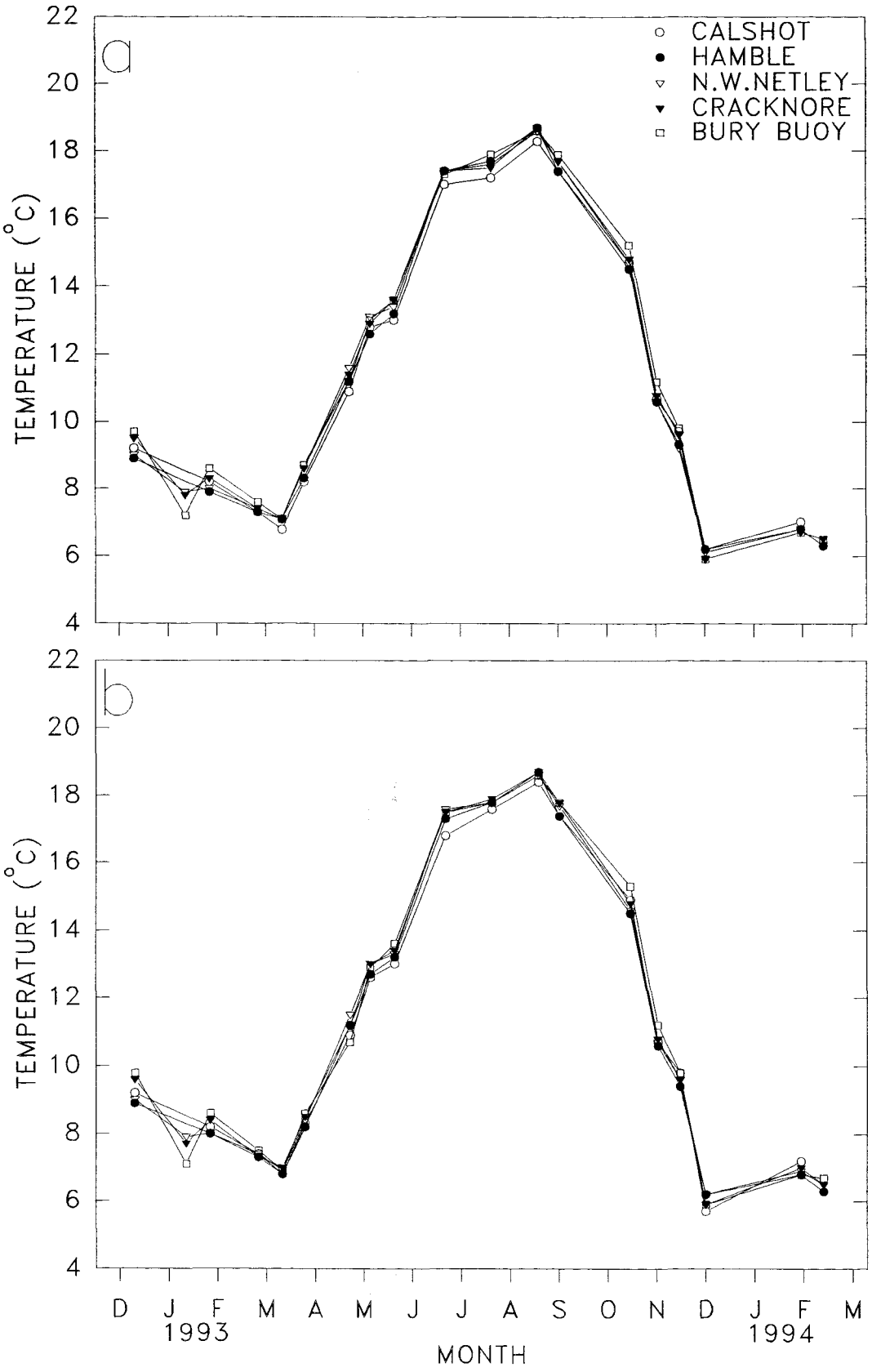


FIGURE 2.3.11 Temperature at the estuarine sites as marked. (a. 5 metres, b. 10 metres).

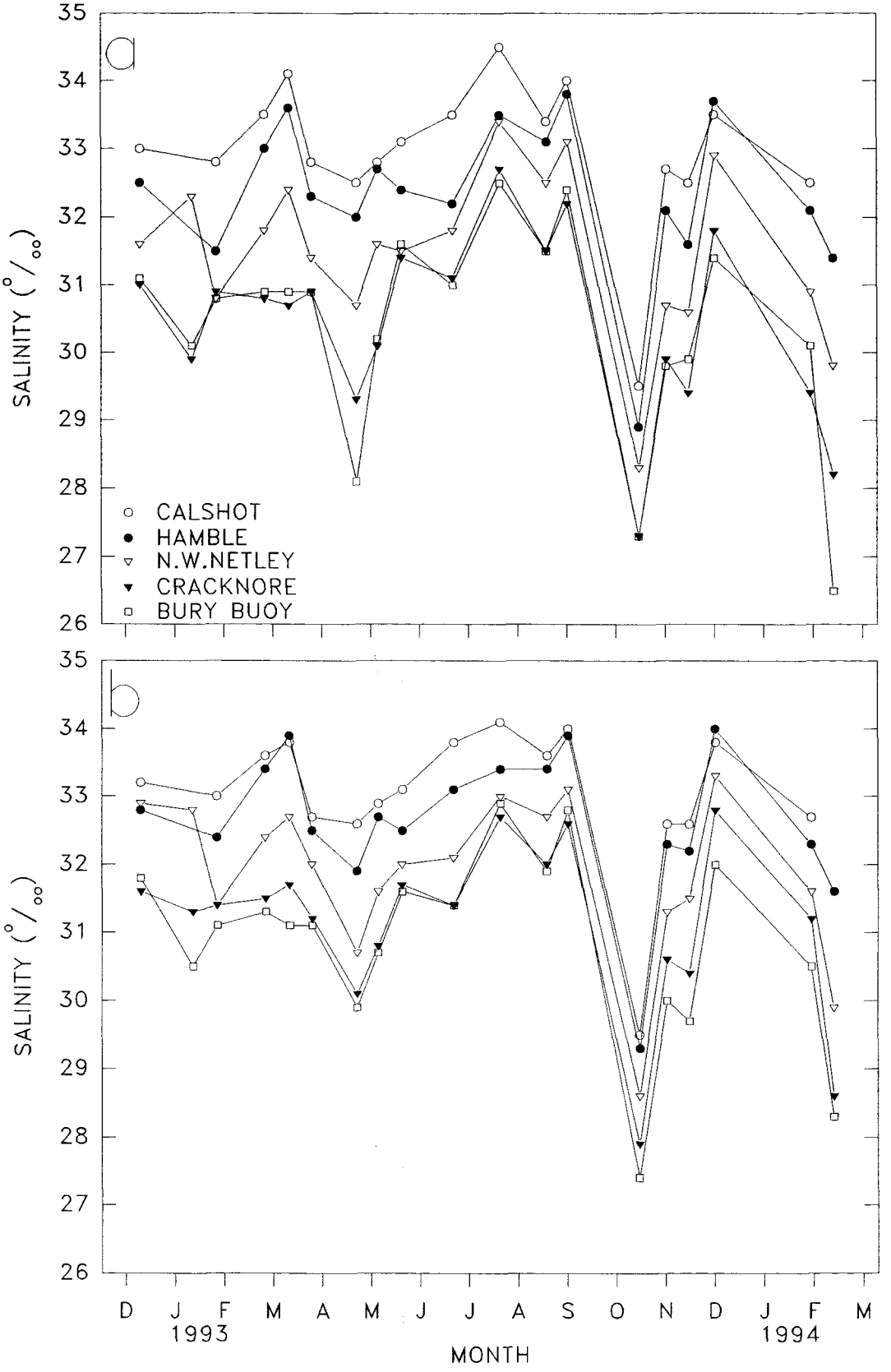


FIGURE 2.3.12 Salinity at the estuarine sites as marked. (a. 5 metres, b. 10 metres).

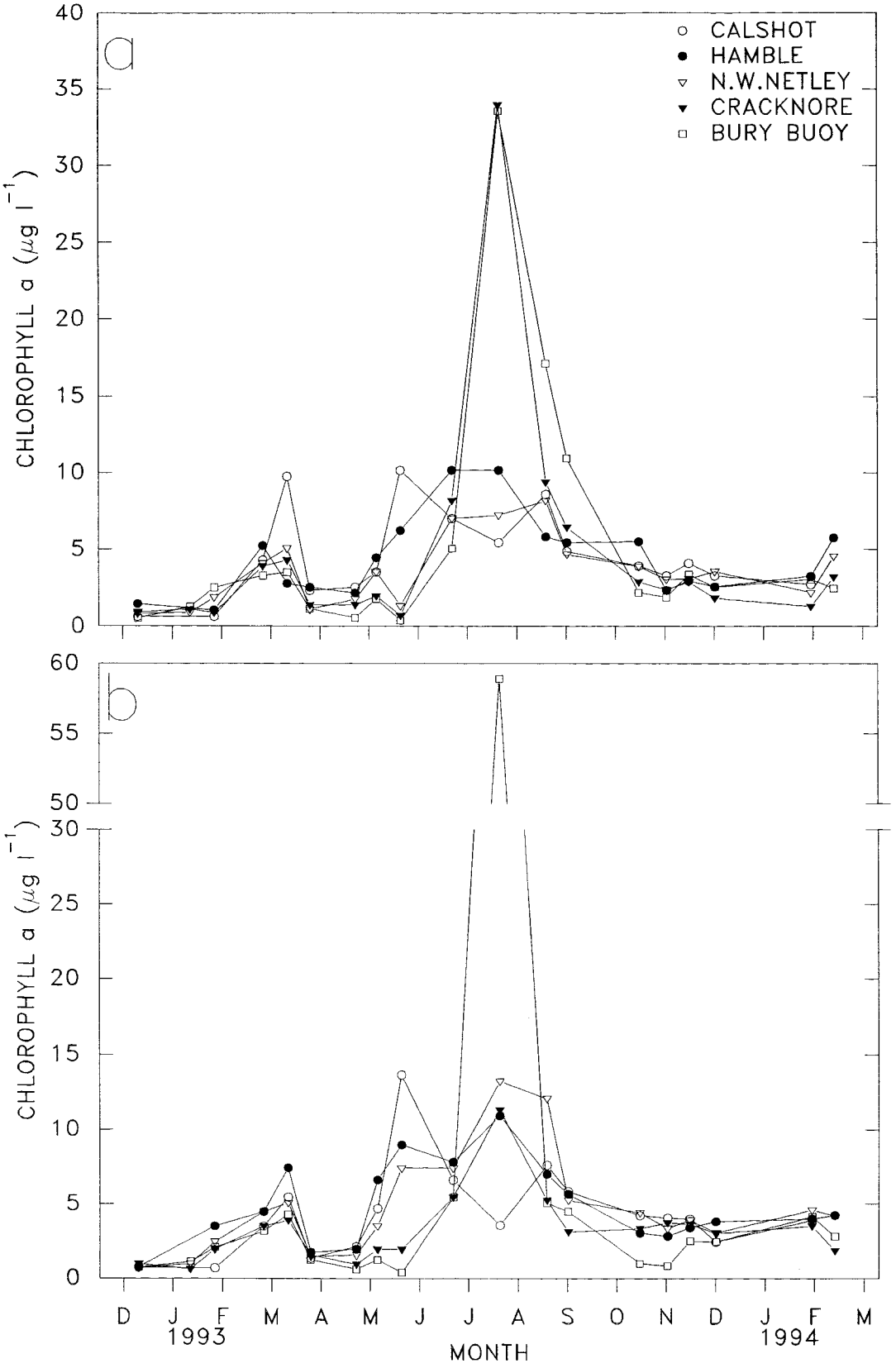


FIGURE 2.3.13 Chlorophyll a concentrations at the estuarine sites as marked (a. 5 metres, b. 10 metres). Note Scale Change.

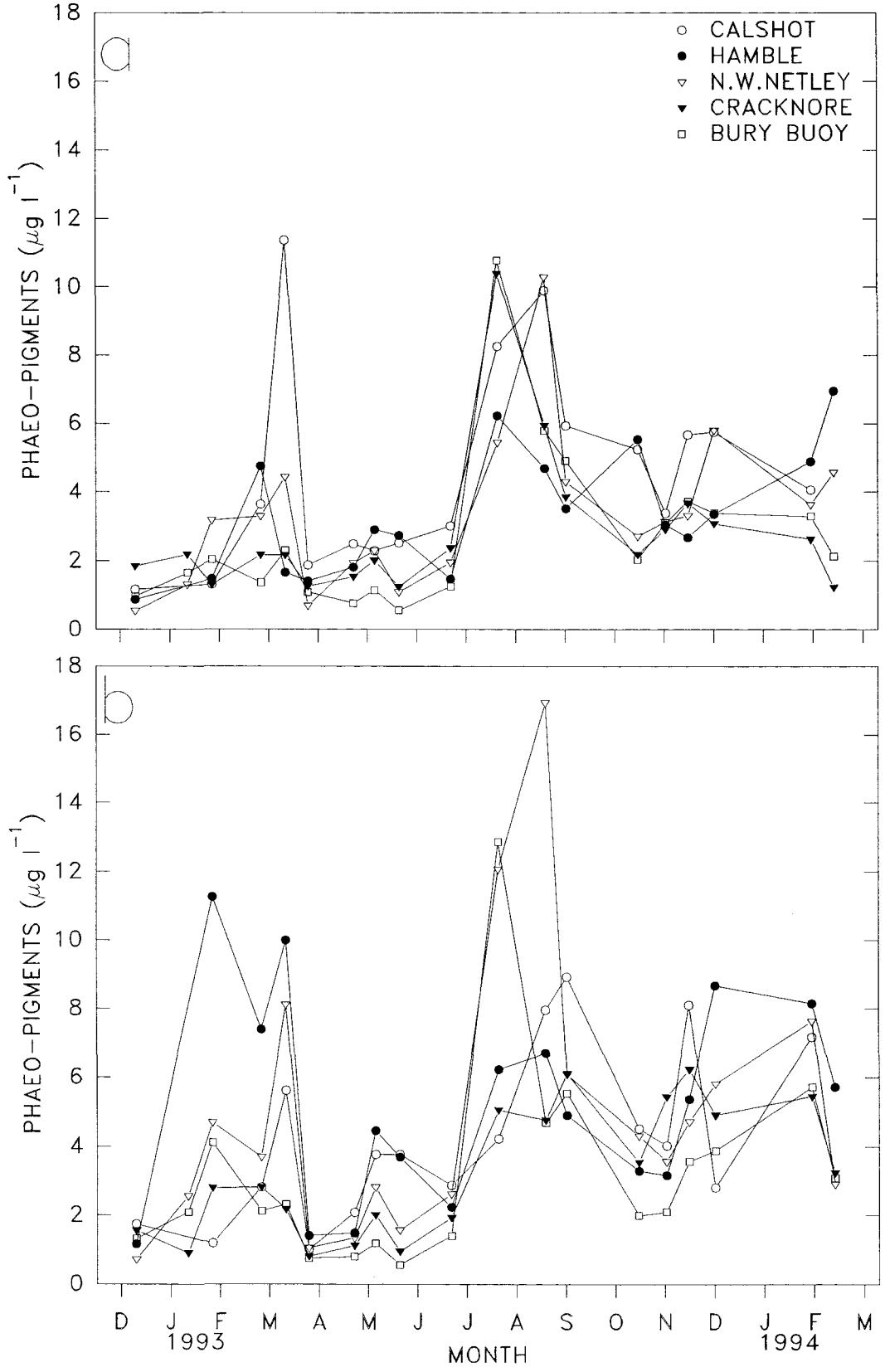


FIGURE 2.3.14 Phaeo-Pigments concentrations at the estuarine sites as marked (5 metres, b. 10 metres).

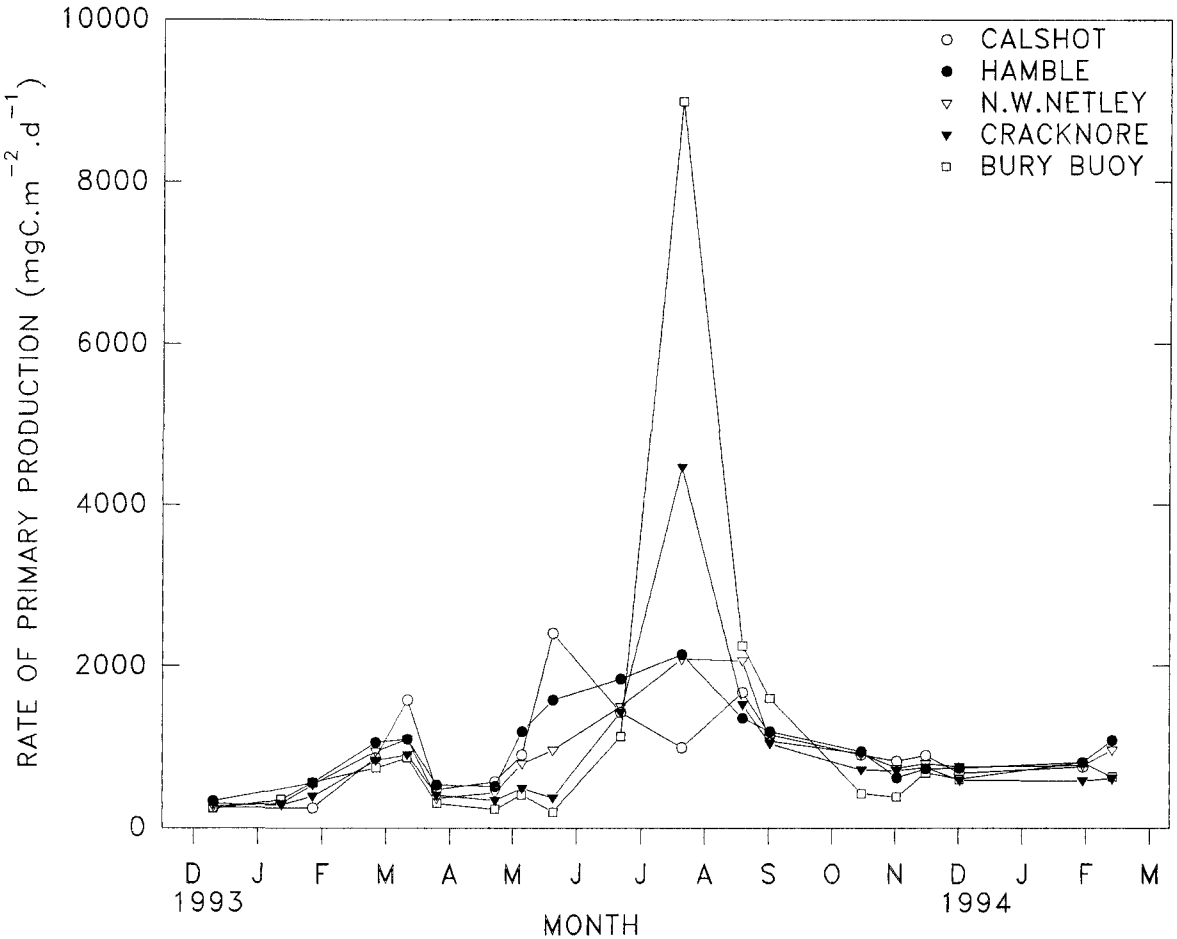


FIGURE 2.3.15 Estimated primary production rates at the estuarine sites as marked.

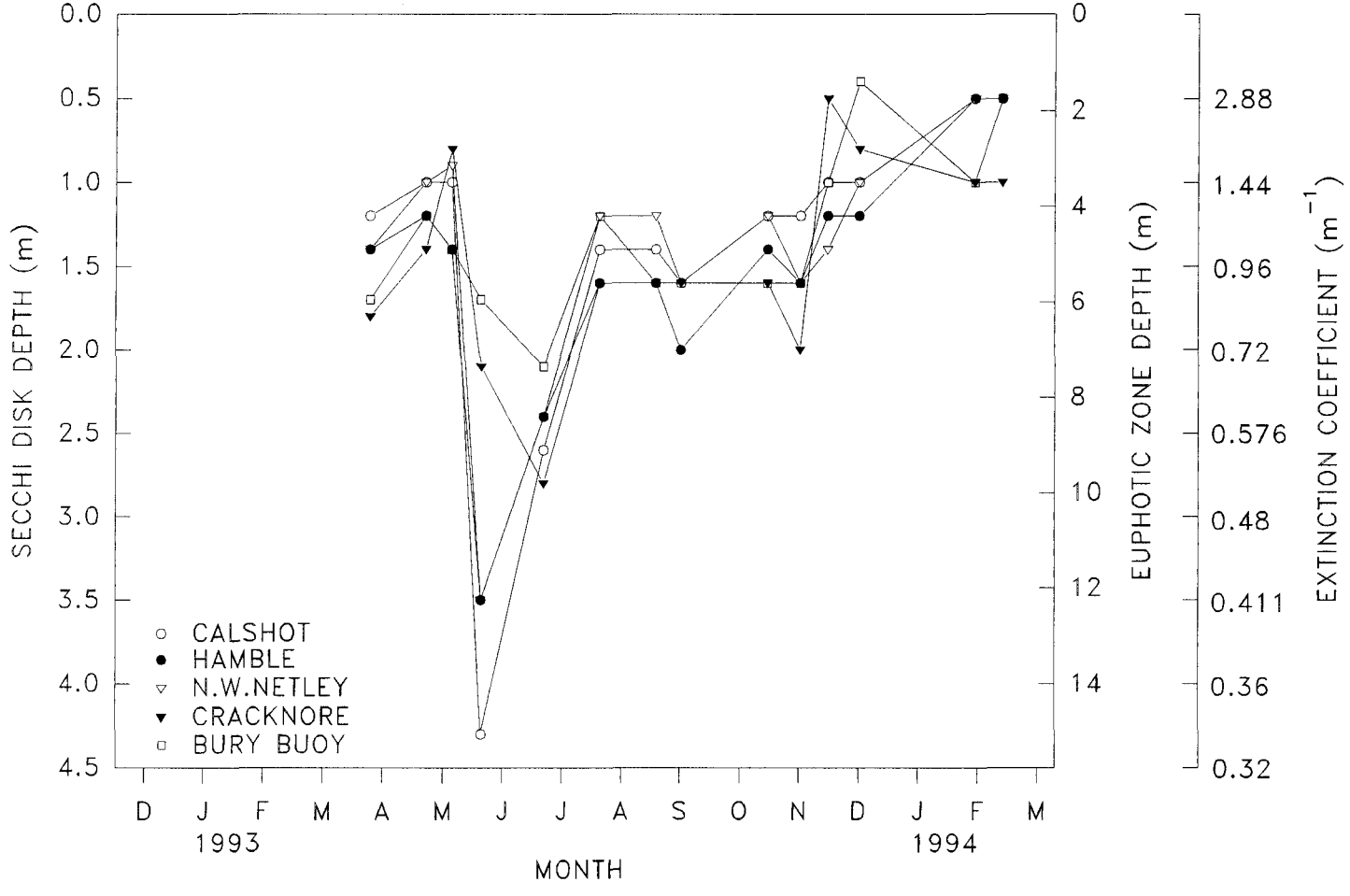


FIGURE 2.3.16 Secchi Disk Depths with associated calculated Euphotic Zone Depths and Extinction Coefficients at the estuarine sites as marked.

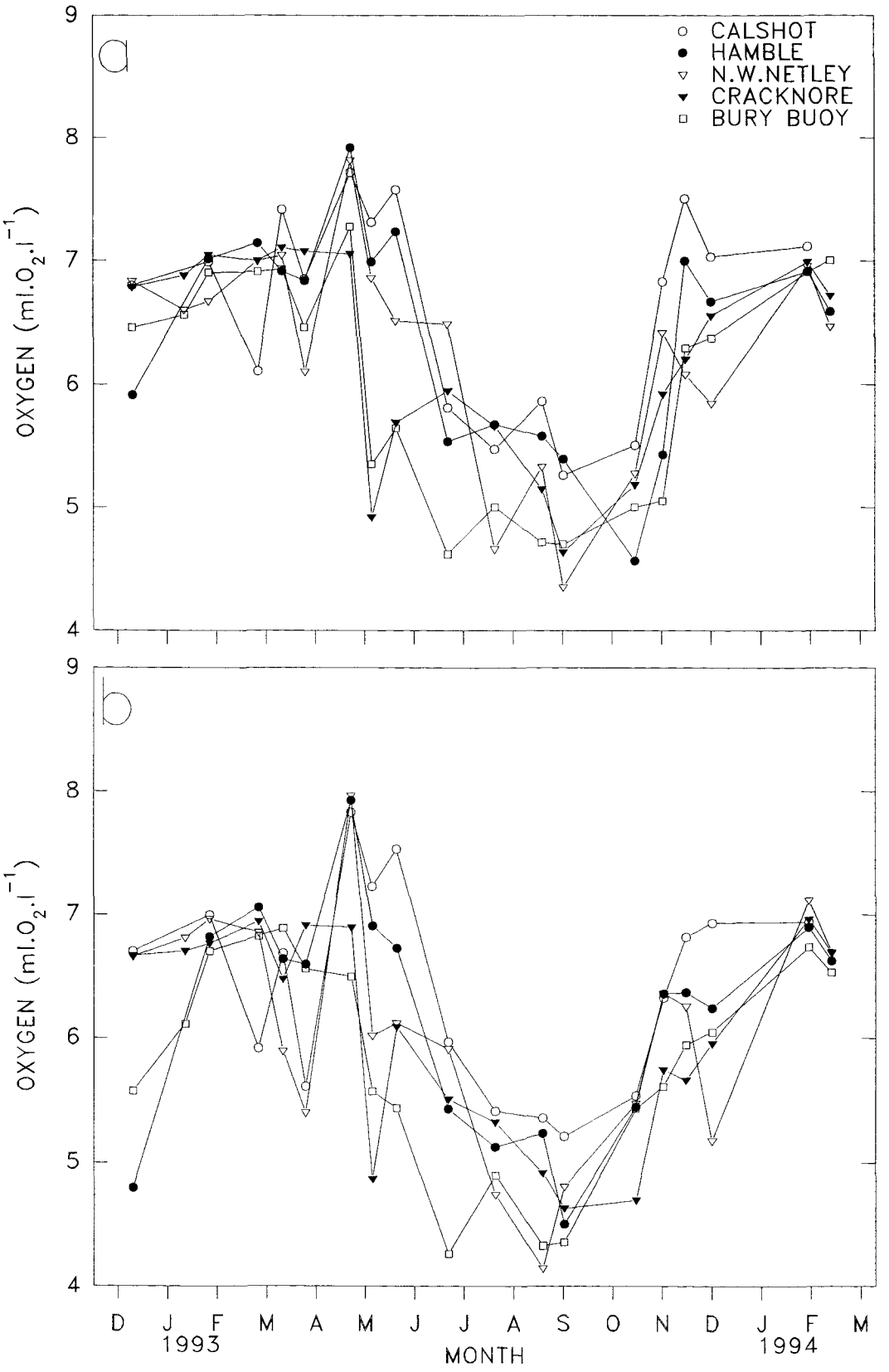


FIGURE 2.3.17 Concentration of Oxygen at the estuarine sites as marked (a. 5 metres, b. 10 metres).

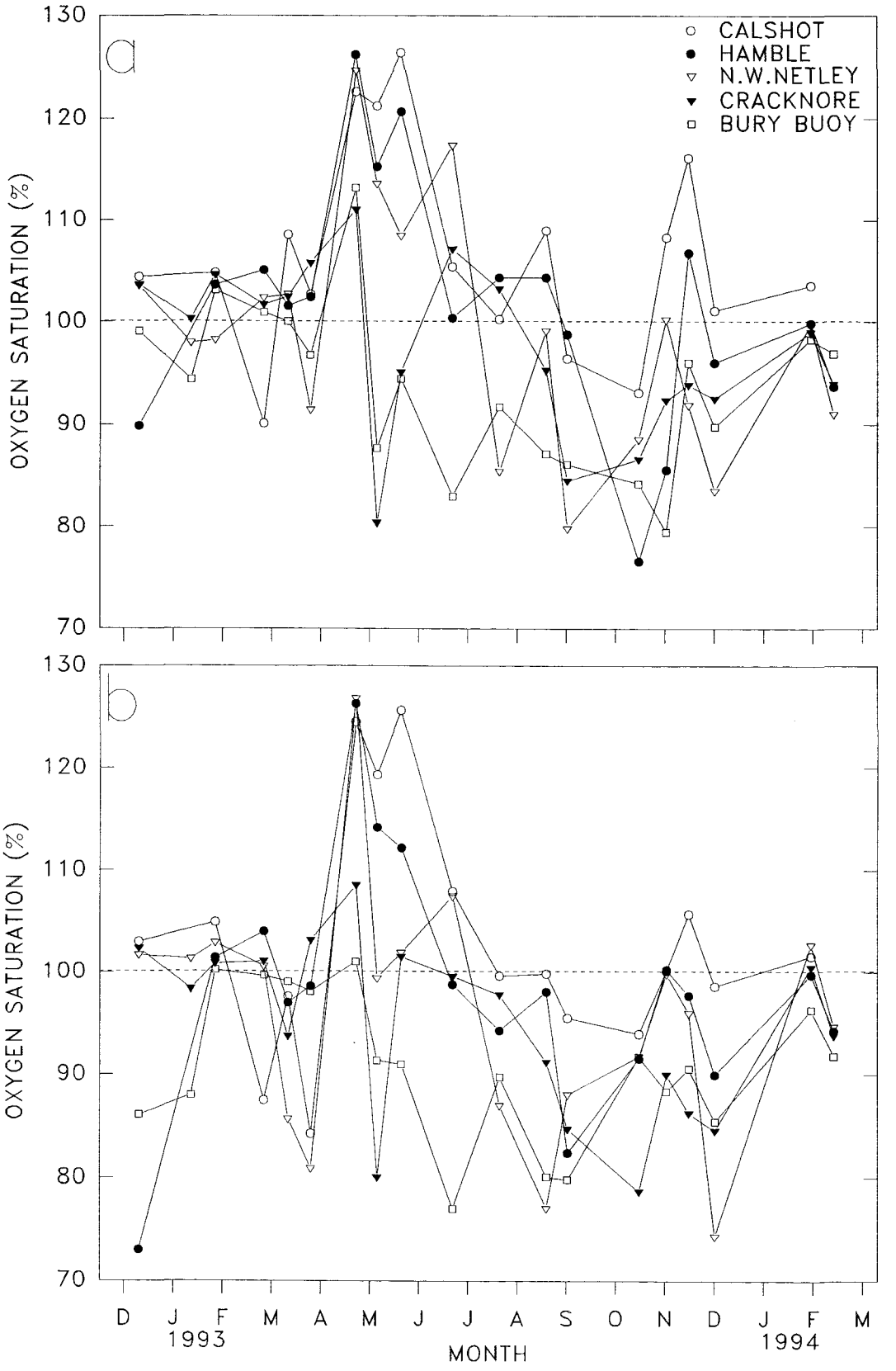


FIGURE 2.3.18 Percentage oxygen saturation at the estuarine sites as marked (a. 5 metres, b. 10 metres).

The calculated primary production rates are presented in Figure 2.3.15. Trends in the primary production rates reflect the changes which occur in chlorophyll a concentrations. The highest rates of primary production occur during July at the Bury Buoy site, when it is estimated to be around 9,000mgCm^{-2}d^{-1} (or 1,125mgCm^{-3}d^{-1}). There is a winter low, followed by an early spring peak at around 1,000mgCm^{-2}d^{-1} throughout the estuary. After this, values fall only to rise once more in March, with values exceeding ~1,000mgCm^{-2}d^{-1} throughout the entire estuary from June to September. Values then fall back to winter lows.

Oxygen concentrations and oxygen saturation percentages are shown in Figures 2.4.17 and 2.4.18. Clear seasonal trends are distinguishable, with oxygen being lowest during the warmer summer months, and highest during the winter and spring period. Maximum peaks in dissolved oxygen occur at most sites and depths in the month of April. The percentage oxygen saturation in the estuary seldom fall below 75%, while peaks of over 125% are apparent during April and May.

Pearson Product Moment Correlation analysis for the various environmental parameters, and density and biomass of various zooplankton groups, measured over the 14 month investigation at the Calshot site, have been carried out. The results from these analyses are presented in Table 2.3.1. Given that many parameters, particularly biological ones, may lag changes in the parameters which influence them, correlation was also conducted after lagging one of the components in each test by 1 measurement (ie. typically 2 to 4 weeks). The results of the second set of tests are presented in Table 2.3.2.

Calanoid copepod biomass and density are positively correlated ($P<0.001$) as might be expected. Calanoid copepod density at Calshot is also significantly positively correlated to temperature ($P<0.001$), although surprisingly more highly correlated that copepod biomass is to temperature ($P<0.05$). Copepod biomass is also positively correlated to oxygen saturation ($P<0.05$). *Sagitta setosa* biomass and density are also highly significantly positively correlated ($P<0.001$). Secchi disk depth is positively correlated to chlorophyll a concentration ($P<0.001$) and primary production ($P<0.001$). *Sagitta setosa* density and salinity are the only variables to be found to be negatively correlated ($P<0.05$).

	CD	CB	SD	SB	Temp	Sal	Chl	Phae	PP	Oxy	Sec
CD	-	**+	ns	ns	**+	ns	ns	ns	ns	ns	ns
CB	-	-	ns	ns	*+	ns	ns	ns	ns	*+	ns
SD	-	-	-	**+	ns	*–	ns	ns	ns	ns	ns
SB	-	-	-	-	ns	ns	ns	ns	ns	ns	ns
Temp	-	-	-	-	-	ns	ns	ns	ns	ns	ns
Sal	-	-	-	-	-	-	ns	ns	ns	ns	ns
Chl	-	-	-	-	-	-	-	ns	ns	ns	**+
Phae	-	-	-	-	-	-	-	-	ns	ns	ns
PP	-	-	-	-	-	-	-	-	-	ns	**+
Oxy	-	-	-	-	-	-	-	-	-	-	ns
Sec	-	-	-	-	-	-	-	-	-	-	-

TABLE 2.3.1 Pearson Product Moment Correlation analysis of various physico-chemical and biological parameters from data collected during the 14 month seasonality investigation at the Calshot site.

Shifted forward by one sampling interval

	CD	*CB*	*SD*	*SB*	*Temp*	*Sal*	*Chl*	*Phae*	*PP*	*Oxy*	*Sec*
CD	-	*+	ns	ns	*+	ns	ns	ns	ns	ns	ns
CB	ns	-	ns	ns	ns	ns	ns	ns	ns	ns	ns
SD	ns	ns	-	ns	ns	ns	ns	ns	ns	ns	ns
SB	ns	ns	ns	-	ns	ns	ns	ns	ns	ns	ns
Temp	**+	*+	ns	ns	-	ns	*+	ns	*+	ns	ns
Sal	ns	ns	ns	ns	ns	-	ns	ns	ns	ns	ns
Chl	ns	*+	ns	ns	ns	ns	-	ns	ns	ns	ns
Phae	ns	ns	ns	ns	ns	ns	ns	-	ns	ns	ns
PP	ns	*+	ns	ns	ns	ns	ns	ns	-	ns	ns
Oxy	ns	*+	ns	ns	ns	ns	ns	ns	ns	-	ns
Sec	ns	ns	ns	ns	ns	ns	ns	ns	ns	*+	-

TABLE 2.3.2 Pearson Product Moment Correlation analysis of various physico-chemical and biological parameters from data collected during the 14 month seasonality investigation, at the Calshot site. Parameters presented horizontally having been shifted forward by one sampling measurement.

(ns= not significant P>0.05; *= significant positive correlation, P<0.05 but >0.001; **= highly significant positive correlation, P<0.001).

+ correlation (increase together)

– correlation (one increases while the other decreases)

Abbreviations:

CD=Total calanoid copepod density (m^{-3})

CB=Total calanoid copepod biomass (μgCm^{-3})

SD=*Sagitta setosa* density (m^{-3})

SB=*Sagitta setosa* biomass (μgCm^{-3})

Temp=Temperature (°C)

Sal=Salinity $^{o}/_{oo}$

Chl=Chlorophyll a concentration (μgl^{-1})

Phae=Phaeopigment concentration (μgl^{-1})

PP=Primary production ($mgCm^{-2}d^{-1}$)

Oxy=Oxygen (% saturation)

Sec=Secchi disk depth (m)

Using a time lagging shows that calanoid copepod biomass is positively correlated to many factors measured at the previous sampling point including; calanoid density, temperature, chlorophyll a concentration, primary production and oxygen (all $P<0.05$). While calanoid copepod density is positively correlated to temperature at the previous sampling point ($P<0.001$). Chlorophyll a concentration and primary production are also positively correlated with temperature at the previous sampling point ($P<0.05$). While oxygen saturation is correlated positively with secchi disk depth at the previous sampling point ($P<0.05$).

2.4 DISCUSSION

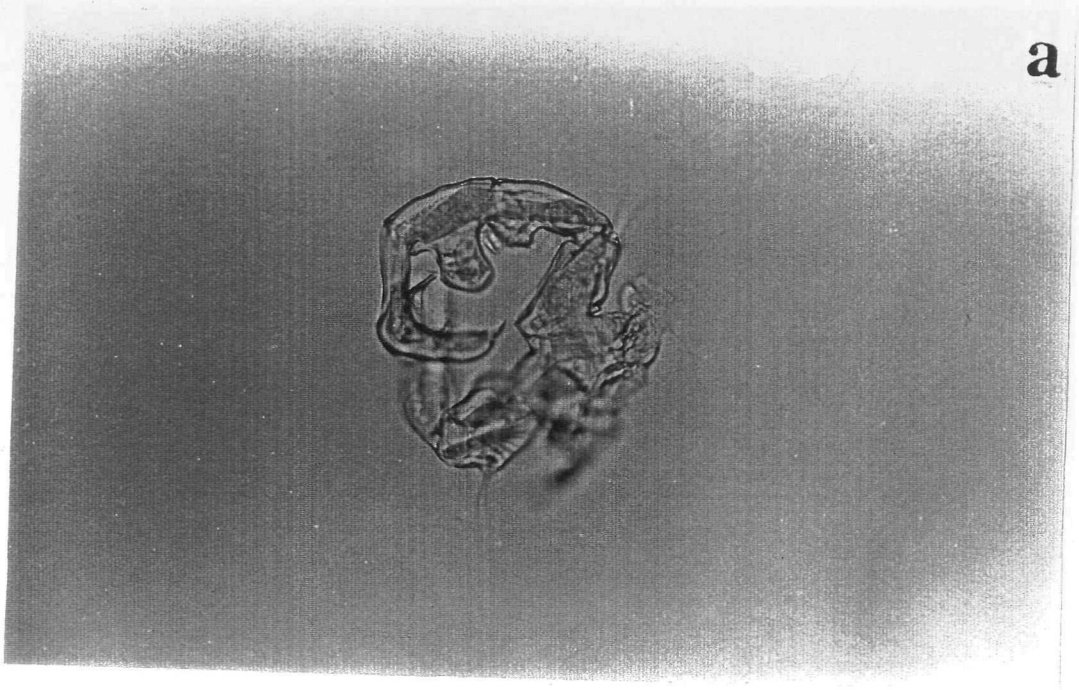
Species present:

The pelagic copepods which have been recorded within Southampton Water in the present, and previous investigations, are given in Table 2.4.1. In the present investigation calanoid numbers and biomass at the Calshot site were overwhelmingly dominated by just 7 species; *Acartia clausi*, *Acartia bifilosa*, *Acartia tonsa*, *Centropages hamatus*, *Temora longicornis*, *Paracalanus parvus* and *Pseudocalanus elongatus*. Biomass and numerical domination by a few species of copepods is a common phenomenon in estuarine waters. Furthermore, the species found in this study are also common in other estuarine, coastal and in some cases offshore areas (Raymont, 1983).

In the present investigation it has been found that the so called *Acartia bifilosa*, recorded by Raymont and Carrie (1964) and Conover (1957), appears under closer scrutiny to show characteristics of both *A.bifilosa* and *A.bifilosa* var.*inermis* (see Rose, 1933). *A.bifilosa* var. *inermis* have been reported in the Loire River estuary, Gibraltan coastal Waters (Rose 1929; Bradford-Grieve, *in press*.), the Bristol Channel, U.K. (Collins and Williams, 1982; Williams and Collins, 1985) and the Forth estuary, U.K. (Taylor, 1984). A personal communication from D.Williamson reported in Taylor (1984), also describes its presence in Irish estuaries. *A.bifilosa* have been reported in the North Sea, Scandinavian and French (Dunkirk) waters (Bradford-Grieve, *in press*.), and the Baltic (Schnack, 1978). Figures 2.4.1 and 2.4.2 show photographs of the fifth leg of adult males and females of *Acartia bifilosa* collected from Storfjorden on the Southern coast of Finland (samples courtesy of M.Koski), and from Southampton Water. These species would appear identical, comparisons with the diagrams of *A.bifilosa* and *A.bifilosa* var. *inermis* given in various descriptions (including; Giesbrecht, 1892; Rose, 1929; Guerney, 1931; Crisafi and Crescenti, 1972), and in the soon to be published ICES Identification Leaflet for Plankton (Bradford-Grieve, *in press*), demonstrate there are clear discrepancies in published descriptions of female and male characteristics.

Examination of specimens from other areas, including the Bristol Channel and Severn Estuary (specimens collected in this area described as *A.bifilosa* var. *inermis* by Collins and Williams, 1982; Williams and Collins, 1985), and also samples lodged by Giesbricht at the Natural History Museum of London (specimens described both as *A.bifilosa* and *A.bifilosa* var. *intermedia*), have all proven not to be divisible on the characters in the currently available keys. It is the belief of the author that *A.bifilosa* and *A.bifilosa* var. *inermis* are one and the same. As a result of slight inaccuracy in the original description of this species, specimens have been redescribed as a variety, unfortunately once again with some error. Only a brief introduction to this work is possible here, but a new description of *Acartia bifilosa* is presently being undertaken by the author and E.Castro-Longoria (Southampton University) to clear confusions which exist in the literature regarding this species and its variety.

While most of the species found at Calshot have been reported in Southampton Water previously, some have not. *Acartia margalefi* for example has not been recorded in the area. Although since its initial finding, it has now been reported in the literature for this area (Castro-Longoria and Williams, 1996). This species occurs only rarely at Calshot, and is more frequent towards the head of the estuary, in more reduced salinity regions (E.Castro-Longoria, *pers. comm.*). *A.margalefi* was originally described from samples collected in the *ria* of Vigo, N.W. Spain (Alcaraz, 1976).



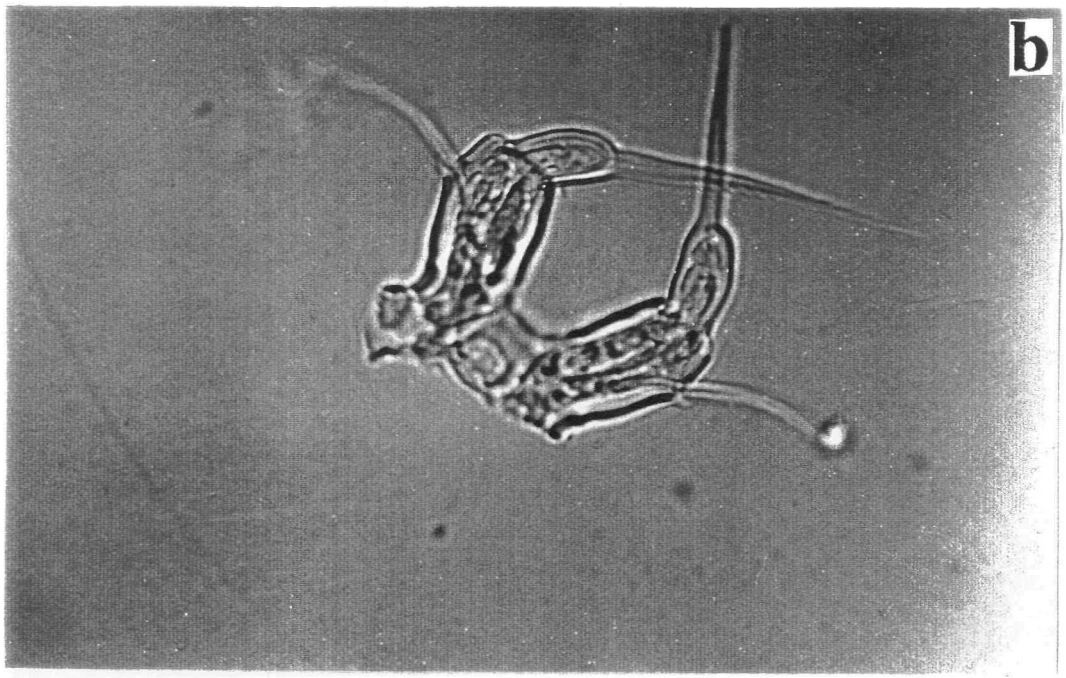
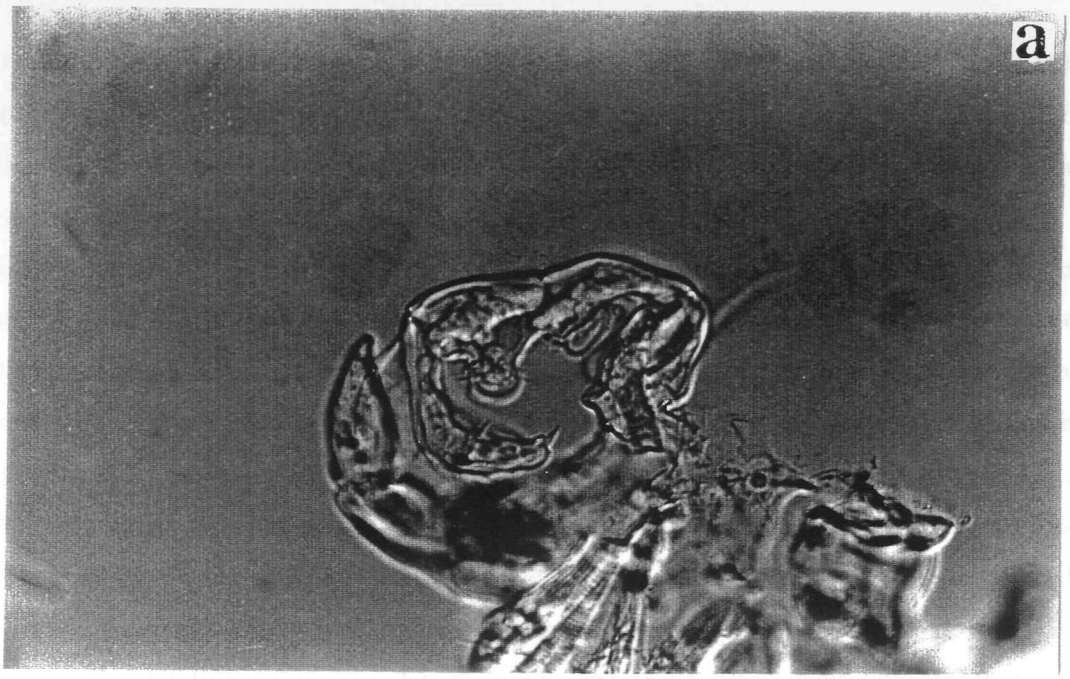


FIGURE 2.4.1 Photographs of the fifth pair of swimming legs of *Acartia bifilosa* collected at Calshot, Southampton Water. (**a**). Adult male P5, (**b**). Adult female P5.



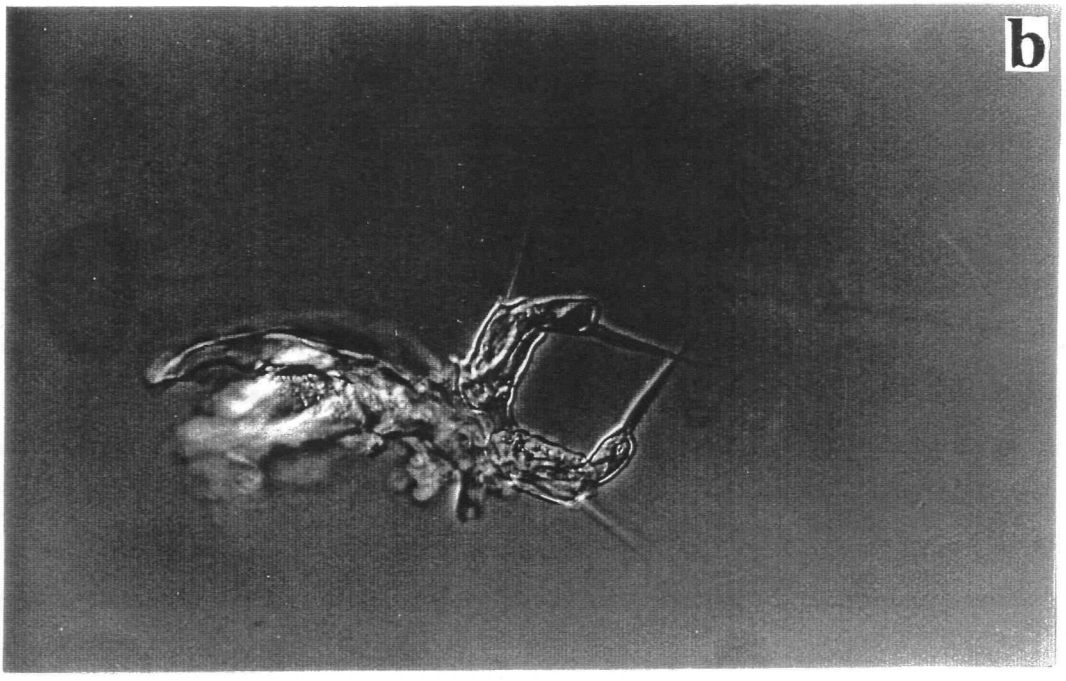


FIGURE 2.4.2 Photographs of the fifth pair of swimming legs of *Acartia bifilosa* collected at Storfjorden, southern coast of Finland, Baltic. (**a**). Adult male P5, (**b**). Adult female P5.

It has since been reported in the rest of the Rias Bajas, the Rivière de Morlaix (France), Huelva estuary (Spain), Killary Harbour (west Ireland), and Genoa Harbour (Italy), as well as possibly in Garaa Achkel (Tunisia), along much of the coast of the Mediterranean Sea and the Black Sea (Bradford, 1976; Alcaraz, 1983; Ryan *et al.*, 1986; Bradford-Grieve, *in press.*). It has been recently found in an enclosed areas of reduced salinity on the south coast of England (eg. Horsea Lake: Castro-Longoria and Williams, 1996). Indeed it has been reported in many semi-enclosed systems such as 'coastal ponds' (Alcaraz, 1977). It is probable that this species has in the past commonly been confused by workers with *Acartia clausi*, given their close similarity, and it may be much more widely spread in European waters. Since it has been described only recently, and is morphologically similarity to *A.clausi*, it is not surprising that earlier workers did not report it in Southampton Water. The two *Acartia margalefi* found by Ryan *et al.* (1986) were described as having a cephalothorax length of 0.55 and 0.68mm (both adult females), while Alcaraz (1976) found *A.margalefi* to have prosome lengths (although described as a metasome length in the original text, but this is presumably wrong) which varied between 0.508 and 0.638mm in males, and 0.508 to 0.648mm in females. In the present investigation prosome length was found to vary between 0.499 and 0.606mm in males, and 0.481 to 0.597mm in females. Female sizes within Southampton Water are within the range previously found, while male lengths overlap previously reported sizes, but do extend below the previous lower limit.

The calanoid *Paracartia grani*, which was reported by both Lance and Raymont (1957) and Raymont and Carrie (1964), was not found in the present study. Only 2 individuals were ever been found at Calshot by Lance and Raymont (1957), while an intensive survey at Marchwood resulted in the discovery of 76 individuals during August to September 1958 (Raymont and Carrie, 1964). At the time of these findings temperatures were at their annual maximum (~22°C). This species is regarded as a warm water species, indeed it was only recorded after water temperatures had been elevated in Southampton Water through warm water discharge by the Marchwood power station (Conover, 1957). As the plant no longer operates, and temperatures may well have declined, then it is not surprising that it may no longer be present in the area. Work still in progress at the Bury Buoy site by E.Castro-Longoria (*pers. comm.*) has revealed no individuals of this species.

The absence of *Acartia tonsa* from samples at Calshot during the present investigation is of interest. This species is found within the estuary but almost always only towards the head at Bury Buoy (Raymont and Carrie, 1964; E.Castro-Longoria, *pers. comm.*). Previously this introduced species has been found to make up to a maximum of 4% of the total *Acartia* individuals at a single point in time at Calshot (Conover, 1957).

SPECIES	PREVIOUS REPORTINGS
Calanoida:	
Acartia discaudata	1,2,4
Acartia clausi	1,2,4
Acartia bifilosa	1,2,4
Acartia tonsa	1,2
Paracartia grani	1,3
Acartia margalefi[+]	4
Centropages hamatus	1,2,4
Centropages typicus	4
Temora longicornis	1,2,4
Paracalanus parvus	1,2,4
Pseudocalanus elongatus	1,2,4
Calanus helgolandicus[†]	1,2,4
Eurytemora hirundoides (*affinis*)	1,4
Parapontella brevicornis	4
Cyclopoida:	
Oithona similis	1,4
Harpacticoida:	
Euterpina acutifrons	1,4
Harpacticus flexus	4
Harpacticus spp.	1
Canuella	1
Monstrilla sp.	4

TABLE 2.4.1 Copepods found in the present investigation at the Calshot site, and reported within the estuary in previous pelagic studies.

Sources:

1 Raymont and Carrie (1964).

2 Conover (1957).

3 Lance and Raymont (1964).

4 Present investigation.

[+] *Acartia margalefi* is also known as *Acartia lefeverae*; having been described separately by both Bradford (1976) and Alcaraz (1976). [†] Revision of the key to *Calanus finmarchicus* and *Calanus helgolandicus* has been made since the early work in Southampton Water. *Calanus* specimens caught in the present investigation have all proven to be *Calanus helgolandicus*, it may therefore be assumed that previous recordings of *C.finmarchicus* are in fact *C.helgolandicus*.

Its sporadic appearance may be the result of inter-annual changes in physical parameters such as temperature and salinity, or may be related to flushing rates.

Of the *Acartia* species at Calshot, *Acartia bifilosa* was dominant during February to June. *Acartia discaudata* and *Acartia clausi* were co-dominant from July to September, after which *A.clausi* was dominant until December, although *A.discaudata* remained second most abundant. After December, *A.discaudata* became dominant once again (see Figure 2.3.2). The successional pattern reported by Conover (1957) at Calshot, during the period October 1954 to June 1955, was very similar to the present study, although there is some deviation. In their work *A.clausi* and *A.discaudata* were found to be the co-dominant *Acartia* species over the winter months of November to January, after which *A.bifilosa* became dominant. From May, *A.clausi* was the most abundant *Acartia* species once again. Raymont and Carrie (1964) also examined the succession of *Acartia* at Calshot and, as in the present study, found that this genus was the dominant calanoid. In common with the present study they also found that *A.discaudata* was dominant during the early months of the year, when almost no other calanoids were found. During February to March *A.discaudata* were found to be replaced by *A.bifilosa*. Unlike the situation in the present study however, they found that *A.bifilosa* dominated until July, when *A.discaudata* increased once more, being dominant until the end of the year. During 1993 although *A.discaudata* did increase in July, *A.bifilosa* decreased earlier in May-June. *A.clausi* was also co-dominant with *A.discaudata* during July and September, and dominant in October and November. Raymont and Carrie (1964) investigated abundance patterns over many years, and found variability in the timing and relative importance of the different *Acartia* species. It is therefore not suprising that there are differences between studies.

Acartia spp., *Centropages hamatus*, *Temora longicornis* and *Eurytemora affinis* have all been shown to produce resting eggs which may be deposited in the sediment (see Viitasalo, 1992), these species are also the most dominant within the estuary. Resting eggs are an important overwinter strategy, which may be particularly important in maintaining populations in neritic areas. Spring peaks in *Acartia bifilosa* numbers have even previously been shown to be the result of egg hatching rather than spawning (Viitasalo, 1992).

The number of coexisting congenerics typically varies between estuaries. The number of coexisting *Acartia* species appears to be maximally five, in Mediterranean harbours and embayments at least (Alcaraz, 1977). In total four species of *Acartia* have recently been found within Southampton Water, and these are temporally and/or spatially separated to some degree (eg. this study, and see Castro-Longoria and Williams, 1996), although there is some coexistence,

detailed spatial analysis is needed to determine species segregation.

Raymont and Carrie (1964) reported that *Centropages hamatus* was the most dominant calanoid after the *Acartia* group. This species was reported as rarely appearing before March/April, but from May and throughout the summer it was moderately common. It was also described as generally persisting through the autumn, disappearing in late December. This pattern is the same as that found in the present investigation (see Figure 2.3.3), with this species being the most dominant after *Acartia*. *Temora longicornis* was found by Raymont and Carrie (1964) to be less common than *C.hamatus* at Calshot, and to be stricter in timing, not appearing until April, and being moderately plentiful until August. It was also much less common than *C.hamatus* in the Autumn. This situation is similar to that in the present study (see Figure 2.3.4). Raymont and Carrie (1964) found *Paracalanus parvus* and *Pseudocalanus elongatus* to be sporadic in appearance at Calshot, the former species being more abundant than the latter. *P.parvus* was also found in greater densities than *P.elongatus* in the present investigation, and occurrence was somewhat sporadic (see Figure 2.3.5).

Raymont and Carrie (1964) found greater peak densities of calanoids at Calshot over the 6 years of their study than found in the present investigation, some 40 years later. They report spring maxima of around 2,000 to 2,500 ind. m^{-3} in 1954, 1957 and 1959, but 5,000 ind. m^{-3} in 1956 and 1958. In 1993 however the calanoid peak in spring was 1,065 ind. m^{-3}, with maximum annual numbers in August of 2,155 ind. m^{-3}. Reports by Raymont and Carrie (1964) of the mean densities of calanoids between September and December are similar to those found in this study. They found mean densities in this period to vary between 433 to 1,263 ind. m^{-3}, whereas in the present investigation average calanoid copepodite numbers during the same period was 900 ind. m^{-3}. Zinger (1989) reported that at Calshot, maximum numbers were found in September-October, reaching 12,646 ind. m^{-3} in 1985 and 9,352 ind. m^{-3} in 1986. Mean densities between September and December were much greater in the years studied by Zinger (1989), at 6,322 and 1,967 ind. m^{-3} in 1985 and 1986 respectively.

The harpacticoid *Euterpina acutifrons* has previously been reported in areas adjacent to Southampton Water, including the Atlantic, North Sea and English Channel (Rose, 1933). Raymont and Carrie (1964) also found it to be extremely common in Southampton Water. *E.acutifrons* was the dominant harpacticoid at Calshot in the present investigation, being most numerous during the summer and autumn period. Over the current investigation there were less than 100 per m^{-3} from the start of the year to mid-summer. In July numbers increased to greater than 1,000 ind. m^{-3}, after which numbers stayed at greater than 2,000 ind. m^{-3} into October,

declining in December and January. A very similar situation, and similar densities were reported by Raymont and Carrie (1964) at Calshot, where a massive domination of the harpacticoids by *E.acutifrons* was recorded. They reported that harpacticoids numbers were below 200 ind. m^{-3} (and often below 100 ind. m^{-3}) from the beginning of the year until mid-summer, after which they increased to ~1,000 ind. m^{-3}, although in some years densities in July and early August were as great at 2,500 ind. m^{-3}. In most years numbers stayed above 1,000 ind. m^{-3} until October, and minimum densities were in December/January. Zinger (1989) found that numbers of harpacticoids at Calshot increased around August in 1985 and 1986, with lowest numbers in winter and spring. Maximum densities were around 2,500 ind. m^{-3} in both years of study. Unfortunately in the work of Zinger (1989) no species distinctions were made, it would seem probable that *E.acutifrons* dominated this group once again.

Cyclopoid copepods were only rarely found in the samples at Calshot in the present investigation, and this was also reported to be the case by Raymont and Carrie (1964). Further, this group was not even reported by Zinger (1989) or Lucas (1994). In the present study numbers never exceeded 20 ind. m^{-3}.

The number of cirripede larvae found over the 14 month investigation was generally much lower than that recorded by Raymont and Carrie (1964), who found that the average density of cirripede larvae between May and September at Calshot, from 1954 to 1959, ranged from 847 ind. m^{-3} to 3,463 ind. m^{-3} (with a mean of 2,164 ind.m^{-3}). In 1993 the average May-September abundance was much lower at only 767 ind. m^{-3}. Zinger (1989) found densities to fluctuate greatly, with great inter-annual variation in the timing of abundance peaks. Maximum numbers reached 13,399 and 17,384 ind. m^{-3} in 1985 and 1986 respectively, while from May to September averages were 4,476 ind. m^{-3} in 1985 and 8,173 ind. m^{-3} in 1986 (Zinger, 1989). Clearly abundances are very variable inter-annually at Calshot.

Seasonal variations in size:

Seasonal variations in size and weight have often been recorded in marine invertebrates including copepods. In the coastal waters of temperate and boreal regions, seasonal variations in size have been found in copepods studied over the greater part of a year (Deevey, 1960). In tropical regions however, systematic seasonal variation in body size is only rarely found, and when variations do occur they have been related to small temperature changes (Chisholm and Roff, 1990a). Mauchline (1995) considered the increasing prosome length within individual *Euchaeta* species with depth to be a result of the decreasing temperature. The amplitude of seasonal change in prosome length, which decreased with depth over a 2,000m water column in

the North Atlantic (Rockall Trough), was reported to reflect increased environmental stability and decreasing influence of epipelagic seasonality with depth. Variations in body size of copepods in coastal areas have been attributed predominantly to temperature and food, although salinity (Kimoto *et al.*, 1986; Moraïtou-Apostolopoulou *et al.*, 1986; Gaudy *et al.*, 1988), predation rates (Warren *et al.*, 1986), and pollution conditions (Moraïtou-Apostolopoulou and Verriopoulos, 1979) have also been described as having effects. Copepod body sizes have been found to be inversely related to temperature, both in nature (Marshall and Orr, 1955; Deevey, 1960, 1966; McLaren, 1965; Moraïtou-Apostolopoulou, 1975; Evans, 1977; Durbin and Durbin, 1978; Landry, 1978; Moraïtou-Apostolopoulou and Verriopoulos, 1979; Uye, 1982a; Uye *et al.*, 1982; Christou and Verriopoulos, 1993a; Huang *et al.*, 1993; Liang *et al.*, 1996; Liang and Uye, 1996) and in the laboratory (Kimoto *et al.*, 1986; Uye, 1991). Relationships however, are typically more markedly significant in older stages for both temperature (commented upon in Uye *et al.*, 1982; and see Kimoto *et al.*, 1986; Jerling and Wooldridge, 1991; Uye, 1991; Huang *et al.*, 1993; Laing *et al.*, 1996; Laing and Uye, 1996) and food concentration (Klein Breteler and Gonzalez, 1982; Berggreen *et al.*, 1988). Indeed, seasonal changes in prosome length of the species in Southampton Water have already been shown to be greater in older stages (see Results section). This commonly observed features is probably the result of environmental factors having accumulative effects through the life of an individual, but adults producing eggs with a fairly stable weight (for example see results of Liang *et al.*, 1994). Changes in body size of copepods have been positively related to food concentration (Digby, 1954; Deevey, 1960, 1966; Moraïtou-Apostolopoulou, 1975; Landry, 1978; Evans, 1981; Klein Breteler and Gonzalez, 1982; Durbin *et al.*, 1983; Berggreen *et al.*, 1988; Christou and Verriopoulos, 1993a), although some of these apparent examples of dependency have been questioned (Corkett and McLaren, 1978; this study, see following discussion).

Regressions of prosome lengths, for each separate stage and sex, against temperature and also chlorophyll a concentration (measured simultaneously), have been completed for each of the species at Calshot. As older stages of copepod may have lengths or weights that are dependent upon past 'associated factors' such as temperature and feeding history, then the analysis has also been completed regressing prosome length against temperature and chlorophyll a concentrations measured at the previous sampling time, ie. from measurements typically 2 or 4 weeks before. The process of lagging the prosome length in time, prior to regression analysis against the independent variables, has been undertaken in previous studies. Christou and Verriopoulos (1993a) regressed *Acartia clausi* prosome lengths against mean chlorophyll over the previous 10 days, while Deevey (1960; 1966) regressed prosome lengths of copepods against temperature and chlorophyll averages of the previous 2 weeks and month. Results from this study are presented in

Table 2.4.2; r^2 and probability levels, together with equations describing the relationships, when they are significant, are given.

The relationships between temperature and prosome lengths are not significant in all cases for all stages and sexes. In all cases where the relationship is significant it is also negative, ie. with an increase in temperature there is a decrease in prosome length. Generally, the relationship between prosome length and temperature on the previous sampling occasion is more significant than the relationship with the temperature on the same date, although this is certainly not the case for all species. With regard to chlorophyll a, there is no clear distinction between lagged and unlagged results, both produce a significant relationship on only three occasions, and in all cases the relationship is a negative one, ie. with decreasing prosome length with increasing chlorophyll a. This is the reverse of the relationship which would be expected (eg. see Deevey, 1960; Landry, 1978), and could simply be the result of the positive relationship between temperature and chlorophyll a. Significant negative relationships exist between temperature on the previous sampling occasion and most *Acartia* non-adult copepodite stages, in addition to *Acartia bifilosa* adults (male and female), and *Acartia discaudata* adult males, although not *A.discaudata* adult females or *Acartia clausi* adults (male and female). Relationships are significant for all stages of *Centropages hamatus* except C5 females, although the relationship is also significant when there is no time lag. Significant relationships between temperature and prosome length are more common for *Temora longicornis* when there is no lag, although both analyses predominantly produce highly significant negative relationships. None of the relationships are significant between temperature and prosome length for the *Paracalanus-Pseudocalanus* group when there is no lagging, and on only 2 significant relationships when regression is completed between length and temperature on previous sampling occasion. The merging of two species in non-adult copepodite stages in this analysis, may make the discernment of species-specific relationships difficult.

Christou and Verriopoulos (1993a) regressed prosome length against chlorophyll averaged over the previous 10 day period, as they believed this gave the best measure of the feeding history of individuals. This was not possible in the present investigation as the samples were only collected on spring tides. Chlorophyll a concentrations can change dramatically on a very short-time scale within Southampton Water (see Kifle, 1992), these changes being possibly related to the spring-neap tidal cycle (*personal observations*, and *pers. comm.* D.Purdie). Rapid changes of this nature mean that fortnightly or monthly sampling does not allow simple comparisons between prosome length and chlorophyll a during an individuals 'feeding history'.

			TEMPERATURE (°C)			CHLOROPHYLL a (µg.l^{-1})				PREVIOUS SAMPLE TEMPERATURE (°C)			PREVIOUS SAMPLE CHLOROPHYLL a (µg.l^{-1})		
SPECIES	**STAGE**	**n**	**r²**	**P**	**Equation**	**r²**	**P**	**Equation**	**n**	**r²**	**P**	**Equation**	**r²**	**P**	**Equation**
Acartia spp.	C1	15	0.111	0.224	-	0.003	0.851	-	14	0.180	0.131	-	0.019	0.641	-
	C2	15	0.250	0.058	-	0.0007	0.926	-	14	0.573	0.002	PL=0.4694-0.0044T	0.006	0.785	-
	C3	15	0.086	0.288	-	0.066	0.356	-	14	0.236	0.078	-	$1.9*10^{-4}$	0.963	-
	C4♀	15	0.348	0.043	PL=0.6435-0.0052T	0.022	0.644	-	12	0.433	0.020	PL=0.6502-0.0058T	0.012	0.732	-
	C4♂	13	0.334	0.039	PL=0.6314-0.0048T	0.093	0.310	-	13	0.398	0.021	PL=0.6401-0.0056T	0.007	0.787	-
	C5♀	13	0.234	0.094	-	0.085	0.333	-	12	0.324	0.053	-	0.069	0.410	-
	C5♂	14	0.478	0.006	PL=0.7720-0.0074T	0.017	0.658	-	13	0.545	0.004	PL=0.7806-0.0079T	0.145	0.199	-
Acartia bifilosa	C6♀	10	0.384	0.056	-	0.026	0.655	-	9	0.836	<0.001	PL=1.0122-0.0244T	0.060	0.524	-
	C6♂	6	0.424	0.161	-	0.516	0.108	-	5	0.922	0.010	PL=0.9740-0.0176T	0.002	0.946	-
Acartia discaudata	C6♀	7	0.757	0.011	PL=0.7473-0.0064T	0.460	0.094	-	7	0.535	0.062	-	0.310	0.194	-
	C6♂	8	0.592	0.026	PL=0.8396-0.0114T	$2*10^{-6}$	0.997	-	8	0.830	0.002	PL=0.8759-0.0139T	0.631	0.018	PL=0.7897-0.0231C
Acartia clausi	C6♀	7	0.182	0.340	-	0.426	0.112	-	7	0.287	0.215	-	0.232	0.274	-
	C6♂	6	0.445	0.148	-	0.015	0.818	-	6	0.200	0.375	-	0.174	0.410	-
Acartia margalefi	C6♀	2	-	-	-	-	-	-	2	-	-	-	-	-	-
	C6♂	2	-	-	-	-	-	-	2	-	-	-	-	-	-
Centropages hamatus	C1	8	0.500	0.050	PL=0.4155-0.0074T	0.019	0.744	-	8	0.913	<0.001	PL=0.4098-0.0074T	0.077	0.507	-
	C2	9	0.737	0.003	PL=0.4983-0.0085T	0.142	0.318	-	9	0.974	<0.001	PL=0.4826-0.0079T	0.028	0.665	-
	C3	9	0.767	0.007	PL=0.6813-0.0145T	0.062	0.519	-	9	0.780	0.002	PL=0.6702-0.0143T	0.009	0.807	-
	C4	12	0.474	0.013	PL=0.7230-0.0116T	0.072	0.399	-	11	0.670	0.002	PL=0.7176-0.0120T	0.454	0.023	PL=0.6322-0.0136C
	C5♀	6	0.806	0.015	PL=0.8732-0.0161T	0.037	0.716	-	6	0.355	0.212	-	0.420	0.164	-
	C5♂	10	0.640	0.005	PL=0.8798-0.0152T	0.019	0.704	-	10	0.714	0.002	PL=0.9101-0.0175T	0.141	0.284	-
	C6♀	9	0.651	0.009	PL=1.1625-0.0224T	0.659	0.008	PL=1.0756-0.0490C	9	0.843	<0.001	PL=1.1945-0.0255T	0.091	0.431	-
	C6♂	5	0.561	0.145	-	0.779	0.048	PL=1.0285-0.0455C	5	0.835	0.030	PL=1.1752-0.0284T	0.354	0.290	-
Temora longicornis	C1	9	0.712	0.004	PL=0.4151-0.0056T	0.0002	0.975	-	9	0.724	0.004	PL=0.4067-0.0054T	0.152	0.300	-
	C2	9	0.647	0.009	PL=0.4797-0.0058T	0.037	0.621	-	9	0.748	0.003	PL=0.4729-0.0057T	0.222	0.201	-
	C3	7	0.792	0.007	PL=0.6398-0.0128T	0.0005	0.961	-	7	0.685	0.021	PL=0.5753-0.0094T	0.529	0.064	-
	C4	7	0.738	0.013	PL=0.7798-0.0177T	0.061	0.592	-	7	0.560	0.053	-	0.204	0.309	-
	C5♀	6	0.251	0.311	-	0.562	0.086	-	6	0.154	0.441	-	0.170	0.417	-

	C5♂	4	0.780	0.011	PL=1.3331-0.0459T	0.585	0.235	-	4	0.436	0.340	-	0.160	0.600	-
	C6♀	5	0.976	0.002	PL=1.2226-0.0318T	$2*10^{-5}$	0.994	-	5	0.773	0.050	PL=1.0375-0.0213T	0.738	0.062	-
	C6♂	7	0.522	0.067	-	0.050	0.630	-	7	0.486	0.082	-	0.254	0.248	-
Para-Pseudocalanus	C1	7	0.008	0.848	-	0.027	0.727	-	7	0.360	0.155	-	0.482	0.083	-
	C2	7	0.176	0.349	-	0.500	0.076	-	7	0.648	0.029	PL=0.6269-0.0168T	0.067	0.574	-
	C3	5	0.102	0.600	-	0.151	0.518	-	5	0.121	0.566	-	0.676	0.087	-
	C4♀	6	0.442	0.150	-	0.067	0.620	-	6	0.763	0.023	PL=0.7195-0.0130T	0.669	0.047	PL=0.6620-0.0243C
	C4♂	2	-	-	-	-	-	-	1	-	-	-	-	-	-
	C5♀	4	0.014	0.884	-	0.635	0.203	-	4	0.169	0.589	-	0.680	0.175	-
	C5♂	3	0.359	0.591	-	0.873	0.232	-	3	0.095	0.800	-	$8.4*10^{-5}$	0.994	-
P.parvus	C6♀	4	0.868	0.068	-	0.989	0.005	PL=1.1224-0.1029C	4	0.660	0.187	-	0.651	0.193	-
	C6♂	4	0.341	0.416	-	0.616	0.215	-	4	0.028	0.832	-	0.001	0.968	-
P.elongatus	C6♀	3	0.700	0.369	-	0.032	0.885	-	3	0.982	0.086	-	0.262	0.658	-
	C6♂	1	-	-	-	-	-	-	1	-	-	-	-	-	-

TABLE 2.4.2 Regression analysis between prosome length and temperature and chlorophyll a concentration, and prosome length and temperature and chlorophyll a measured on the previous sampling occasion. Equations are only given in the cases where the relationship is significant eg. $P<0.05$.

n is the number of points, PL is the prosome length in μm, T is temperature (°C), and C is chlorophyll a concentration in $\mu g.l^{-1}$.

Re-analysis of the data of Christou and Verriopoulos (1993a) is possible from the presentation of raw data in their Table 1. Using Stepwise Backward Regression of $\log_{10}$ transformed prosome length against $\log_{10}$ transformed temperature and chlorophyll (with F-to-Enter set at 4.0 and F-to-remove at 3.9), chlorophyll was removed from the regression in all cases (ie. C1, C2, C3, C4, C5♀, C5♂, C6♀ and C6♂), leaving temperature alone as the independent variable. As transformed chlorophyll is significantly related to transformed temperature (P=0.027), this may explain some of the apparent dependence in this instance. Other reports have also shown there may be no apparent significant relationships between prosome lengths and chlorophyll concentrations. Deevey (1960) found that temperature was significantly negatively related to prosome lengths of *Pseudocalanus minutus*, *Temora longicornis*, *Acartia clausi* (*hudsonica*?) and *Acartia tonsa* in Long Island Sound; however, chlorophyll concentrations were not significantly related (with and without any time lagging). In the same study, adult female *Centropages typicus* from Castellón, Spain, were shown to be significantly positively related to phytoplankton abundance (in Harvey Units) and negatively to temperature. Indeed reanalysis of this data using Backwards Stepwise regression (with F-to-Enter set at 4.0 and F-to-remove at 3.9) also shows that both variables should be included in regression analysis. The conclusions of Deevey (1960) however, were criticised by Corkett and McLaren (1978), who believed that size was related to temperature at time of development alone. They pointed out that some of the apparent positive relationships with phytoplankton were simply a result of the size of over-wintering adults being attributed to the wrong temperature, in that it should be compared with temperature at time of development. They reviewed much of the literature and predominantly found that food only affected individual weights when it was particularly low, and suggested that 'the association between body size and food supply in nature is indirect: that food shortages may retard development and therefore diminish the correlation between size and current temperatures, but that body size is not ultimately affected by this shortage'.

Figure 2.4.3 shows the relationships between *Acartia clausi* prosome lengths and temperature at Calshot, together with the values given by; Marshall (1949) for *A.clausi* from Loch Striven (Clyde Sea area, U.K.); Christou and Verriopoulos (1993a) for *A.clausi* in the Eastern Mediterranean (Saronikos Gulf, Aegean sea); and Digby (1950) for *A.clausi* taken off Plymouth (U.K.). Other prosome length-temperature data have been reported for *A.clausi* in the literature (eg. Deevey, 1966; Uye, 1982a), however, as these were derived in non-European waters, and are probably conspecific eg. *Acartia hudsonica* and *Acartia omorii*, they were not used. Temperatures have been estimated in the case of the results of Digby (1950) by averaging measures made at 1 and 30 metres depth (zooplankton tows being depth integrated from 30 metres to the surface).

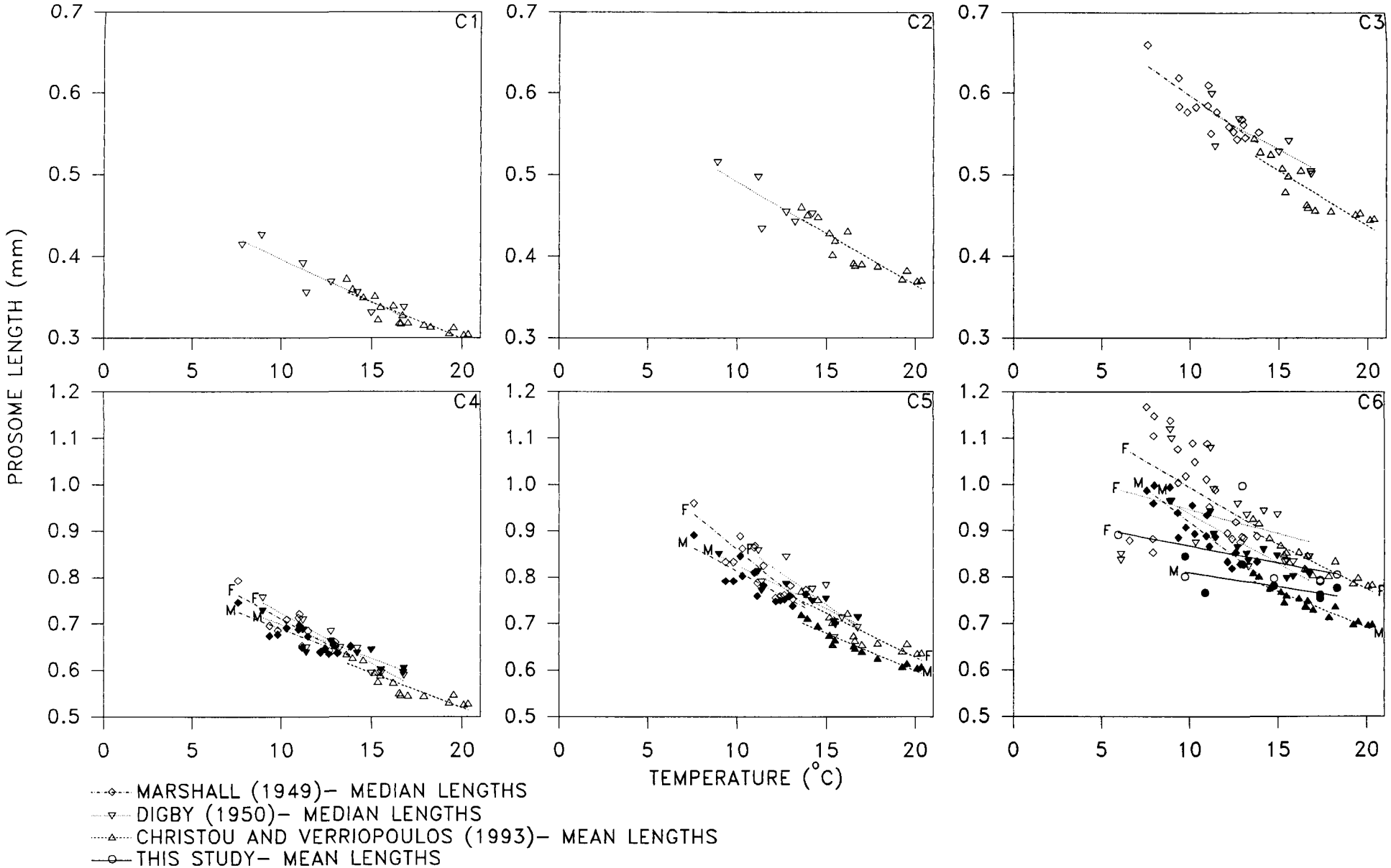


FIGURE 2.4.3 Relationships between Acarta clausi prosome lengths and temperature for individuals collected at Calshot, and also compiled from reports of Acartia clausi in other areas: for C4–C6 filled symbols represent males, when distinguished. (Note Scale Change).

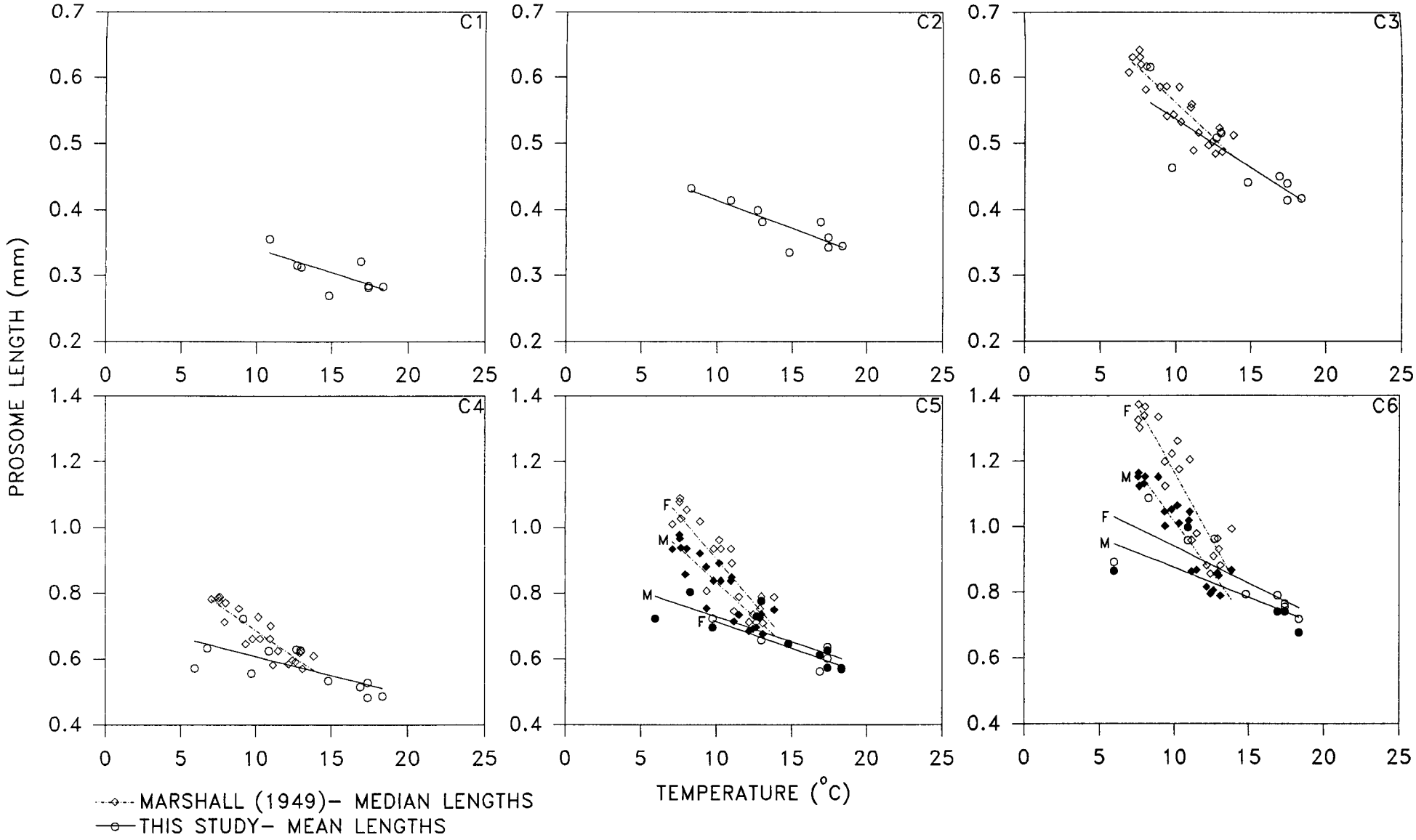


FIGURE 2.4.4 Relationships between Centropages hamatus prosome lengths and temperature for individuals collected at Calshot, and also compiled from reports of Centropages hamatus in other areas: for C5–C6 filled symbols represent males, when distinguished. (Note Scale Change).

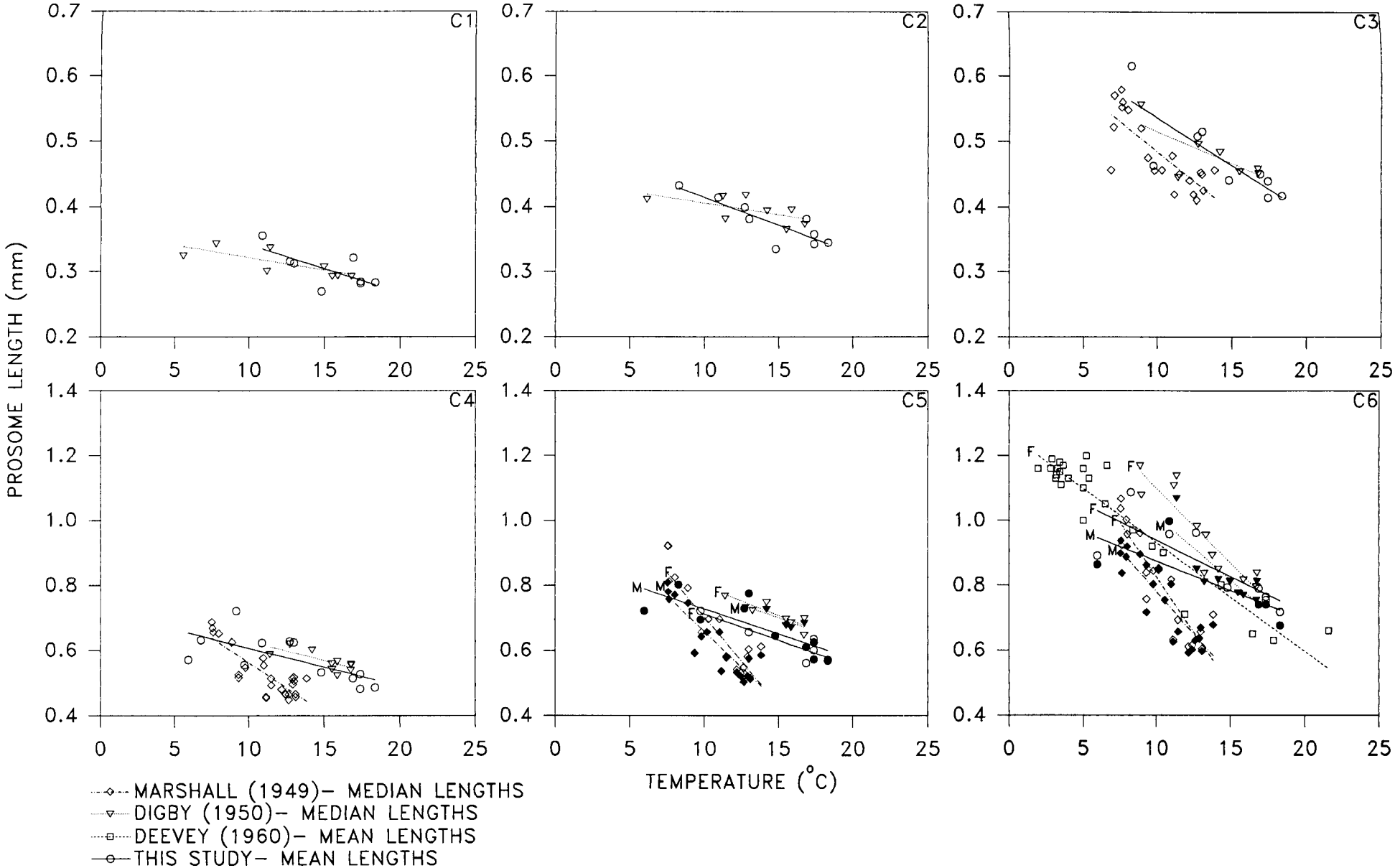


FIGURE 2.4.5 Relationships between Temora longicornis prosome lengths and temperature for individuals collected at Calshot, and also compiled from reports of Temora longicornis in other areas: For C5–C6 filled symbols represent males, when distinguished. (Note Scale Change).

Temperatures were different at these two depths throughout much of the year, although the maximum difference recorded was only 4.8°C (ie. actual values being maximally 2.4°C from the utilised value). Simultaneous temperature recordings taken at the same location as zooplankton were not presented in the original study of Marshall (1949). These measurements were made, and are given in Marshall *et al.* (1934), from which they have been taken. In this case temperatures have been averaged for 0 and 30 metres (zooplankton tows being depth integrated from 30 metres to the surface). Temperatures did differ between these two depth extremes, and in this case the maximum range of temperatures on any single date was 7.5°C (ie. the real value would maximally be 3.75°C different from the utilised mean), however, typically the differences are very much less, the average difference between the two measures being only 2.9°C (ie. ±1.45°C from the utilised mean). In both the studies where temperatures have had to be depth averaged (ie. Marshall *et al.*, 1934 and Digby, 1950), given the typically small differences between the mean and the extremes, then the errors associated will only be minor. In Figure 2.4.3 stages C1 to C5 of *Acartia clausi* appear to demonstrate a single linear relationship between temperature and prosome length for all of the combined data sets (although individual regressions have still been included in the figures). In C5 and C6, the females appear larger than the males, although the slopes are similar. For adult *Acartia clausi* the relationship is more variable both within studies and between studies, although a single relationship would still appear valid. The combined data for adult males and females also appears to show a non-linear relationship, with size decreases being greater per unit temperature at lower temperatures. Negative, curvilinear, and potentially asymptotic relationships of this form have previously been used to describe the relationship between temperature and prosome length (see McLaren, 1965; Corkett and McLaren, 1978). Some of the variation in the relationships are likely to be the result of not comparing prosome length against the temperature experienced during copepod developmental history.

Development stage and sex specific prosome lengths of *Centropages hamatus* versus temperature (at time of collection) for both Southampton Water and Loch Striven (Marshall, 1949) are presented in Figure 2.4.4. The results of Marshall (1949) show strongly significant negative linear relationship between length and temperature, and the slope of the relationship also appears to be much steeper than the Southampton Water population ie. for each increase in unit temperature the decline in prosome length is greater. Without more information it is difficult to ascribe these differences to any particular feature, although food abundance and the temperature range differences may play a part (see Deevey, 1960). Individuals subjected to conditions of higher food quality/quantity may typically grow larger (eg. Ban, 1994). There may also be genetic differences between the populations in the two areas. Differences in the size-temperature relationships in marine copepods have previously been attributed to genetic differences (ie.

Pseudocalanus: Corkett and McLaren, 1978), with evidence suggesting that size is markedly heritable and related to cell size, these differences being related to variations in DNA content and nucleus size (Alcaraz, 1976; McLaren, 1976). The differences brought to light in this study need further attention to determine if there are important genetic differences (and possibly even different species). Taxonomic and laboratory breeding work could be rewarding in an effort to determine if there may in fact be separate species in these areas.

Prosome lengths for each stage and sex versus temperature (at time of collection) for *Temora longicornis* collected at Calshot (this study), Loch Striven, U.K. (Marshall, 1949), coastal waters off Plymouth, U.K. (Digby, 1950) and Long Island Sound, USA (Deevey, 1960), are presented in Figure 2.4.5. The results from the present investigation and those from Digby (1950) appear to be very similar for C1 to C5 stages, the slopes of the regressions are parallel in most instances, and lie close to one another. The adults appear less similar although still close. The data gfor adult females from Southampton Water are also similalr to those given by Deevey (1960). The results from Loch Striven (Marshall, 1949) are very different from those collected at Plymouth, Southampton Water and Long Island Sound. Although the overall ranges in size are within those for the other studies, the slope fitted to Marshall's data is much steeper. This is similar to the situation found for *Centropages hamatus*, when comparing between Loch Striven and Southampton Water. The factors controlling inter-population differences could therefore be common to both of these species. It is of interest to note however, that such differences were not observed for *Acartia clausi* between Loch Striven and the other 3 areas of collection (see Figure 2.4.3). Similar ranges in size appear commonly between areas, however, the slope of the relationships were found to be very different between some areas. More work needs to be completed before the factors controlling such remarkable differences in some species but not others can be identified. Such factors are important given the dependence of production rates upon body size and weight.

Acartia clausi has been reported in the eastern Atlantic (Bradford-Grieve, *in press*.), North Sea (Evans, 1977) and eastern Mediterranean (Christou and Verriopoulos, 1993a). Earlier reports from the western Atlantic, eastern Pacific and Japanese waters, have now been shown to be other species, predominantly *Acartia hudsonica* and *Acartia omorii* (see Bradford, 1976; Ueda, 1986a;1986b). From Calshot collections individuals were found to exhibit a range of prosome length from 0.712 to 0.998mm in males, and from 0.614 to 0.855mm in females. Digby (1950) found the prosome length of *A.clausi* off Plymouth to vary between at least 0.761mm to 0.973mm in males, and at least 0.708 to 1.13 in females. While Marshall (1949) found individual prosome lengths to vary between at least 0.644 to 1.009mm in males and at least 0.644 to 1.218

in females. The sizes of male of *A.clausi* collected at Calshot, fall within the ranges of sizes found by both Digby (1950) and Marshall (1949). The female lengths predominantly fall within the ranges of Digby (1950) and Marshall (1949), but do also extend below it. During the period when sizes were outside the range of these two studies, temperature was also greater (at ~17-18°C), this factor probably accounts for the differences. Unfortunately only mean prosome lengths are given by Christou and Verriopoulos (1993a); these were found to range in adult females between 0.780 to 0.925mm, and 0.695 to 0.808mm in adult males. Mean prosome lengths of *A.clausi* collected in Northumberland coastal waters by Evans (1977) were found to vary between ~0.85 and 1.14mm in adult females.

Acartia clausi were found in Southampton Water from April to December, when temperatures ranged from 5.95°C to 18.4°C. Christou and Verriopoulos (1993a) found *A.clausi* when temperatures ranged from 13.6°C to 20.3°C during the period November to June, they also reported it to be virtually absent during the summer-autumn in the same area. Marshall (1949) reported *A.clausi* presence between 6.3 and 13.8°C (depth integrated averages). Digby (1950) found that *A.clausi* were present, in waters off Plymouth, in every month except December, at temperatures between 5.6 and 16.8°C. This species therefore has a more temporally restricted range at Calshot in comparison to Plymouth (both being sites on the south coast of England). Whether this is attributable to competition with other *Acartia* species, or the result of food or physical restrictions is not clear. It would appear that *A.clausi* populations have been found over a range of temperatures from at least 5.6 to 20.3°C, although they may occur over a greater range than this.

Calanoid abundances:

Maximum *Acartia clausi* adult abundance in Southampton Water was found in July when they reached 140 ind. m^{-3}. Digby (1950) reports that off Plymouth *A.clausi* adults reached a maximum density in June with 760 ind. m^{-3}, sampled using a net with an aperture of less than 127μm (estimated from net details, ie. 200 meshes to the inch). Ryan *et al.* (1986) found in Killary Harbour, western Ireland, that *A.clausi* was the most abundant of the calanoid copepods. In this area copepodite numbers increased in late winter and spring, reaching a maximum in early July at 7,899 ind. m^{-3} (using a 90μm mesh aperture net). Although non-adults were not identified to species in the present investigation, maximum total *Acartia* copepodite numbers reached only 1,665 ind. m^{-3}, and while the copepodites may have been under sampled slightly, the differences between the density in this study and those reported by Ryan *et al.* (1986) allowing for under sampling are still very dramatic. Numbers at Calshot were high until September, when they declined sharply, small winter peaks were also observed. Maximum densities of *Acartia* spp.

copepodite C1 to C5 for all stages at Calshot were in August (although these were almost certainly dominated by *Acartia discaudata*) when densities reached 362 (C1), 429 (C2), 298 (C3), 232 (C4), 182 (C5) and 1,503 (total non-adult copepodites) ind. m^{-3}. When *A.clausi* adults were most abundant, the copepodite numbers were only 104 (C1), 100 (C2), 110 (C3), 104 (C4), 77 (C5) and 496 (total non-adult copepodites) ind. m^{-3}. Digby (1950) found that maximum abundances for each stage of *A.clausi* were between May and June, at 1,340 (C1), 740 (C2), 580 (C3), 520 (C4), 300(C5) and 3,480 (total non-adult copepodites) ind. m^{-3}. Evans (1977), sampling copepods in Northumberland coastal waters (North Sea) during 1972-1973 using a water bottle found that *A.clausi* adult abundance peaked in September, reaching 834 ind. m^{-3}. While non-adult copepodite numbers peaked in May and September at 1,188 and 1,042 ind. m^{-3} respectively, the adult numbers were therefore much greater than in the present investigation.

Acartia discaudata has been previously reported in British, Scandinavian and French (Dunkirk) waters (Bradford-Grieve, *in press.*). Adults were found at Calshot in April to May, and from July to December, adult numbers reaching a maximum of 105 ind. m^{-3} in mid-August. Ryan *et al.* (1986) found that *A.discaudata* copepodites in Killary Harbour reached a maximum density of 168 ind. m^{-3} in early July, throughout much of the rest of the year numbers were very low (typically less than 4 ind. m^{-3}). This species is therefore more prevalent at Calshot than in the estuarine site studies of Ryan *et al.* (1986).

Acartia bifilosa has been reported from many locations including the North Sea, Baltic and Channel waters (Bradford-Grieve, *in press.*). Its absence from other estuaries in the British Isles has been also commented upon. Ryan *et al.* (1986) for example found no *A.bifilosa* in Killary Harbour during an extensive sampling program. *A.bifilosa* adults were found at Calshot from January through to May, and in July, November and December. Maximum numbers reached 575 ind. m^{-3} in early May. Koski *et al.* (1994) reported that in the Baltic, off the southern coast of Finland, the abundance of *A.bifilosa* adults exceeded 3,000 ind. m^{-3}, while copepodite densities (including adults) could exceed ~12,000 ind. m^{-3}. Densities at Calshot were very much lower than at the site of their investigation.

Temora longicornis have been reported in the coastal North Sea (Evans, 1977), Dutch Wadden Sea (Klein Breteler and Gonzalez, 1986) as well as in the English Channel, Baltic and Norwegian Sea (Farran, 1948), and the Mediterranean (Rose, 1933). Within Southampton Water adult males were found to vary between 0.579 and 0.802mm in prosome length, while adult females varied between 0.650 and 0.936mm. Deevey (1960) found that the mean prosome length of *T.longicornis* from Long Island Sound varied between 0.63 to 1.20mm. Marshall (1949) found

that prosome lengths of this species collected in Loch Striven, varied between at least 0.539 and 1.218mm in adult males, and at least 0.539 to 1.270mm in adult females. Evans (1977) found adult female *T.longicornis* mean prosome lengths to vary between ~0.77 and 1.2mm. The sizes of adults collected from Southampton Water were therefore within the previous extremes of size reported. *T.longicornis* copepodites were found at Calshot between the months of March to November, with maximum total abundance in May. Maximum adult abundance was recorded as 39 ind. m^{-3}, which is much less than the adult abundance recorded off Plymouth by Digby (1950) of 340 ind. m^{-3}. The maximum recorded abundances for all copepodite stages off Plymouth was a month later than in Southampton Water ie. during June. From Evans' (1977) data it is evident that *T.longicornis* copepodite numbers in Northumberland coastal waters peaked in May-June, adults attained 1,166 ind. m^{-3}, while total non-adult copepodites reached a maximum of 583 ind. m^{-3}. In Southampton Water no *T.longicornis* were found between December and February. Digby (1950) also found that this species was very scarce/absent in the winter months of November to January, nauplii and a few copepodites were found from February onwards. Evans (1977) reported that in the coastal waters off Northumberland, *T.longicornis* adults never quite disappeared in winter, but densities of <1 ind. m^{-3} were not unusual. Marshall (1949) found only nauplii of this species in January in Loch Striven. Unfortunately no abundance data were collected during October to December. This species has been shown to be able to produce a dormant egg, which may be deposited in sediment, and may be viable for periods of at least 6 months (Lindley, 1986). Ryan *et al.* (1986) found in Killary Harbour that *T.longicornis* occurred in every month of the year, although were most abundant in early July at 4,675 ind. m^{-3}, and numbers remained high until late September. Within Southampton Water total copepodite numbers reached only one fifth of this value, at 562 ind. m^{-3}.

Centropages hamatus has been recorded in Atlantic waters as far north as Iceland, and as far south as coastal Portugal (Lindley and Hunt, 1989). It has also been found in the North Sea, Baltic, English Channel, inshore Norwegian, Barent and Kara seas (Raymont, 1983), and also the Mediterranean (Rose, 1933). Within Southampton Water, prosome lengths were found to vary between 0.668 and 1.096mm in adult males, while females varied between 0.668 and 1.087mm. Marshall (1949) found that adult male *C.hamatus* from Loch Striven varied between at least 0.696 and 1.270mm, while adult females varied at least between 0.748 and 1.479mm. Those collected in Southampton Water had a size range extending below these limits, the lower sizes being found at temperatures of 17.4°C, which was higher than that achieved in Loch Striven. *C.hamatus* reached maximum densities during July and August at Calshot, with adults reaching 53 ind. m^{-3}, this is similar to the maximum of 42 ind. m^{-3} for *Centropages typicus* found off Plymouth (Digby, 1950). Raymont and Carrie (1964) also report in their multi-year study of

zooplankton at Calshot, that in the 1950's, the maximum numbers of *C.hamatus* were found typically in July, and that over the 6 years of study, maximum densities were >1000 copepodites m^{-3}. In the present investigation the maximum density recorded was 453 copepodites m^{-3} in August. Unfortunately Raymont and Carrie (1964) give no indication of variation from their maximum densities, so comparisons with more typical densities are not possible. Ryan *et al.* (1986) found that in Killary Harbour, *C.hamatus* occurred in every month of the year, and was one of the most abundant species in spring and early summer, maximum total numbers being found in spring, when numbers reached 3,292 ind. m^{-3}. Lindley and Hunt (1989) found from CPR data that *C.hamatus* declined in abundance across the North Atlantic and North Sea from August-September. Marshall (1949) and Wiborg (1940) also found decreasing densities of late copepodites and adults in Loch Striven and Oslo fjord respectively, after July. The proposition that a July disappearance was a consequence of competition by *C.typicus*, as suggested by Lindley and Hunt (1989), should be questioned given that this species was extremely rare in Southampton Water, and was not found by Marshall (1949) in Loch Striven. At Calshot, adult numbers decreased after July, however, late stage copepodites did not decline until August and September. Individuals of *C.hamatus* were found at Calshot throughout the year except in January-February. This is similar to the situation found by Raymont and Carrie (1964) at Calshot, reporting that over their 6 years of study, hardly a specimen was recorded in January-February. Lindley and Hunt (1989) also reported that CPR data for the North Atlantic and North Sea showed it to be very rare during January and February, and most abundant and widespread in June to August. As already described, *C.hamatus* is a species for which resting eggs have been found (Pertzova, 1974; Marcus, 1984; both from Uye, 1985). These eggs are commonly deposited in sediment, where they may lay dormant for periods of up to one year (Lindley, 1990). Lindley and Hunt (1989) found that pelagic populations of *C.hamatus* persisted over the winter in a limited number of regions, mainly confined to areas with high phytoplankton stocks (possibly greater than 1mg.Chl a. m^{-3}) and low temperature (<5°C). Neither of these prerequisites were satisfied within Southampton Water (ie. chlorophyll a often <1mg.m^{-3} and temperatures >5°C during winter), and hence it could be predicted that the pelagic population should indeed be absent. Whether there are resting eggs in the region from which populations develop has not as yet been confirmed.

Paracalanus parvus and *Pseudocalanus elongatus* have been recorded in the North Sea (Evans, 1977), Channel waters off Plymouth (Digby, 1950), and having also been found together in the Black Sea (Rose, 1933). *Paracalanus parvus* is frequently very abundant in parts of the temperate North Atlantic, and may be plentiful not only inshore but in surface offshore waters (Raymont, 1983). At Calshot *Paracalanus parvus* copepodite numbers were found to reach a

maximum of 182 ind. m^{-3}, with an adult maximum of just 31 ind. m^{-3} in the following month. Off Plymouth, Digby (1950) found densities of *Paracalanus parvus* (including nauplii) to reach their maximum in May, at 5,180 ind. m^{-3}, with non-adult copepodite and adult numbered 1,220 and 200 ind. m^{-3} respectively at this time. Maximum non-adult and adult numbers off Plymouth however were found in June, when adult numbers reached 420 ind. m^{-3}, and non-adult copepodite numbers reached 3,264 ind. m^{-3}. Digby (1950) also found densities of *Pseudocalanus elongatus* copepodites to reach densities of 2,220 ind. m^{-3} in May and 3,510 ind. m^{-3} in July. *Pseudocalanus elongatus* were fairly rare at Calshot however, copepodite numbers reaching a maximum of 36 ind. m^{-3} in late April, with a second peak in December.

Physico-chemical parameters:

Oxygen concentrations throughout the sites sampled showed clear trends on an annual basis (see Figure 2.3.17 and 2.3.18), there is also a general trend of increasing oxygen concentration in a seaward direction. This trend may be expected given the landward trend in eutrophication (Kifle, 1992). Lowest concentrations of oxygen were found from June to October. Although patterns are more variable in terms of percentage saturation, the summer to late autumn months are dominated by sub-saturation levels. Levels of saturation barely fall below 80% at any time, however. Values at Bury Buoy below 40% have been recorded previously in July (Hayes *et al.*, 1989). Many studies have reported the occurrence of hypoxic and anoxic conditions in eutrophic estuaries and coastal areas, which were associated with water column stratification, high temperatures and freshwater inputs. Southampton Water is however shallow, and generally regarded as being well-mixed, which may reduce oxygen depreciation. Oxygen concentrations are not easy to interpret since they are affected by biological and physical processes. Periods when photosynthetic activity exceeds respiration rates may also result in oxygen super-saturation. Wind and wave action may increase the rate at which oxygen is dissolved.

Kuosa (1989) found in the laboratory that *Acartia bifilosa* at 18°C, exhibited increased mortality at 2 and 4.5mgO_2l^{-1}, but not at 7.0mgO_2l^{-1} (control level being 10mgO_2l^{-1}), and could be induced into inactivity because of the low oxygen concentrations. In the present study oxygen levels varies between 6.1 and 11.6mgO_2l^{-1}. At times oxygen levels could certainly have an effect upon copepod survival and activity. In this study oxygen levels were generally measured in the morning to late afternoon. Levels may be lowest during dark periods however, when there is no net production of oxygen by autotrophic algae. Whether levels would fall sufficiently to have an important effect upon zooplankton needs to be investigated. In the present investigation oxygen saturation percentage over the 14 month investigation was positively correlated with copepod biomass at Calshot ($P<0.05$; see Table 2.3.1).

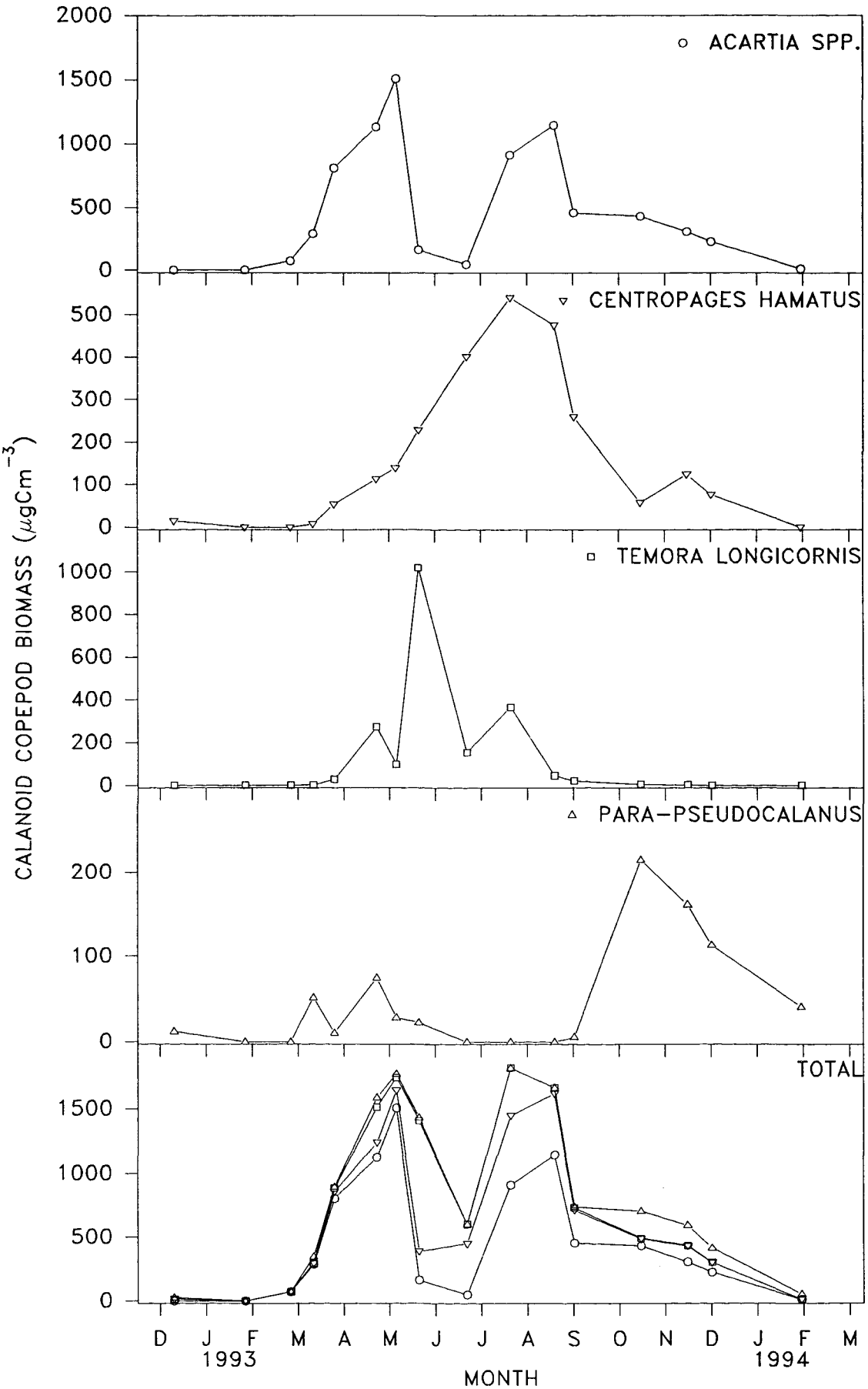


FIGURE 2.4.6 Estimated species-specific calanoid copepod biomass at the Calshot site (Note Scale Change).

However, oxygen saturation decreases in a landward direction and yet copepod abundance and probably biomass increase away from the estuary mouth (see Figure 2.4.8). This probably indicates that biomass is not infact controlled by the oxygen concentration at Calshot.

Secchi disk depths, extinction coefficients and depth of the euphotic zone are given in Figure 2.3.16. Secchi disk depths ranged from 4.3m in May 1993 at Calshot, to 0.4m in December 1993 at Calshot and Hamble. Lowest values were recorded during the winter months, while secchi depths were greatest in May, June and July. These recorded extremes give estimated depths of the euphotic zone of 15.05 to 1 metre respectively. Calshot is a site characterised by high winter sediment-loads (Head, 1969), although the recorded Secchi disk depths for the other sites are very similar during the winter period, and sediment loads may be high throughout the sampling area. Secchi disk depths are indicative of the amount of suspended particulate material in the water column, whether this material is living or dead. Values fall rapidly during June to August, this probably reflects an increase in biological material. The reduced values during the winter months may be the result of higher concentrations of suspended non-living material, particularly detritus and re-suspended sediment. Although there is no consistent increase in secchi disc depth moving seawards, it is common for the more seaward sites to have greater Secchi disc depths. Secchi disc readings given in Leakey (1990) for Calshot and N.W.Netley are very similar in value and seasonal patterning to those found in the present investigation. Once again low values are found in late spring (around May-June), being much reduced in late June, and being low in winter (October-December). Secchi disc depth was found to be significantly positively related to chlorophyll a concentration ($P<0.001$). As the Secchi depth relates to euphotic zone depth then the association may be simply a result of favourable algal growth condition during periods of deeper light penetration. This result tends to suggest that the eutrophic zone depth is strongly related to suspended particulate material (SPM) of a non-algal from. Such material could be dominated by suspended sediments which will be greatest in winter.

Calanoid biomass estimates and population parameters:

Biomass estimates for the dominant calanoid copepod species (excluding nauplii) are presented for Calshot in Figure 2.4.6. Biomass patterns broadly reflected changes in the density of species, although biomass is of course not simply a function of the density of copepods but dependent upon their size, with this varying with stage and season. In this study copepod biomass appears to be strongly seasonal at the Calshot site. Given that the mesh used will not catch all copepod stages, then samples may typically be regarded as giving estimates below their true value (excluding patchiness effects). *Acartia* was the single most dominant group in terms of biomass throughout much of the year, although in the winter the *Para-Pseudocalanus* group and

Centropages hamatus had greatest biomass, and in May and June of 1993, when *Acartia* biomass was reduced from its spring and late summer-autumn peaks, the individual biomass of both *Centropages hamatus* and *Temora longicornis* were greater. *Acartia* biomass was at its highest in April-May, when it reached 1,508μgCm^{-3}, and in August, when it reached 1,144μgCm^{-3}. *C.hamatus* biomass increased from February, when no individuals were found, to the end of July, when its biomass reached its maximum at 541μgCm^{-3}. After this peak the biomass fell steadily until November, when there was a small second peak, after which biomass fell into winter. There were three discrete peaks of *T.longicornis* biomass, in April when biomass reached 273μgCm^{-3}, in May at 1,021μgCm^{-3} and in July at 365μgCm^{-3}. *Para-Pseudocalanus* biomass was greatest in October, when it reached 215μgCm^{-3}.

Total calanoid copepod biomass was lowest in January, increased until April-May, when it reached 1,772μgCm^{-3}. It fell from this value and reached a mid-year low in June, after which it rose once again reaching a second even greater peak of 1,818μgCm^{-3} in July. After this point biomass declined, although values were sustained above 400μgCm^{-3} until January 1994. Biomass estimates for calanoid copepods during the present study are lower than those found in many other temperate nearshore areas. Fransz (1981) for example found in the western Dutch Wadden Sea, that *Temora longicornis* populations had an annual biomass maximum of around 3,200 to 24,000μgCm^{-3}, the lowest value being some three times the value found in the present investigation for this species at Calshot. Estimated annual maximum biomass of *Pseudocalanus elongatus* in the same area (Fransz, 1981) was found to be typically around 800μgCm^{-3} (although in one year it was as high as ~20,000μgCm^{-3}). At Calshot the *Para-Pseudocalanus* group had a maximum value in 1993 of 215μgCm^{-3}. *Acartia clausi* was estimated to have an annual biomass maximum of around 1,200 to 24,000μgCm^{-3} in the Dutch Wadden Sea (Fransz, 1981). The value for *Acartia* in the present study falls within this range, but is very much towards its lower end at 1,144μgCm^{-3}. *Acartia bifilosa* biomass in the Baltic, off the southern coast of Finland, was reported by Koski *et al.* (1994) to reach as much as 3,400mgCm^{-2}. Which is over 180 times the total calanoid biomass found at Calshot during this investigation (where it reached 18.18mgCm^{-2}). Escaravage and Soetaert (1995) report maximum *Acartia tonsa* biomass values in the Westerschelde estuary, Netherlands, of 25,000μgCm^{-3}, this value being 14 times greater than that the total calanoid biomass estimated for Southampton Water. They also report a maximum *Eurytemora affinis* in the same region of 180,000μgCm^{-3}. *Centropages hamatus* biomass, excluding nauplii, was estimated in the Dutch Wadden Sea to reach an annual maximum of around 1,600 to 22,000μgCm^{-3}, whilst in the present study it was only 541μgCm^{-3}. Low calanoid copepod biomass and low densites in comparison to other nearshore areas were therefore both observable at Calshot. These low values may be the result of high flushing rates, and as

demonstrated in the following chapter, also the result of rather low growth rates.

Ratios of adult females to adult males for calanoid copepods in this investigation have been estimated for cases where more than 20 adult individuals of any given species were identified. The results show that for *Acartia bifilosa* females were always more abundant than males (where the number of times such a measurement [n] was made was equal to 4), with females making up between 54 to 73% of the adults. *Acartia discaudata* females were also always more abundant than males (where n=3), making up between 67 and 76% of adults. *Acartia clausi* females were more abundant on the same number of occasions as males, although for this species n was only equal to 2. Unfortunately adults of *Temora longicornis* and *Centropages hamatus* were rarer than *Acartia*, and numbers of adults exceeded 20 on only one occasion for both species. Females were more abundant on these occasions, while examining abundances when adult number were less than 20 shows no single dominance by one sex or the other. Schnack (1978) determined the sex ratio of calanoid copepods in Kiel Bay, Baltic, and reported that *A.bifilosa* adult females were more abundant than males, making up an average 63% of the total adults. This is very similar to the average of 67% estimated for this species in Southampton Water. *A.discaudata* sampled in the Kiel Bay were found to make up 69% of adults on average, as compared to 71% in Southampton Water. Digby (1950) found that for *A.clausi*, collected in coastal waters off Plymouth, females were dominant over the males on 10 of 15 occasions (considering only occasions when the total number of adults was greater than 20). Females made up between 38 and 90%, with an average of 56% (with regression analysis giving no significant relationship between; proportion females [dependent variable] and adult and total abundance as the [independent variables]). Marshall (1949) found that for *A.clausi* collected in Loch Striven, Scotland, females were more abundant than males on only 13 out 32 of occasions, making up between 27 and 80% of the adults (and an average of 49%), this situation is somewhat different from the other reports.

Centropages hamatus and *Temora longicornis* adult males were found to be more abundant than females in Kiel Bay, making up in both cases an average 51% of adults (Schnack, 1978). In Southampton Water, males of these two species made up around 45% of the adults. Digby (1950) found that off Plymouth, *T.longicornis* males were usually more abundant than were females, being dominant on 7 out of 11 occasions, with females making up between 33 and 100% of the adults (with an average of 50%). Marshall (1949) found that in Loch Striven, Scotland, male *T.longicornis* and *C.hamatus* were also both more abundant than females in this species, with females making up between 20 and 57% of adults (average 43%) in *Temora longicornis*, and between 9 and 72% (average 34%) in *Centropages hamatus*. Evans (1977)

found for the year 1971 in offshore Northumberland waters, that *Temora longicornis* males were once again not always more abundant than the females. Females did however make up, on average, 40% of the adults (estimated from all dates regardless of number of individuals found, as numbers were almost always very low). In the same study, *A.clausi* and *A.longiremis* were both more typically female dominated, with females making up on average 68 and 73% respectively (once again estimated from all dates regardless of number of individuals found).

Females of calanoid copepods have commonly been found to be more abundant than males, although for *Centropages hamatus* and *Temora longicornis* the reverse may be more common (Marshall, 1949; Digby, 1950; Eriksson, 1973a). Marshall (1949) and Eriksson (1973a) both suggested that for most species the females were longer lived than the males, this could explain the greater number of females even if the two sexes were produced in equal numbers. Martens (1981) believed that the longer lived nature of females meant that *Acartia* populations showing larger proportions of females to males were older than populations with lower proportions, this hypothesis does not however explain why the number of males may exceed that of females. Food species supplied (Paffenhöfer, 1970) and temperature (Katona, 1970) have also both been shown to effect the sex ratio under experimental conditions. Field and laboratory results have also shown that the density of a population may cause differences in the sex ratio, with higher proportions of females at low densities (Heinle, 1970), although for some species there have been no relationships of this type found (Hillebrandt, 1972; Schnack, 1978; this study).

For *Acartia bifilosa* and *Acartia longiremis*, and in some years for *Acartia tonsa* and *Pseudocalanus* sp., Schnack (1978) found that the proportion of females to males appeared to increase as density declined. Given the cyclical nature of abundance of these species, these changes could probably just as well be related to temperature or food abundance. Least squares linear regression found no significant relationship between sex ratio and density of *Acartia* or *Acartia bifilosa* adults, or temperature for this species in Southampton Water, although the results did only span ~2 months of the year.

It is of interest to note that in the present investigation individual adult and late copepodite stages of *Acartia* were found in Southampton Water which displayed both female and male characteristics. There appears to be no such descriptions of intersexual individuals in the current literature, and potential causes appear as yet undescribed. The cause could be attributable to developmental effects (environmental; possibly pollution related; the result of parasitic attack [although these were not evident]), or a result of genetic abnormality. This anomaly has been

noted in other crustaceans, notably amphipods (M.Sheader, *pers. comm.*; Sudo and Azeta, 1996)

Unfortunately the length-weight regressions chosen from the literature for application in this investigation, was not specific to this location (or to any season). It has been shown that the dry weight per unit length for individual species may vary between locations (eg. *A.clausi* (*hudsonica*?), Durbin and Durbin, 1978; and also see comparisons in Figures 2.2.5 to 2.2.7). As such the accuracy of the biomass estimates may be open to question, particularly as single equations have been used, and these were derived not within Southampton Water. To give an example, for an individual *Acartia clausi* with a prosome length of 500μm, all the equations derived for this genus in Table 2.2.2, gives values which range from 0.396μgC to 0.855μgC. The lower limit to the range is estimated from an area very different from Southampton Water (and the North Sea, from which the equation applied to the Southampton Water population was adopted), namely the Eastern Mediterranean, where temperature at time of collection was 16.5°C. Unfortunately biomass was not determined through the weighing of samples either, as recommended by Chisholm and Roff (1990a), and therefore no attempt at estimating the true deviation from the estimates made using length weight regressions is possible.

Both total calanoid copepod biomass and total calanoid copepod density are positively correlated with simultaneous measurements of temperature and temperature in the previous month (see Table 2.3.1 and 2.3.2). This may be expected given the usual dependence of biomass growth and reproduction upon this factor. Hernroth and Ackefors (1979) state that 'In many sea areas temperature is the master factor, affecting both the physiology and the ecology of zooplankton. Temperature influences physiological factors such as mortality, survival, metabolic rate, feeding rate, embryonic development and ecological features such as community structure, diapause and energy flow'.

The slight decrease in water temperature towards the more seaward sites apparent in the present study, has been shown by other workers (Crawford *et al.*, 1985; Zinger, 1989; Kifle, 1993; Lucas, 1993). Because of the well mixed nature of the shallow water column, changes in temperature with depth were only slight (as previously noted by Raymont and Carrie, 1964). The maximum difference recorded in the present investigation was only 0.5°C. Temperature has a very significant effect upon biological processes; however, given the similarity in temperature between the sites examined in this study, other factors are likely to be more important in terms of the differences found between sites.

Salinity fluctuations within Southampton Water reflect the rate of input of fresh water

GROUP	REGION	WATER DEPTH (m)	ANNUAL BIOMASS RANGE	MEAN*	SOURCE
Calanus finmarchicus	Scotian Shelf, Canada		0.594-19.246mgCm^{-3}	6.36mgCm^{-3}	Tremblay and Roff, 1983[3]
		89.3	53.04-1,718.67mgCm^{-2}	567.95mgCm^{-2}	
Oithona similis	Scotian Shelf, Canada		0.120-0.779mgC^{-3}	0.395mgCm^{-3}	Tremblay and Roff, 1983[3]
		89.3	10.72-69.56mgCm^{-2}	35.27mgCm^{-2}	
Metridia lucens	Scotian Shelf, Canada		0.771-1.938mgC^{-3}	1.342mgCm^{-3}	Tremblay and Roff, 1983[3]
		89.3	68.85-173.06mgCm^{-2}	119.84mgCm^{-2}	
Centropages typicus	Scotian Shelf, Canada		0.004-2.488mgC^{-3}	0.742mgCm^{-3}	Tremblay and Roff, 1983[3]
		89.3	0.36-222.18mgCm^{-2}	66.26mgCm^{-2}	
Pseudocalanus minutus	Scotian Shelf, Canada		0.157-0.635mgC^{-3}	0.430mgCm^{-3}	Tremblay and Roff, 1983[3]
		89.3	14.02-56.71mgCm^{-2}	38.40mgCm^{-2}	
Paracalanus parvus	Scotian Shelf, Canada		0.0032-0.717mgC^{-3}	0.170mgCm^{-3}	Tremblay and Roff, 1983[3]
		89.3	0.29-64.03mgCm^{-2}	15.18mgCm^{-2}	
Calanus hypoboreus	Scotian Shelf, Canada		0-3.258mgC^{-3}	0.776mgCm^{-3}	Tremblay and Roff, 1983[3]
		89.3	0-290.94mgCm^{-2}	69.30mgCm^{-2}	
Clausocalanus sp.	Scotian Shelf, Canada		0.024-0.290mgC^{-3}	0.102mgCm^{-3}	Tremblay and Roff, 1983[3]
		89.3	2.14-25.90mgCm^{-2}	9.11mgCm^{-2}	
Calanus glacialis	Scotian Shelf, Canada		0-0.765mgC^{-3}	0.267mgCm^{-3}	Tremblay and Roff, 1983[3]
		89.3	0-68.31mgCm^{-2}	23.84mgCm^{-2}	
Candacia armata	Scotian Shelf, Canada		0.019-0.170mgC^{-3}	0.067mgCm^{-3}	Tremblay and Roff, 1983[3]
		89.3	1.70-15.18mgCm^{-2}	5.98mgCm^{-2}	
Acartia tonsa	Rhode River Sub-Estuary, USA		0.068-6.52mgCm^{-3}	2.06mgCm^{-3}	Allan *et al.*, 1976
		1.94	0.132-12.65mgCm^{-2}	4.00mgCm^{-2}	

Eurytemora affinis	Rhode River Sub-Estuary, USA		0.016-87.448mgCm^{-3}	-	Allan *et al.*, 1976
		1.94	0.031-169.65mgCm^{-2}	-	
Acartia tranteri	Westernport Bay, Australia		~0.8-8.4mgCm^{-3}	2.92mgCm^{-3}	Kimmerer and McKinnon, 1987
		10	~8.0-84.0mgCm^{-2}	29.2mgCm^{-2}	
Copepoda	Continental Shelf Waters, USA		~0.1-10.5mgCm^{-3}	~4.0mgCm^{-3}	Curl, 1962
		-	-	-	
Copepoda	Mikawa Bay, Japan		-	-	From Koga, 1986
		-	85.8-777.9mgCm^{-2}	268.6mgCm^{-2}	
Copepoda	Osaka Bay (st.4), Japan		9.46-11.05mgCm^{-3}	10.37mgCm^{-3}	Joh and Uno, 1983
		30	283.8-331.5mgCm^{-2}	311.1mgCm^{-2}	
Centropages abdominalis	Inlet, Inland Sea of Japan		0-97.1mgCm^{-3}	-	Liang *et al.*, 1996
		7.5	0-728.25mgCm^{-2}	-	
Acartia omorii	Inlet, Inland Sea of Japan		0-80.5mgCm^{-3}	-	Liang and Uye, 1996
		7.5	0-603.74mgCm^{-2}	-	
Copepods	Inlet, Inland Sea of Japan		?-165mgCm^{-3}	39.1mgCm^{-3}	Uye and Liang, 1996
		7.5	?-1,237.5mgCm^{-2}	293.3mgCm^{-2}	
Calanus sinicus	Harima-nada, Inland Sea of Japan		~0-26.0mgCm^{-3}	-	Huang *et al.*, 1993
		~29	~0-754mgCm^{-2}	-	
	Kii Channel, Inland Sea of Japan		~0.5-15mgCm^{-3}	-	Huang *et al.*, 1993
		~48	~24-720mgCm^{-2}	-	
	Coastal Pacific		~0.1-1.7mgCm^{-3}	-	Huang *et al.*, 1993
		<200	-	-	
	Offshore Pacific		~0.1-0.9mgCm^{-3}	-	Huang *et al.*, 1993
		~200-1,500	-	-	

Acartia bifilosa	Baltic, S.Coast Finland		-	-	Koski *et al.*, 1994
		-	~30-340mgCm^{-2}	-	
Eurytemora affinis	Baltic, S.Coast Finland		-	-	Koski *et al.*, 1994
		-	~10-260mgCm^{-2}	-	
Copepods	Southern Kattegat	28	~3.6-39.3mgCm^{-3}	-	Kiørboe and Nielsen, 1994
			~100-1,100mgCm^{-2}	-	
Eurytemora affinis	Westerschelds estuary, Netherlands		~0-180mgCm^{-3}	28.5mgCm^{-3}	Escaravage and Soetaert, 1995
		7	~0-1,260mgCm^{-2}	199.5mgCm^{-2}	
Acartia tonsa	Westerschelds estuary, Netherlands		~0-25mgCm^{-3}	7.0mgCm^{-3}	Escaravage and Soetaert, 1995
		7	~0-175mgCm^{-2}	49.0mgCm^{-2}	
Eurytemora affinis	Bristol Channel, U.K.		0.0003-0.009mgCm^{-3}	0.003mgCm^{-3}	Burkill and Kendall, 1982
		-	-	-	
Omivorous zooplankton	Inner & Outer Bristol Channel		<4mgCm^{-3}	~1mgCm^{-3}	Collins and Williams, 1982
(predominantly copepods)		-	-	-	
Calanoid Copepods	Calshot, Southampton Water		0.0006-1.818mgCm^{-3}	0.846mgCm^{-3}	This Study for 1993
		10	0.006-18.18mgCm^{-2}	8.46mgCm^{-2}	
	Calshot, Southampton Water		0.206-15.175mgCm^{-3}	3.211mgCm^{-3}	Estimated from data of Zinger for 1985[1]
		10	2.06-151.75mgCm^{-2}	32.11mgCm^{-2}	
	Calshot, Southampton Water		0.728-11.222mgCm^{-3}	3.873mgCm^{-3}	Estimated from data of Zinger for 1986[1]
		10	7.28-112.22mgCm^{-2}	38.73mgCm^{-2}	
	Hamble, Southampton Water		0.120-12.128mgCm^{-3}	3.008mgCm^{-3}	Estimated from data of Zinger for 1985[1]
		10	12.0-121.28mgCm^{-2}	30.08mgCm^{-2}	
	Hamble, Southampton Water		1.306-6.791mgCm^{-3}	2.920mgCm^{-3}	Estimated from data of Zinger for 1986[1]
		10	13.06-67.91mgCm^{-2}	29.20mgCm^{-2}	

Greenland, Southampton Water	0.038-3.169mgCm^{-3}	1.318mgCm^{-3}	Estimated from data of Lucas for 1990[2]
10	0.38-31.69mgCm^{-2}	13.18mgCm^{-2}	
Greenland, Southampton Water	0.151-15.729mgCm^{-3}	2.204mgCm^{-3}	Estimated from data of Lucas for 1991[2]
10	1.51-157.29mgCm^{-2}	22.04mgCm^{-2}	
N.W.Netley, Southampton Water	0.118-15.411mgCm^{-3}	3.619mgCm^{-3}	Estimated from data of Lucas for 1991[2]
8	0.94-123.29mgCm^{-2}	28.95mgCm^{-2}	
Cracknore, Southampton Water	0.0206-17.844mgCm^{-3}	2.957mgCm^{-3}	Estimated from data of Zinger for 1985[1]
8	0.17-142.75mgCm^{-2}	23.66mgCm^{-2}	
Cracknore, Southampton Water	0.732-15.651mgCm^{-3}	5.448mgCm^{-3}	Estimated from data of Zinger for 1986[1]
8	5.86-125.21mgCm^{-2}	43.58mgCm^{-2}	
Cracknore, Southampton Water	0.485-15.287mgCm^{-3}	4.830mgCm^{-3}	Estimated from data of Lucas for 1990[2]
8	3.88-122.30mgCm^{-2}	38.64mgCm^{-2}	
Cracknore, Southampton Water	0.097-13.289mgCm^{-3}	2.837mgCm^{-3}	Estimated from data of Lucas for 1991[2]
8	0.78-106.31mgCm^{-2}	22.70mgCm^{-2}	

TABLE 2.4.3 Comparisons of copepod biomass values reported in various neritic and shelf areas, together with estimates for Southampton Water. All values when given in dry weight have been converted to carbon assuming carbon to be 40% of dry weight (Omori and Ikeda, 1984; Båmstedt, 1986). *Means when calculated for this study are simple arithmetic, commonly original texts do not give mean type although commonly also arithmetic (however, in Kimmerer and McKinnon (1987) means are explicitly described as geometric).

1 Estimated from abundance data, and assuming mean weight of 1.2μgC per individual (for details see Chapter 5). 2 Estimated from abundance data, and assuming mean weight of 2.0μgC per individual (for details see Chapter 5). 3 Biomass units converted from kJ to carbon by assuming 25kJ gDW^{-1} (mid-range value of Tremblay and Roff, 1983), and carbon to be 40% of dry weight (Omori and Ikeda, 1984; Båmstedt, 1986). Depth integrated measures estimated assuming a mean water depth of 89.3 metres (as given in original paper).

and the rate of flushing. As already discussed, flushing may play an important role in the biomass and density of copepods in the estuary. Salinity is affected by rates of freshwater input and mixing, and will therefore also be important in determining species composition along the length of the estuary. During October 1993 there was an extremely dramatic decline in salinity throughout the estuary. This was the result of due to extreme freshwater inputs, from heavy rainfall and flooding in the Southampton catchment area. At Calshot salinity fell from 34.0‰ in September to 29.5‰ in October. By the beginning of November this had risen back to a more typical level at 32.7‰ (see Figure 2.3.12). Comparisons of copepod densities prior to the salinity fall with those after, show a substantial drop in total calanoid numbers, with densities falling from 1,981 to 993 ind. m^{-3}. However, not all species showed a decline in abundance over this period, with the *Paracalanus/Pseudocalanus* group showing a marked increase from 5 to 182 ind. m^{-3}. Salinity was not significantly correlated (with and without lagging) to copepod biomass or density. The dependence upon more important factors such as temperature may cause any effects of salinity to be masked.

The biomass of calanoid copepods is almost certainly exceeded by the biomass of *Euterpina acutifrons* at Calshot during the months of September to November. Although biomass of this harpacticoid was not estimated, it has a similar body size to the calanoids, and reached densities of 2 to 4 times those of the total calanoid copepodites. The biomass of cirripede nauplii was also not assessed, again these were more abundant than calanoids from December 1992 until April 1993 and in June and October 1993 and January 1994. Cirripede larvae may therefore at times contribute a similar or greater proportion of total biomass than the calanoids. Given the size and density of the other mesozooplankton groups identified (eg. polychaete larvae, gastropod larvae, *Oikopleura* and ascidians), these may be regarded as probably having much lower biomass than the three most dominant groups at Calshot detailed above, namely the calanoids, *Euterpina acutifrons* and barnacle nauplii.

It is difficult to fully appreciate biomass fluctuations at Calshot without some idea of inter-annual fluctuation. Biomass and densities found were generally lower than those reported for other estuarine and neritic areas (see Table 2.4.3), although the biomass maxima were comparable to those found by Collins and Williams (1982) in the outer and inner Bristol Channel. Estimated biomass values of calanoids appear to never exceed ~18mgCm^{-3} in the main body of the estuary, this value apparently being exceeded in many other coastal areas. It has previously been shown in neritic areas that zooplankton abundance and biomass may fluctuate greatly between years (Fransz, 1981), and there are obvious differences between years in terms of the abundance and biomass found in Southampton Water (see Figures 2.4.2 to 2.4.1,

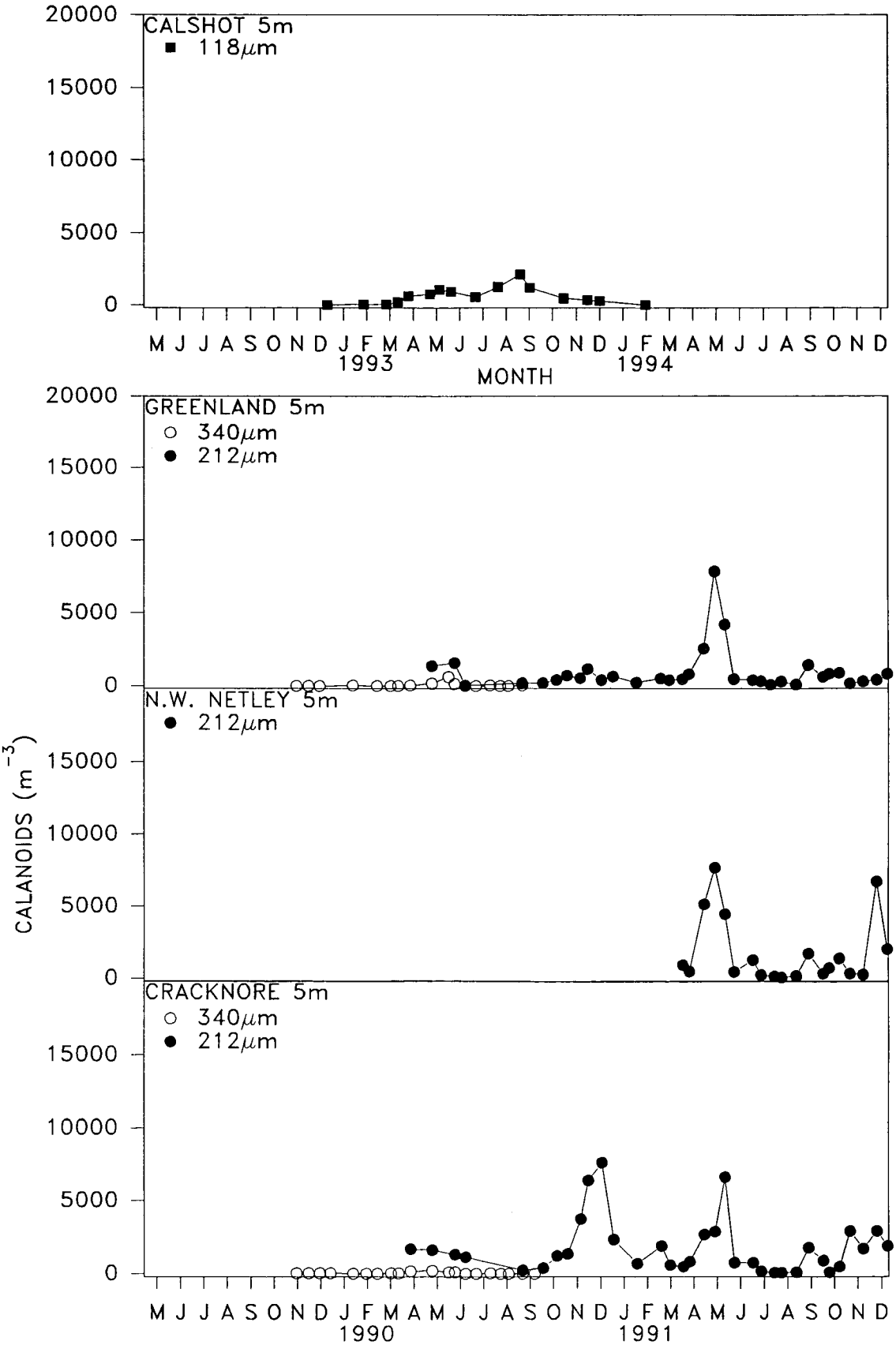


FIGURE 2.4.7 A comparison of the data on calanoid abundance at various sites in Southampton Water. Top graph data collected at Calshot during the present investigation, lower graphs from data given in Lucas (1993).

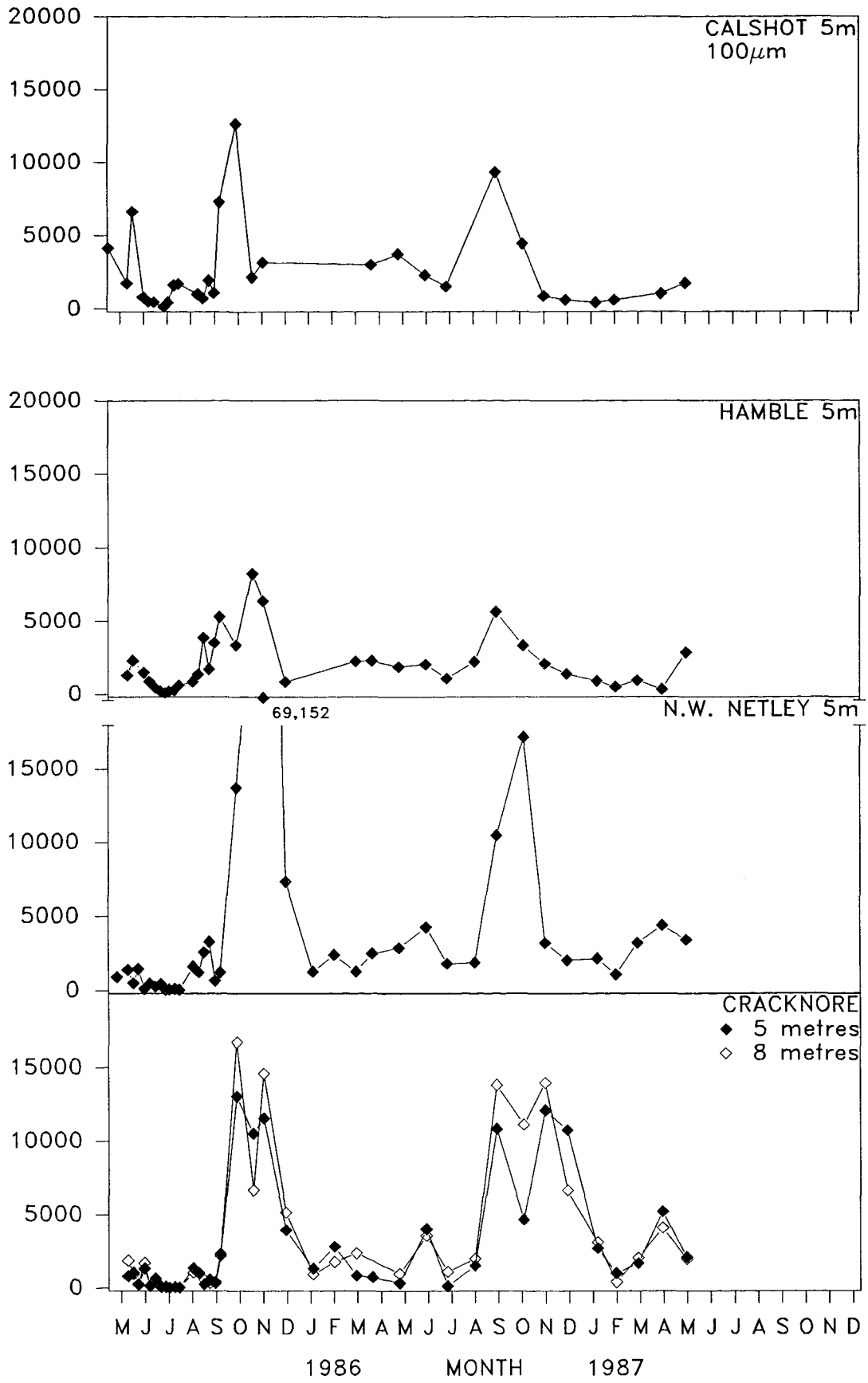
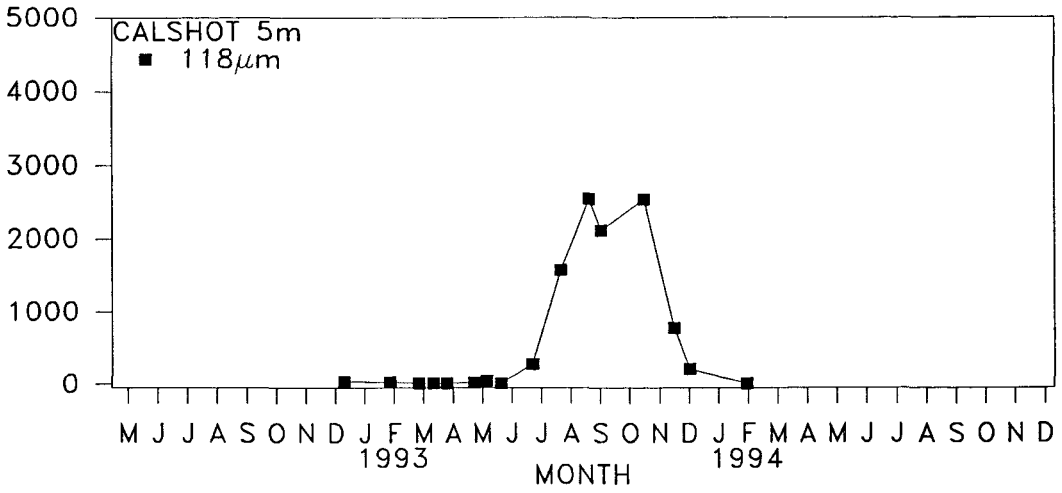


FIGURE 2.4.8 A comparison of the data on calanoid abundance at various sites in Southampton Water. Data from Zinger (1989). All samples taken with a 100μm mesh net.



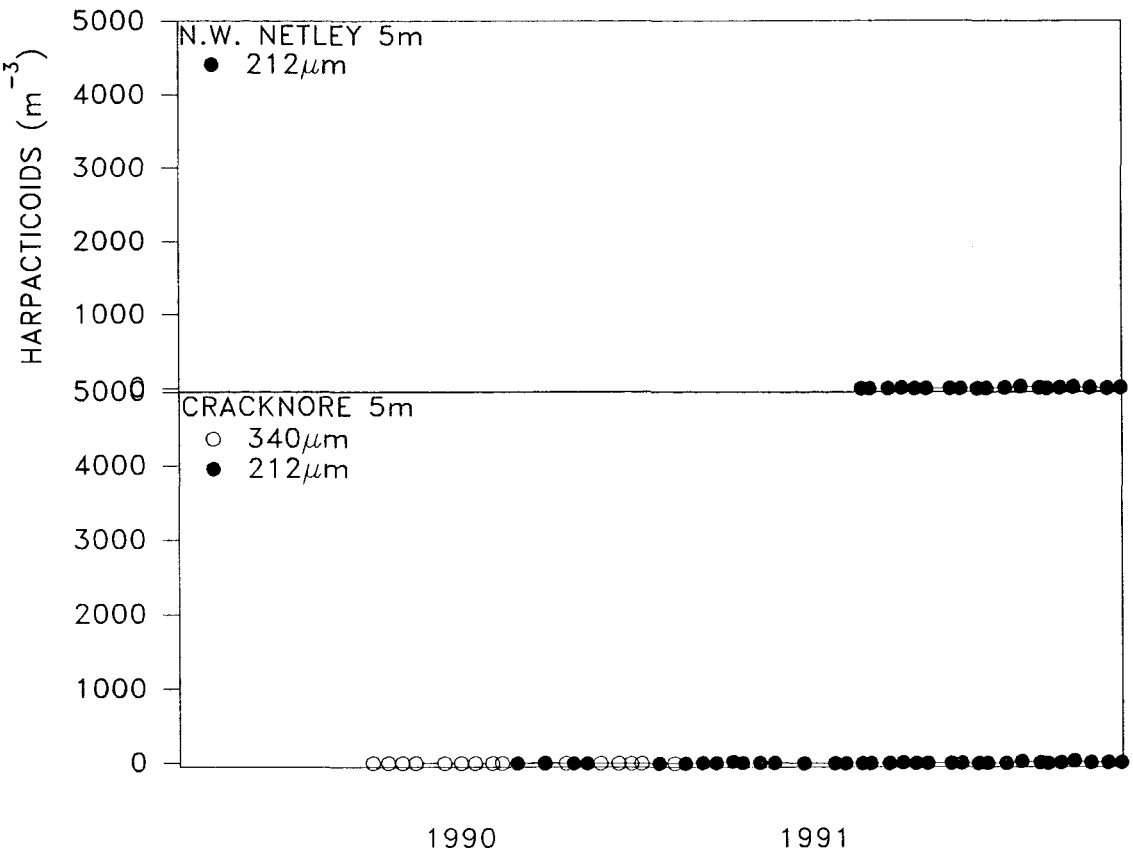


FIGURE 2.4.9 A comparison of the data on harpacticoid abundance at various sites in Southampton Water. Top graph data collected at Calshot during the present investigation, lower graphs from data given in Lucas (1993).

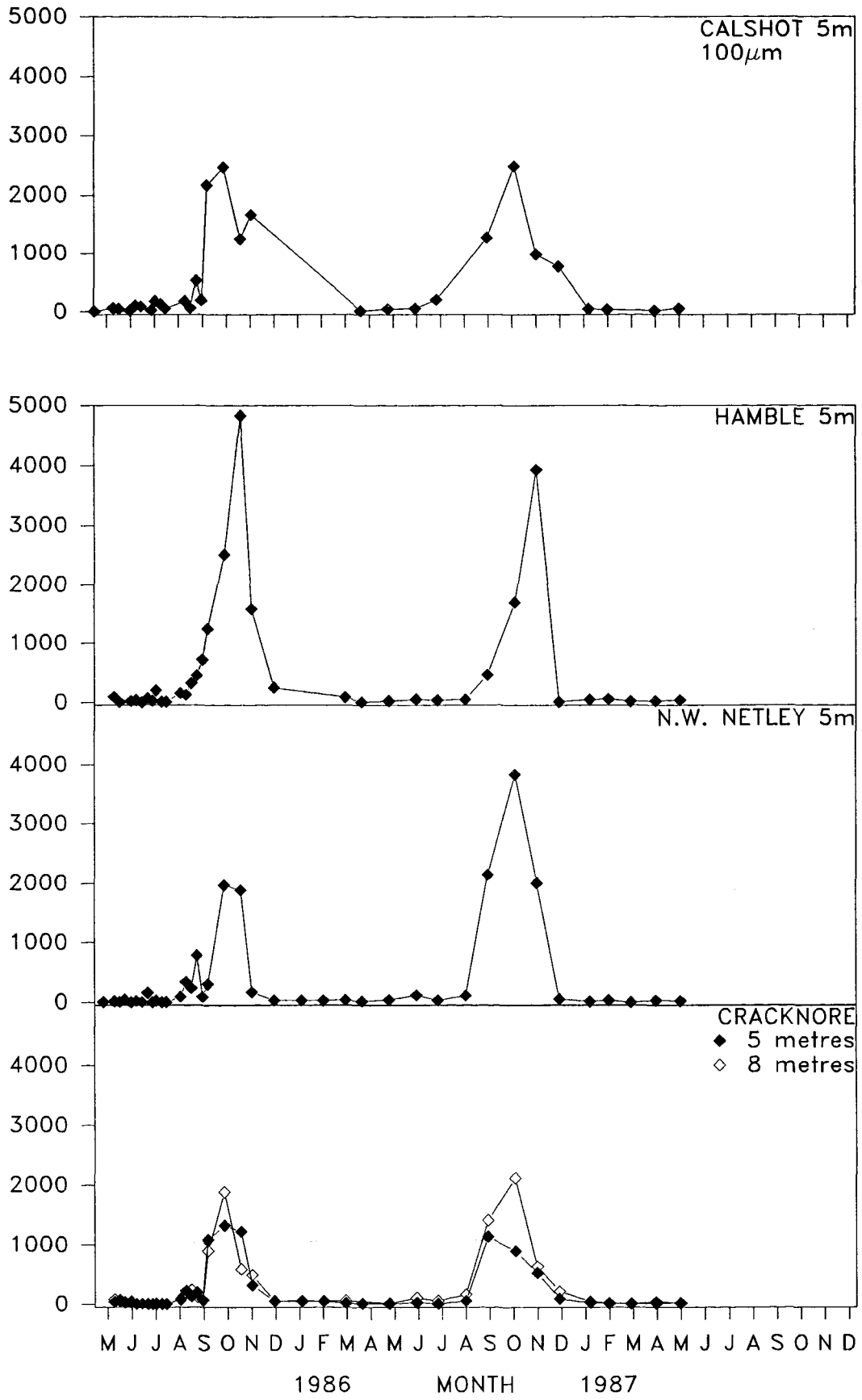


FIGURE 2.4.10 A comparison of the data on harpacticoid abundance at various sites in Southampton Water. Data from Zinger (1989). All samples taken with a 100μm mesh net.

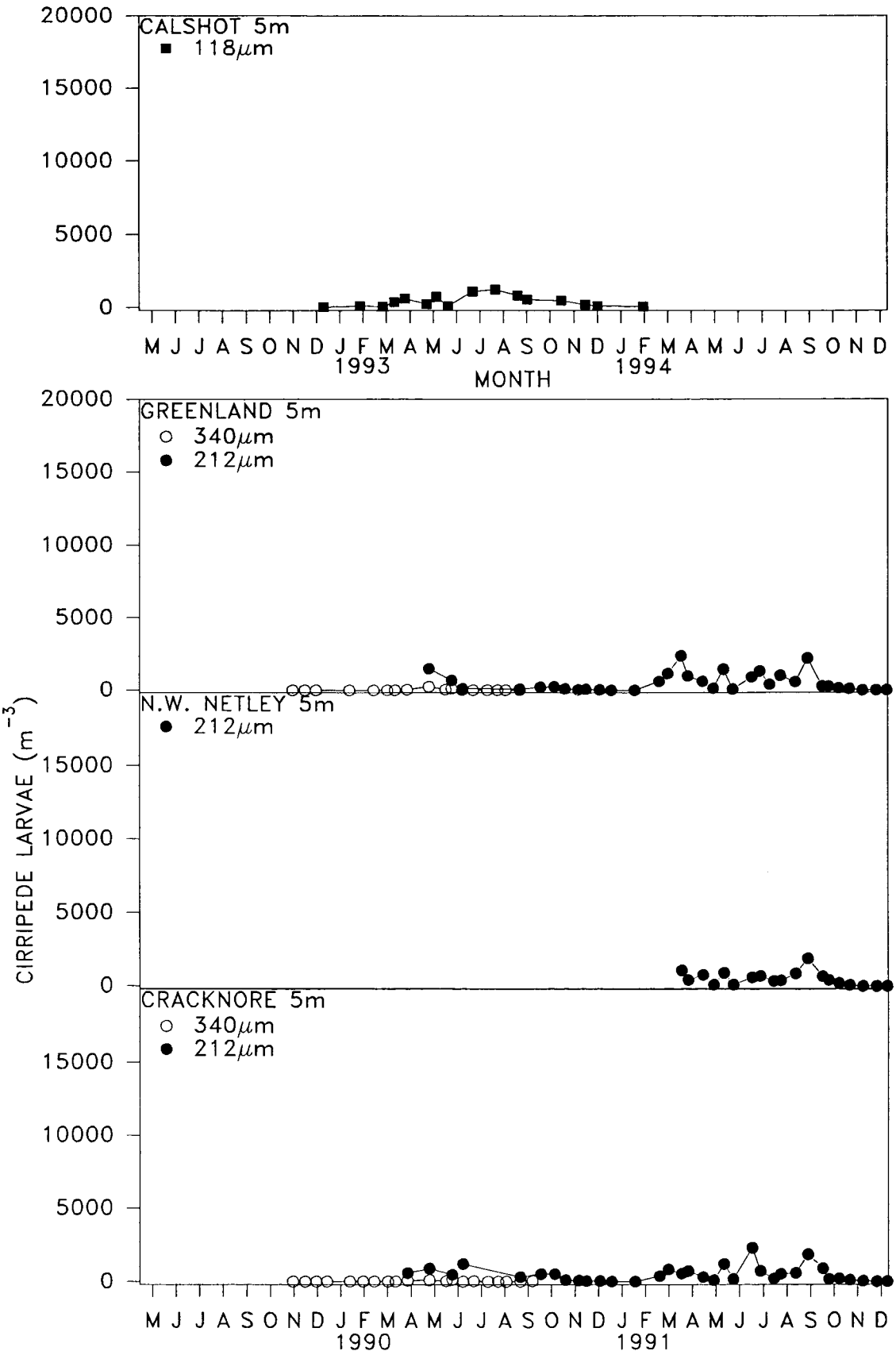


FIGURE 2.4.11 A comparison of the data on cirripede larvae abundance at various sites in Southampton Water. Top graph data collected at Calshot during the present investigation, lower graphs from data given in Lucas (1993).

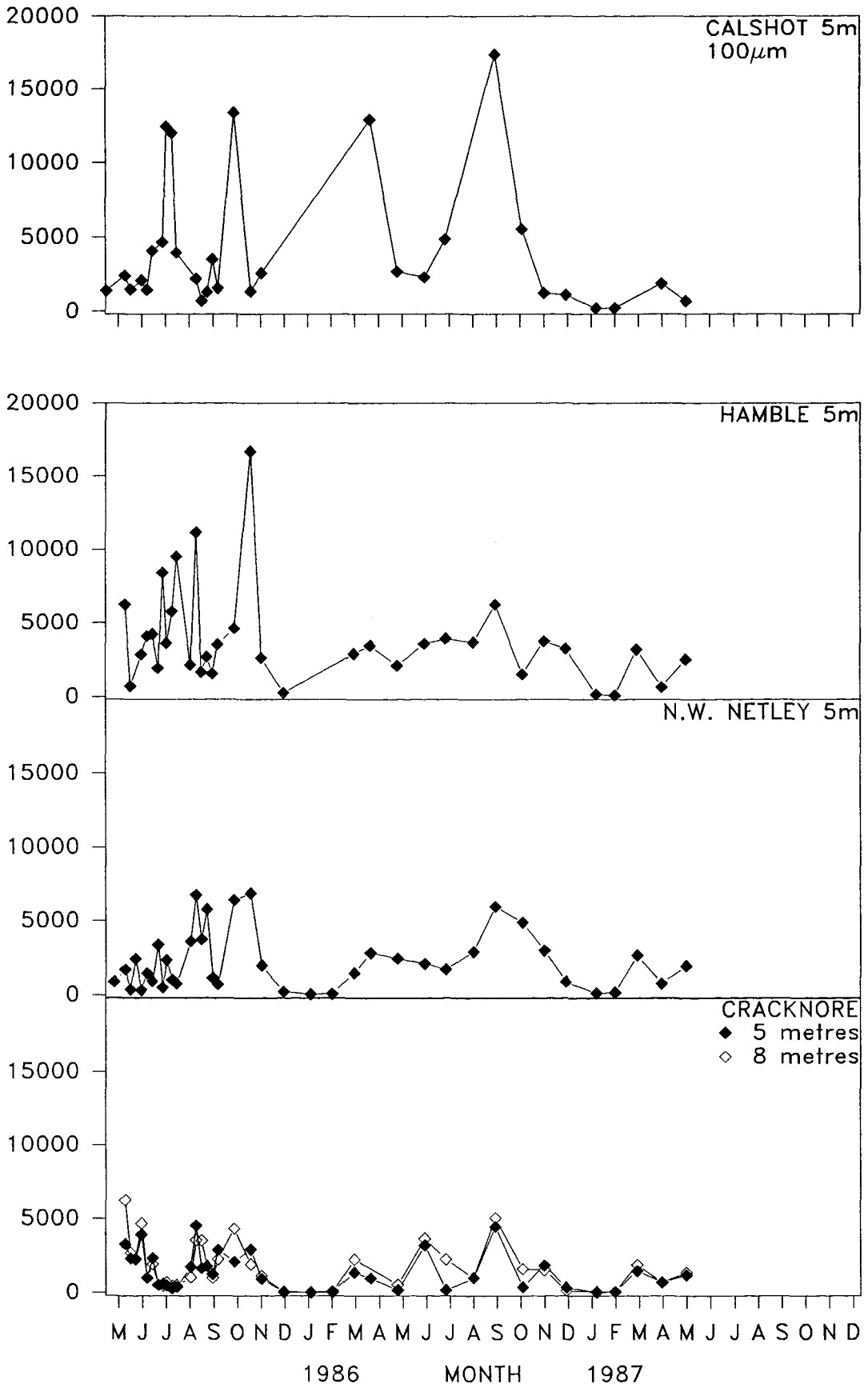


FIGURE 2.4.12 A comparison of the data on cirripede larvae abundance at various sites in Southampton Water. Data from Zinger (1989). All samples taken with a 100μm mesh net.

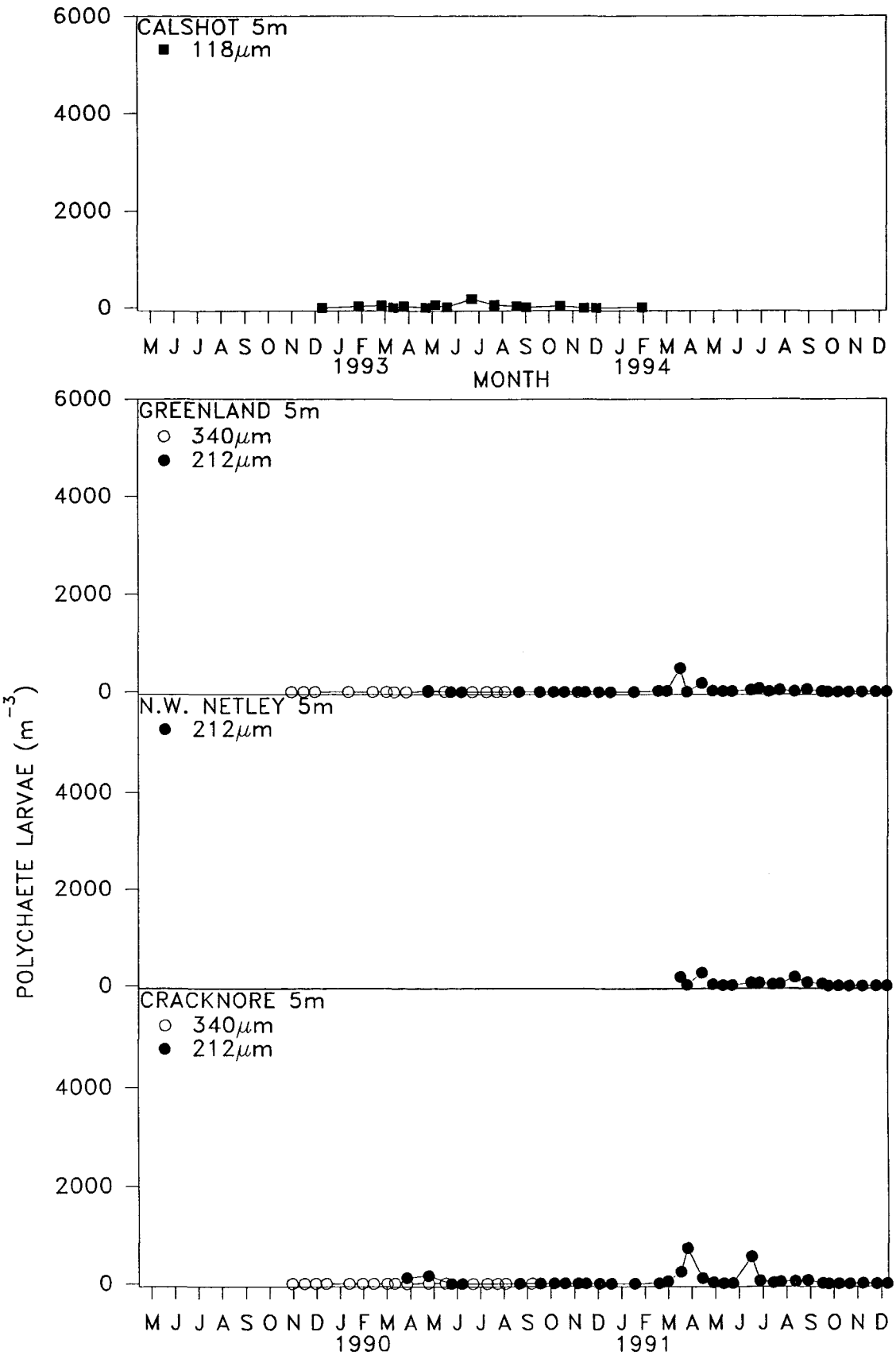


FIGURE 2.4.13 A comparison of the data on polychaete abundance at various sites in Southampton Water. Top graph data collected at Calshot during the present investigation, lower graphs from data given in Lucas (1993).

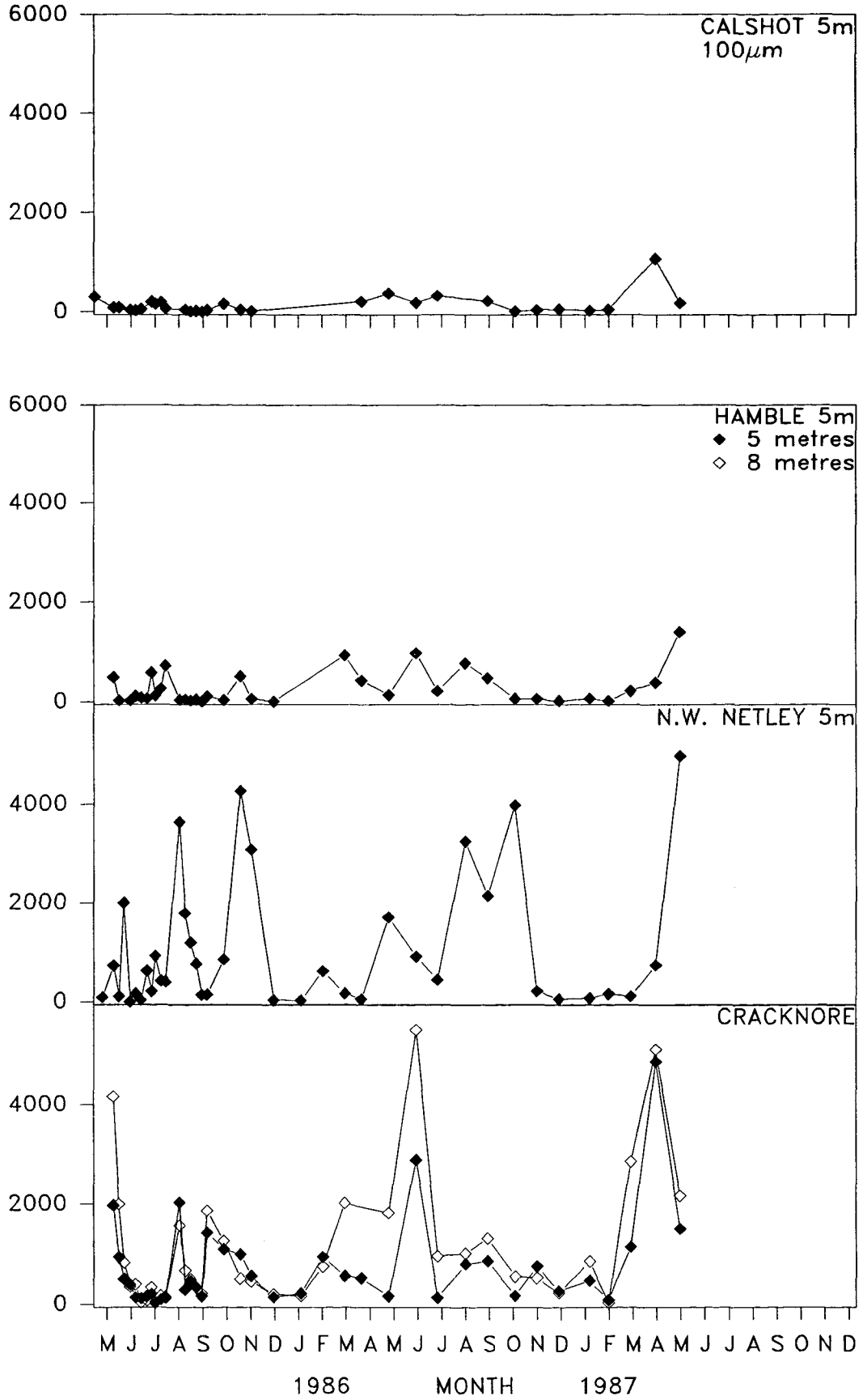


FIGURE 2.4.14 A comparison of the data on polychaete abundance at various sites in Southampton Water. Data from Zinger (1989). All samples taken with a 100μm mesh net.

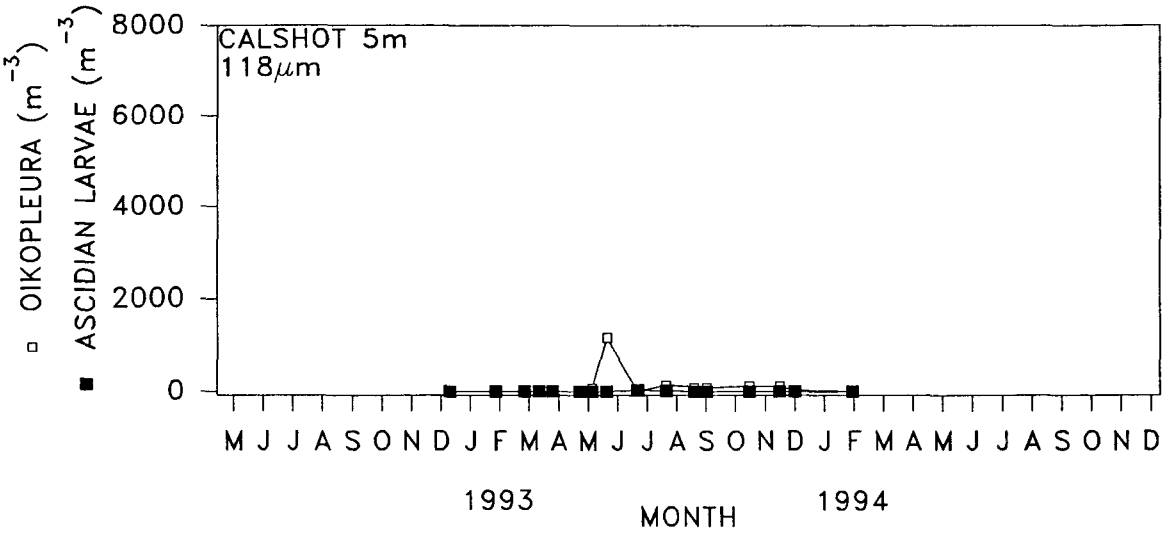


FIGURE 2.4.15 A comparison of the data on ascidian larvae and Oikopleura sp. abunadance at Calshot during the present investigation.

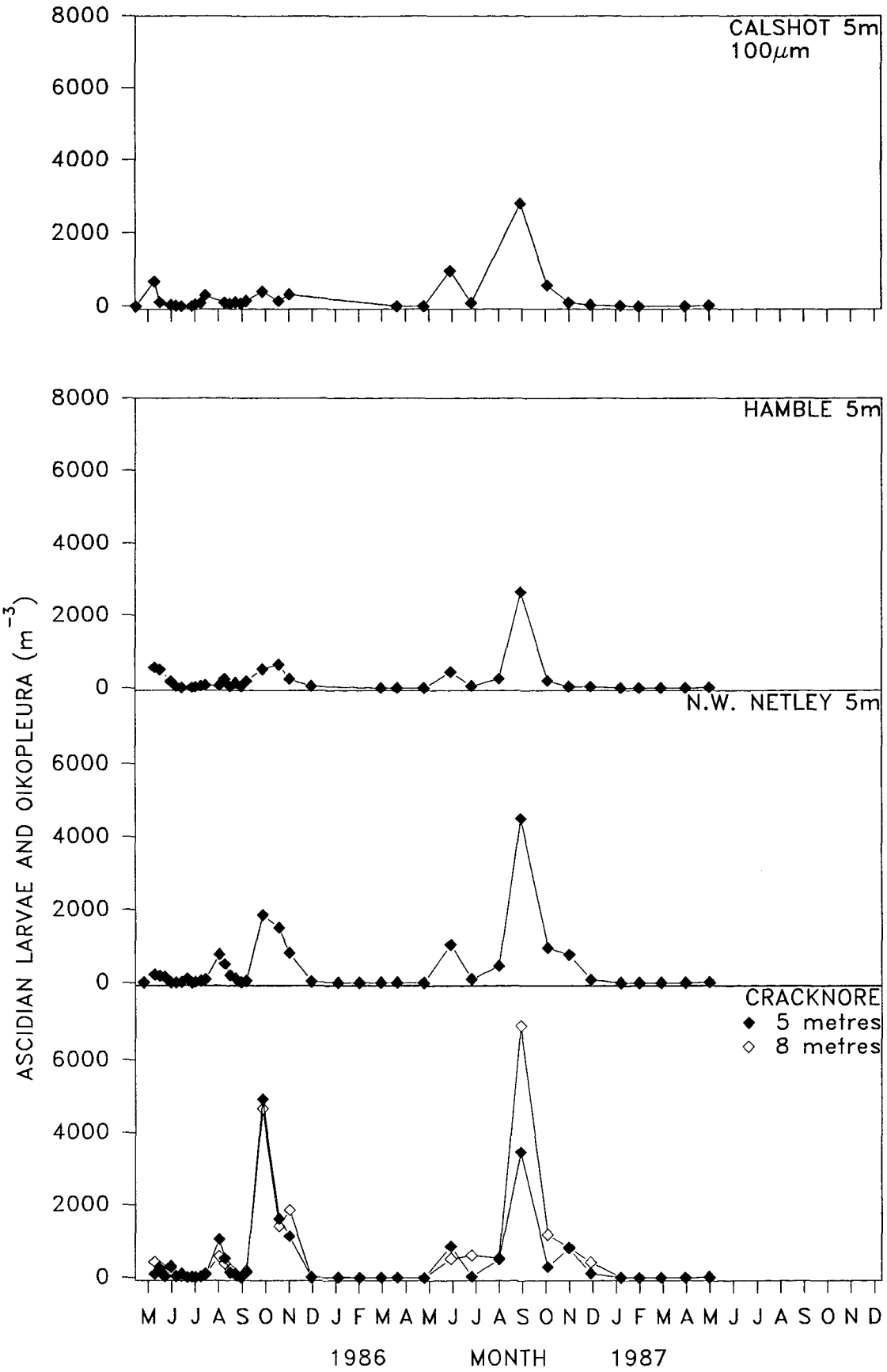


FIGURE 2.4.16 A comparison of the data on ascidian larvae and Oikopleura sp. abundance at various sites in Southampton Water. Data from Zinger (1989). All samples taken with a 100μm mesh net.

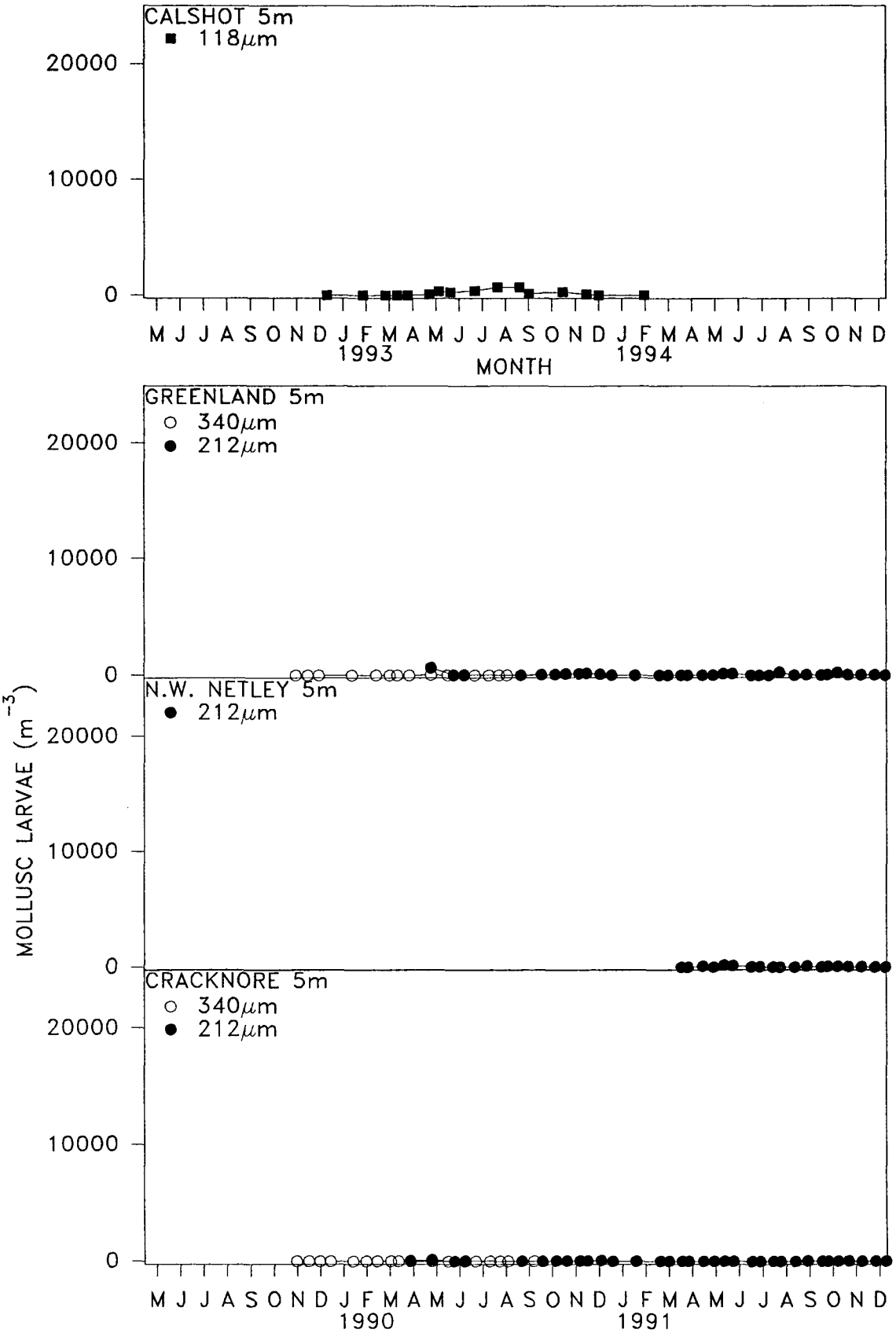


FIGURE 2.4.17 A comparison of the data on mollusc larvae abundance at various sites in Southampton Water. Top graph data collected at Calshot during present investigation, lower graphs from data given in Lucas (1993).

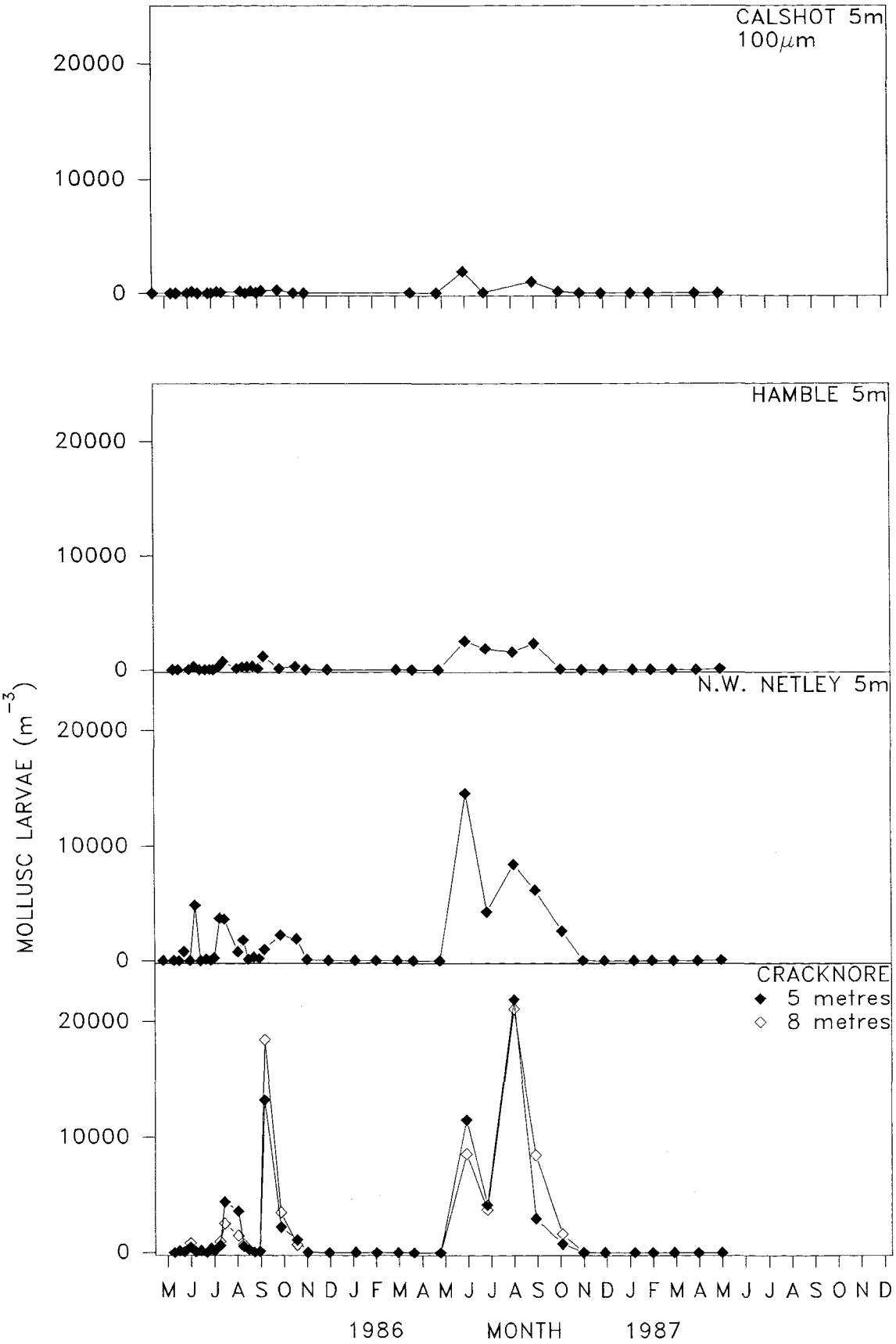


FIGURE 2.4.18 A comparison of the data on mollusc larvae abundance at various sites in Southampton Water. Data from Zinger (1989). All samples taken with a 100μm mesh net.

and Table 2.4.3). Until a longer time series is available it will be difficult to fully appreciate the situation in a 'typical' year in the current study area. Comparisons of density between the data from this study, together with the data collected by Lucas (1993) and also Zinger (1989) have been compiled in an attempted to gain a better understanding of the inter-annual variation, and also along-estuary trends. The 100μm mesh net used by Zinger (1989) was similar to that used in the present study ie. 118μm. The densities of the mesozooplankton groups as recorded by Lucas (1993), are generally much lower than those reported for the same sites, or similar sites, in Zinger (1989). This will predominantly be the result of the use of larger mesh sizes by Lucas (1993) which was 212μm. Many groups appear to have been greatly under sampled by Lucas (1993), including polychaetes, mollusc larvae, harpacticoids and cirripedes. Although calanoid copepod numbers have also been under sampled, after appropriate conversions to allow for biomass estimation it would appear that biomass may not be dramatically underestimated for this group given the values compiled into Table 2.4.3. The degree to which a larger mesh will under sample any of these groups will probably not be a simple proportion, as it will be controlled by the degree of avoidance on any given date, clogging, and the size of the animals themselves, which will also of course change through the year.

Figure 2.4.7 and 2.4.8 give calanoid copepod abundance estimates over several years, and at various sites. Clear differences in the timing of calanoid abundance increases can be seen, and the relative abundances achieved also appear to vary dramatically inter-annually. Calanoids in 1993 were found to reach a maximum of 2,155 in August. This is remarkably small in comparison to the peaks in August-September at 12,646 and 9,352 ind. m^{-3}, in 1985 and 1986 recorded by Zinger (1989). The data of Zinger (1989) also shows there to be an increase in abundance with distance into the estuary. Apart from one very high abundance peak of 69,152 ind. m^{-3} during the winter of 1985 at N.W.Netley, the abundances at N.W.Netley and Cracknore are very similar.

High densities of calanoid copepods were found by Zinger (1989) during the winter, this period being associated with low chlorophyll a, and when live algal biomass and primary production are typically at their lowest during the annual cycle (see Figure 2.4.19). These peaks in calanoid copepod abundance which are also in evidence in the 212μm mesh net samples of Lucas (1993) are typically *Acartia discaudata* (*personal observation*), although presumably at the upper estuary sites this period is also when *Acartia tonsa* may be most abundant. Unfortunately no data were collected on the diet in the present investigation, however, there is a report in the study of Lucas (1993) that the guts of copepods collected during the winter blooms consist predominantly of sedimentary particles. Presumably living organic material associated with these

sedimentary particles and dead particulate organic matter may both be particularly important. Concentrations of suspended particulate material has previously been cited as a possible cause of reduced diversity of zooplankton. Kimmerer and McKinnon (1985) believed that lower diversity in Westernport Bay, Australia, in comparison to the adjacent Port Phillip could be due to the suspended detritus and sediment. Detrital material is believed to be of poor feeding quality for copepods (Heinle *et al.*, 1977), and is unsuitable for the continued survival of some groups (Richman and Dodson, 1983).

Mesozooplankton abundance:

Maximum *Euterpina acutifrons* densities found at Calshot in 1993 were during October, when they reached 2,524 ind. m^{-3}, although densities exceeded 1,000 ind. m^{-3} from July to October. Total harpacticoid abundance patterns at Calshot in 1993 reflected changes in *E.acutifrons* density, this single species being greatly dominant, with maximum harpacticoid densities between July and October, when they ranged between 1,587 and 2,544 ind. m^{-3}. Zinger (1987) also found that harpacticoids were very much restricted to the months of August to November-December. Maximum densities at Calshot were recorded as 2,468 ind. m^{-3} in 1985 and 2,497 ind. m^{-3} in 1986, both of these values being similar to the densities in 1993. Densities of harpacticoids appeared to be greatest at Hamble, declining in a landward direction from this site, with lowest numbers at Cracknore. When the distribution of harpacticoids sampled with the 100 and 118μm mesh nets are compared with the distribution of calanoids along the length of the estuary (see Figures 2.4.8 and 2.4.10), there would appear to be clear similarities in seasonal patterns of these two groups. Harpacticoids increase dramatically after August, and reach densities typically greater than 2,000 to 4,000 ind. m^{-3} throughout the main body of the estuary. Calanoid copepods increase after August reaching densities typically greater than 1,500 ind. m^{-3} at the higher sites. Comparisons with other regions are possible, Roper *et al.* (1987) for example found that densities of *Euterpina acutifrons* in the Avon-Heathcote estuary reached a maximum of 1,609 ind.m^{-3}. Given that harpacticoids may migrate into the water column during darkness, and that this may be very pronounced (Peters, 1968), then the densities estimated in the present investigation may greatly underestimate the densities which are achieved at times. If this group also feed when in the water column, then they may also have an important impact upon their prey species.

Cirripede larvae in the present study at Calshot in 1993 reached a maximum of 1,242 ind. m^{-3} in late June, although they were present with numbers typically above 100 ind. m^{-3} throughout most of the year. The data of Zinger (1989) is in marked contrast to that in the present study (see Figure 2.4.12). Where number at Calshot reach 13,399 ind. m^{-3} in 1985 and

17,384 ind. m^{-3} in 1986. Densities appeared to decline into the estuary, with lowest numbers at Cracknore, the site where maximal inputs are likely, given the suitable substrates for adult attachment in this area, ie. hard dock walls. The densities found in Southampton Water may also be compared to other areas. Ryan *et al.* (1987) in Killary Harbour found cirripede abundance to reach 7,197 ind. m^{-3} in April, after a dramatic increase in late May. Roper *et al.* (1983) found that in the Avon-Heathcote estuary, New Zealand, that cirripede nauplii reached a maximum density of 212 ind. m^{-3}, while cyprids reached 960 ind. m^{-3}.

Polychaetes larvae reached a maximum density in 1993 of 189 ind. m^{-3} at Calshot in late June (see Figure 2.4.13). They were found to be present in every sample during the 14 month abundance investigation. Zinger (1989) found similar densities at Calshot, with numbers rarely increasing above 200 ind. m^{-3}. Peaks were very sporadic for this group, probably because of multiple release by single species and also the release by different species at different times in the year. Although densities at Hamble were broadly similar to those found at Calshot, densities at Cracknore and N.W.Netley were much greater, with peak densities exceeding 4,000 ind. m^{-3} at these two sites in 1986-1987 (see Figure 2.4.14). Ryan *et al.* (1987) found that maximum polychaete densities were 7,639 ind. m^{-3} in early June, in Killary Harbour. Roper *et al.* (1983) found polychaete larvae to reach 1,283 ind. m^{-3} in the Avon-Heathcote estuary, New Zealand.

Ascidian larvae in 1993 were found to reach a maximum of 30 ind. m^{-3} at Calshot in June. In Killary Harbour, that maximum abundances were found during September and October, when they reached 37 ind. m^{-3} (Ryan *et al.*, 1987). While Roper *et al.* (1987) recorded maximum densities of only 5 ind. m^{-3}. *Oikopleura* sp. were found to reach densities as high as 1,172 ind. m^{-3} at Calshot in 1993, with a second peak after this May maximum during November at 113 ind. m^{-3} (see Figure 2.4.15). A seasonal study of *Oikopleura dioica* in a eutrophic temperate inlet in the Inland Sea of Japan (Uye and Ichino, 1995) revealed maximum recorded abundances of 53,200 ind. m^{-3}, during July, when temperature were 25°C. Minimum abundances were found in February to April (mean abundance 978 ind. m^{-3}) and August to September (mean abundance 1,440 ind. m^{-3}). The absolute smallest density was recorded in February, when numbers were 88 ind. m^{-3}. At Calshot numbers of *Oikopleura* sp. were greatest during May, when they reached 1,172 ind. m^{-3}, at this point temperatures being 13.0°C. Individuals were absent during the winter months of January to March, and present from April to November-December. Acuna *et al.* (1995) found that appendicularians were present off Plymouth all year around, but total abundances never exceed ~400 ind. m^{-3}. There have been several studies on *Oikopleura* in the North Sea (see review in Paffenhöfer, 1976b). Hansen and Anderson (1962) found a maximum of 3,500 ind. m^{-3}, during August at Bloden Ground.

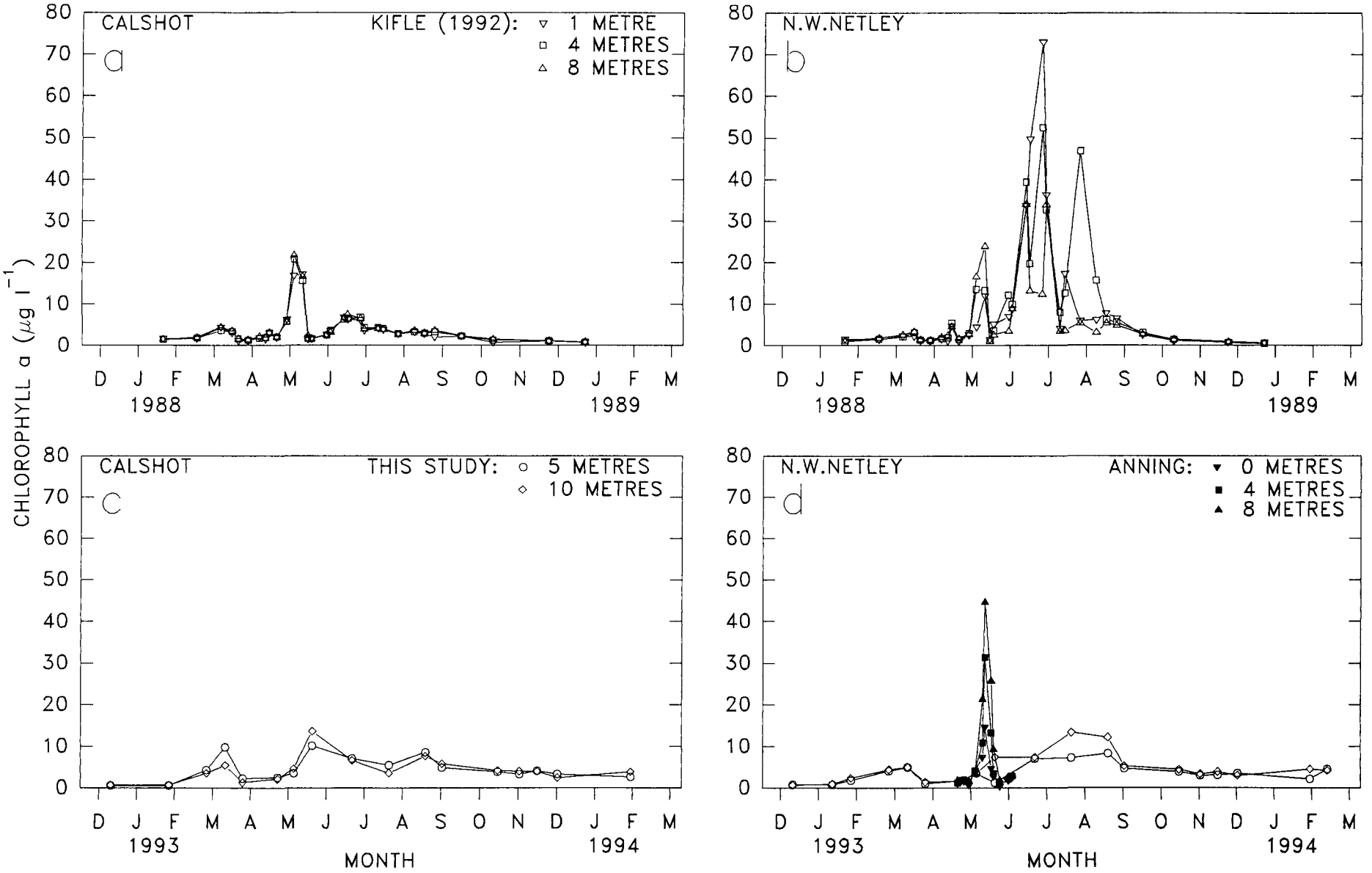


FIGURE 2.4.19 A comparison of the concentrations of Chlorophyll a at Calshot and N.W.Netley sites for 1988 by Kifle, 1992 (a–b) with that produced in the present investigation, 1992–1994 (c–d). High resolution sampling undertaken by T.Anning at N.W.Netley during 1993 also shown.

On the east coast of England, Cushing and Vucetic (1963) recorded a low in March of 1.0-1.5 ind. m^{-3}, to 21-63 ind. m^{-3} in May. In the southern Bight, Wyatt (1971) found more than 500 ind. m^{-3} at the end of February. Eriksson (1973b) found appendicularian abundance near the coast of Sweden reached a maximum in July, at 301 ind. m^{-3}. In the Southern North Sea (nr. Sylt), Paffenhöfer (1976b) found that *O.diocia* abundance was greatest in June-July, when numbers reached a maximum of ~8,500 ind. m^{-3}. Ryan *et al.* (1986) found *O.dioica* in Killary Harbour throughout the year, with numbers increasing in February, March and April, subsequently declining in May, before rising to a peak in June of 3,054 ind. m^{-3}. Roper *et al.* (1983) found that *O.dioica* occurred at maximal densities of 548 ind. m^{-3} in the Avon-Heathcote estuary, New Zealand, with mean densities increasing as one travelled towards the more saline mouth. Unfortunately, Zinger (1989) grouped ascidian larvae and *Oikopleura* sp. together the density estimates, comparisons are somewhat difficult therefore. However, densities of this group increased into the estuary, and there were clear differences between 1985 and 1986 in the abundances achieved (see Figure 2.4.16), and both were much greater than the present study.

Bivalve larvae reached a maximum abundance of 313 ind. m^{-3} during July at Calshot in 1993, with lowest numbers in winter and spring. Raymont and Carrie (1964) found that the bivalves sampled at Marchwood were dominated by *Mytilus edulis*. Unfortunately in the present investigation no attempt was made to identify the larvae further. It is known however, that there have been dramatic changes in the composition of the benthic fauna since the study of Raymont and Carrie in the 1950's (M.Sheader, *per. comm.*). Ryan *et al.* (1986) found that in Killary Harbour, bivalve numbers reached their maximum in April, and a greater one in August at 31,388 ind. m^{-3}. While Roper *et al.* (1987) found in the Avon-Heathcote estuary, New Zealand, maximum bivalve larvae densities of 402 ind. m^{-3}, and recorded that gastropod veligers reached densities of 1,010 ind. m^{-3}. As Zinger (1989) described a mollusc group, then gastropod veligers and bivalve larvae have been combined to allow comparisons between studies (see Figures 2.4.17 and 2.4.18). At Calshot in 1993 the total gastropod abundance was reached in July at 724 ind. m^{-3}, whereas in 1985 and 1986 densities reached 255 ind. m^{-3} in 1985 and 1,887 ind. m^{-3} in 1986. Numbers appeared to increase into the estuary with maximum annual densities exceeding 13,000 ind. m^{-3} in both 1985 and 1986.

One of the striking features of the mesozooplankton within Southampton Water, is that there is a strong trend of increased abundance as one travels from the mouth of the estuary at Calshot to the upper reaches at Cracknore. This gradient of increasing meroplankton abundance may be the result of higher benthic faunal abundances in the higher reaches, in part due to the abundance of harbour walls, necessary for the attachment of some forms with meroplankton

larvae.

From the results of the present study, throughout much of the year there would appear to be no strong trends in chlorophyll a concentration with position in the estuary, although there are isolated periods at which the up estuary sites have much greater concentrations of chlorophyll a, eg. in July 1993 (see Figure 2.3.13). The chlorophyll a concentrations measured in the present study may therefore give a false picture of algal biomass and production, given that blooms may have been missed as a result of sampling on spring tides. Indeed, the data of Kifle (1992) does suggest much greater concentrations of chlorophyll a at the inner site of N.W.Netley than at Calshot. This is exemplified in Figure 2.4.19, where comparisons between chlorophyll a at Calshot and N.W.Netley are made in the present investigation and in 1988 (from Kifle, 1992). Indeed Bryan (1979) found that primary production increased up the estuary, with a maximum just above the confluence of the Test and Itchen. The gradient in mesozooplankton numbers may therefore also be related to a primary production gradient.

During the period of the present investigation, chlorophyll a concentrations were measured at the N.W.Netley site by T.Anning (data *pers. comm.*). These samples were collected at the surface, 4 metres and 8 metres depths, over the period 21/04/93 to 04/06/93. Since all samples for the 14 month investigation were taken on or close to spring high tides, all the pigment concentration data points produced are also from these periods. Anning's sampling points were made regularly (average period 4.4 days) over a total program period of 44 days, samples being collected over the whole of a spring-neap cycle. The reason for making comparisons of the data produced by the two investigations are clear. Chlorophyll a concentrations (which reflect the algal biomass, and are strongly correlated with primary production rates) may be reduced during the periods of spring tides compared with the periods of neap tides. The reasons for this is the higher flushing rates which will accompany the spring tides and the lower flushing rates which will accompany the neap tides. The gradient in epi-benthic and holoplankton may therefore be related to the abundance of algae, and also detritus and ciliates, which increase in an up estuary direction (Leakey, 1990; Kifle, 1992).

The inter-annual variability is remarkable for many species, although some are relatively stable eg. harpacticoids. Although there are no estimates of the variability in biomass of the different planktonic groups. Other workers have also reported great variation in the densities achieved by copepods and other groups between years. Taylor (1984) reported that copepod densities were 58 times greater in 1981 than 1980 in the Forth estuary, U.K. Plankton records since 1948 also show much annual variation in the southern North sea (Gieskes and Kraay,

1977). While Fransz (1981) reported that inter-annual variation in zooplankton biomass and composition in the western Wadden Sea is 'irregular and probably based on shifts in the coincidence of the zooplankton development and the phytoplankton spring bloom (Fransz, 1976), and in the phytoplankton species composition of the spring bloom. Both are influenced by unknown stochastic factors.' Given the dependence of some species upon recruitment from dormant eggs deposited in previous years, changes in sedimentation, re-suspension and dredging may also have important effects upon recruitment.

FUTURE IMPROVEMENTS

Regressions of length to weight should to be completed for the calanoid copepod species within Southampton Water. The use of length:weight equations from other regions may result in some discrepancy in biomass estimates, given the apparent variation. Such inter-study application of these equations are remarkably common, but are far from ideal. The production of such equations may also need to take in to account the fact that length-weight relationships can also change with season. Equations are also needed for other mesozooplankton, in addition to length measurement through the year.

Calanoid copepods were examined most intensively in this investigation. It is clear however, that other mesozooplankton including benthic meroplankton, and harpacticoids are quantitatively important food-web participants, both in terms of their grazing, and also their production. Given their dominance during some periods, their biomass and growth needs to be examined with some urgency. As all sampling of zooplankton in Southampton Water has occurred during daylight hours, and yet holo-planktonic inlet copepods may be more homogenously distributed during night-time (Ueda, 1987), and harpacticoids may migrate into the water column in darkness (Peters, 1968). Effort needs to be invested in determining the errors associated with daytime sampling, such errors may prove to be great.

As a result of time constraints it was not possible to have extensive estuarine wide coverage. Currently, meroplanktonic investigation is being undertaken at sites higher in the estuary. The results of this work may help in examination of spatial variation in biomass and production. Investigations of algal concentrations with respect to the possible spring neap cycles in bloom formation need investigation. Such blooms, which may be missed through coarse resolution sampling may provide food. The diet of copepods within the estuary also needs further investigation in this area, particularly during copepod blooms. Feeding by copepods during the winter periods needs particular attention given the size of the calanoid populations then.

CHAPTER 3

MEASURING *IN SITU* GROWTH RATES OF THE DOMINANT CALANOID COPEPOD SPECIES.

3.1 INTRODUCTION

When situations permit, cohort distinction and generation time methods are generally the most easy to apply in the estimation of growth, development and production rates of natural populations *in situ*. Cohorts or generation times have been identified, and used for growth and production estimation in many coastal locations (eg. McLaren, 1969, 1978; Landry, 1978; Ueda, 1978; McLaren and Corkett, 1981; Uye, 1982a; Liang and Uye, 1996; Liang *et al.*, 1996). Indeed, studies which utilize the identification of natural population parameters may be preferable to those where the natural population must be artificially manipulated. However, prolonged recruitment, a short generation time, variable mortality and growth rates may make the discernment of cohorts doubtful or impossible. Development and cohort methods should also not be used when there are age-dependent movements or mortality of the animals under study (Rigler and Cooley, 1974), and there is, typically, little or no information about such processes. Additionally, cohorts or generations may be unrecognizable or inaccurate in estuarine areas where populations are subject to great spatial movements as a result of flushing and tidal effects and as a result of patchiness. Most annual data sets are also too poorly resolved in time to allow any form of cohort identification, or accurate stage specific development/growth rate estimates. Many workers have relied upon some form of experimental incubation method to estimate growth rates when cohort or population change methods are inapplicable. Such methods do involve manipulation of a population, which may be a disadvantage, but they also have an advantage in allowing much greater spatial and temporal resolution of growth and production, and do not require some of the assumptions made in *in situ* work.

The dependence of growth on food quality and quantity, and other growth influencing factors such as suspended sediment and suspended particulate concentrations (Burkill and Kendall, 1982; Irigoien and Castel, 1995), and predator behaviour and prey patchiness, requires that growth rates should be determined in conditions as close as possible to those in the field if they are to be applied to natural populations (eg. Burkill and Kendall, 1982; Kimmerer, 1983; Kimmerer and McKinnon, 1987; Peterson *et al.*, 1991; Irigoien and Castel, 1995; Peitsch, 1995;

Peterson and Hutchings, 1995). Often, copepod growth and development rate studies have been examined in the laboratory under food saturated conditions, the results being directly applied to field biomass measures to estimate *in situ* production (Heinle, 1966; and extensive Soviet material in Winberg, 1971; Roff *et al.*, 1988). Although generation times of field populations of copepods may at times be very similar to the maximum food saturated laboratory rates (see Huntley and Lopez, 1992), this does not necessarily infer that growth in nature is maximal. There is evidence that development rates and growth are very often sub-optimal in nature, even under conditions of apparently high algal abundance (eg. Burkill and Kendall, 1982). Differences observed between laboratory development rate studies and *in situ* rates often linked to differences in the concentrations of food, or the feeding environment (Landry, 1978b; Burkill and Kendall, 1982; Kimmerer and McKinnon, 1987; Irigoien and Castel, 1995). Saturating concentrations, commonly used in the laboratory, are typically much greater than those found in nature using 'traditional' sampling techniques (eg. Harris and Paffenhöfer, 1976a). In laboratory culture, food has also often been supplied in the form of single algal species (eg. Paffenhöfer, 1976a), while natural diets may be very varied (see Turner, 1984, 1985, 1986a, 1986b, 1987, 1991), and food quality can affect the growth of copepods (McLaren,1965; McLaren and Corkett, 1981; Landry, 1975a, 1975b; Paffenhöfer, 1976a; Vidal, 1980b; Burkill and Kendall, 1982),. Attempts have increasingly been made therefore, to reproduce environmental conditions of food quality as well as quantity.

Many problems may be overcome in *ex situ* work by keeping recently collected, field copepods in freshly collected natural water, the water may be changed frequently, or the animals may be kept in relatively large volumes for short periods of time, to prevent change in the food concentrations (eg. Jerling and Wooldridge, 1991; Peterson *et al.*, 1991; Hay, 1995; Peterson and Hutchings, 1995). Flow-through systems (eg. Burkill and Kendall, 1982; Peterson and Hutchings, 1995), and containers with mesh which allow exchange of the feeding environment have also been developed (eg. Newbury and Bartholomew, 1976; Kimmerer, 1983; Kimmerer and McKinnon, 1987). Models used to predict copepod growth have also been established and applied to natural populations, allowing prediction of *in situ* growth rates and production from a minimum of more easily measurable parameters (see Chapter 4). In this investigation a field incubation technique was chosen to determine *in situ* growth rates of the dominant copepods in Southampton Water. It was adapted from that described by Kimmerer and McKinnon (1987), after a method proposed by Tranter (1976), and involves the containerization and re-introduction into the environment of artificially produced cohorts of natural assemblages.

3.2 METHOD

Field growth rate studies were conducted at fortnightly to monthly intervals, when conditions permitted, from August 1994 to May 1995 (see Appendix 3 for details of the timing of sampling events). This allowed the seasonal changes in calanoid copepod growth rates to be examined. The site chosen for zooplankton incubation was Calshot pier, situated on the east side at the mouth of Southampton Water (see Figure 2.2.1 for site location). Previously, attempts had been made to moor samples from mid-channel buoys but these proved unsuccessful.

Zooplankton samples for the growth rate measures were collected using a 160μm mesh net (mouth opening diameter 50cm, length approximately 125cm), with a 3 litre non-filtering cod-end, just off the incubation site. Net towing was conducted at the lowest possible speed, and made to a depth of around 5 metres. Tows were typically undertaken for a duration not exceeding 3 minutes, although in winter months it was necessary for this to be extended to allow adequate numbers to be collected. Once collection was complete, the zooplankton sample was immediately emptied into a large insulated opaque container. This had been half filled prior to the collection of zooplankton with sea water, collected on site, which had been passed through a 45μm nylon mesh net. This procedure minimized thermal and light shock and ensured that the density of copepods was reduced immediately. Overcrowding is known to greatly influence predation and mortality rates, and small temperature changes are recorded as a factor which may stimulate moulting bursts (Miller *et al.*, 1984). All equipment which was brought into contact with the live samples had been washed, then soaked for 24 hours in aquarium sea water, and finally rinsed thoroughly on site using sea water collected on station. Size fractionation was then completed, to produce a zooplankton sample of less than 200μm but greater than 180μm. The procedure used in the size fractionation process was as follows, a 10cm diameter PVC cylinder, which had a 200μm polyester mesh covering its bottom end, was gently lowered into the plankton sample. Water from inside the PVC cylinder was then siphoned out, using a length of plastic tubing (diameter 1.5cm) into a second PVC cylinder, with a 180μm mesh covering its lower end. This second cylinder was kept half submerged in a collected sea water which had been passed through a 45μm mesh. The sample volume transferred to the second cylinder was carefully mixed and partially drained several times to allow most of the organisms and particulates less than the 180μm mesh net to be flushed out. At no point was the mesh in this second cylinder raised above the water surface, as this could lead to damage of the live sample. The size fractioned plankton sample was then siphoned from the cylinder into a bucket, which was part filled with 45μm filtered sea water. A sub-sample was then removed, and an assessment of the density of copepods made on station using a binocular microscope. Sub-samples were then removed by dipping

beakers of appropriate volume from the stirred sampled. The sub-samples were placed into the 3 incubation containers of 2.9 litres volume, which had been part filled with on site collected 45μm filtered seawater. Although filtering may potentially reduce food available and affect the particles encountered, microscope analysis of the >45μm fraction on several occasions revealed no discernible phytoplankton. Furthermore, replicate chlorophyll a and phaeo-pigment analysis of both the <45μm fraction and of unfractionated water samples, showed no significant differences ($P>0.05$) when compared using t-test.

The density of copepods was controlled so that around 20-60 individuals were present in each of the three incubation containers. These containers were then topped with 45μm filtered surface water before the lid with mesh was screwed in place, they were then enclosed in a wide meshed holding bag, and tied closed. The whole apparatus was then weighted with a large lead weight and suspended at a mid-water column depth from the end of Calshot pier, where it would stay submerged over the entire incubation period of either around 24 or 48 hours. 3 sub-samples were also collected from the original zooplankton size fraction, and fixed with 4% formaldehyde, these samples representing time zero. The whole process from the collection of the sample to submersion of containers containing artificial cohorts typically took less than 15 minutes.

After incubation, the moored samples were reclaimed. The contents were stained by adding neutral red to make a solution with a concentration of $1.1 mg.l^{-1}$. Kimmerer and McKinnon (1987) suggest a concentration of $1\text{-}2\mu g.l^{-1}$ was sufficient; however, using laboratory kept copepods this proved not to be the case. Only the much greater concentrations were found to be great enough (the concentration given in Kimmerer and McKinnon (1987) is believed to be a printing error, as in earlier work using a similar method Kimmerer (1980) quotes a value of $1\text{-}2mg.l^{-1}$, again this is similar to the concentration found adequate in this study). After a period of 45 minutes, during which time the stain was taken up by only living individuals, the contents were fixed using 4% formaldehyde. During this entire staining period the incubation containers were kept submerged in large insulated containers filled with on site collected seawater. Prior to the addition of neutral red, 50ml of water was removed from each container and filtered for chlorophyll a and phaeo-pigment analysis. On each sampling occasion (time 0 and time t) measurements of chlorophyll a, phaeo-pigments and suspended particulate matter were also made upon water samples collected from the surface, 5 and 10 metres depth. 6 samples were taken from each depth for the chlorophyll a and phaeo-pigment analysis. 3 were filtered through a 45μm mesh net while 3 were left unfractioned. Chlorophyll a and phaeo-pigments concentrations were measured in the same manner as in the 14 month investigation, however, rather than storing samples in a cool box they were filtered immediately and stored in the freezing compartment on

board. Seston dry weights were estimated upon return to the laboratory, by filtering whole sea water through tared, pre-combusted 4.25-cm GF/C filters. The filters were then dried for 24 hours at 60°C and re-weighed. They were then ashed at 500°C for 4 hours and weighed again.

Time zero samples were sorted on return to the laboratory. Individuals were staged and sexed when possible, and prosome lengths were measured using a calibrated eye-piece graticule (as detailed in Chapter 2). Time t samples were also sorted upon immediate return to the laboratory in the same manner. Copepods which failed to take up the stain were counted but excluded from the calculations, although only very rarely was an individual found with no stain (typically less than 2%). Individual prosome lengths were converted to individual carbon body weights using the equations detailed in Chapter 2, the equations for *A.bifilosa* being used for all *Acartia* copepodite individuals. In one instance (incubation from 19th to the 21st October 1994), none of the individuals appeared to take up the stain, there was no apparent explanation for this, and the sample was therefore discounted from all analysis. Daily weight-specific growth rates were then determined from the slope of a type I least squares regression plotted for the $\log_e$ transformed mean weight versus incubation time (in days) as shown in Figure 3.3.1.

3.3 RESULTS

Acartia spp. were the dominant calanoid copepods in terms of numbers and probably biomass, while other species made up generally a minor component within the incubation samples. When the total number of individuals of a given species was greater than or equal to 15 individuals per incubation container, then growth rates were estimated, when they did not they were not included in the analysis. Figure 3.3.1 demonstrates $\log_e$ mean carbon weights at the beginning and end of each of the incubation experiments, for each of the species for which data are available.

To determine if chlorophyll a changed significantly in the containers during incubation, the initial measures were compared to the final measurements using t-tests. In no instance was there significant change ($P>0.05$) in the concentration. Thus indicating that food was not depleted from initial ambient.

Figure 3.3.2 demonstrates the salinity measurements throughout the sampling program, and Figure 3.3.3 the secchi disk depth readings. Measured surface salinities varied much throughout the year, from greater than $34^{o}/_{oo}$, to less than $25^{o}/_{oo}$. The salinities at 5 and 10 metres where however, much more stable, varying by less than $4^{o}/_{oo}$.

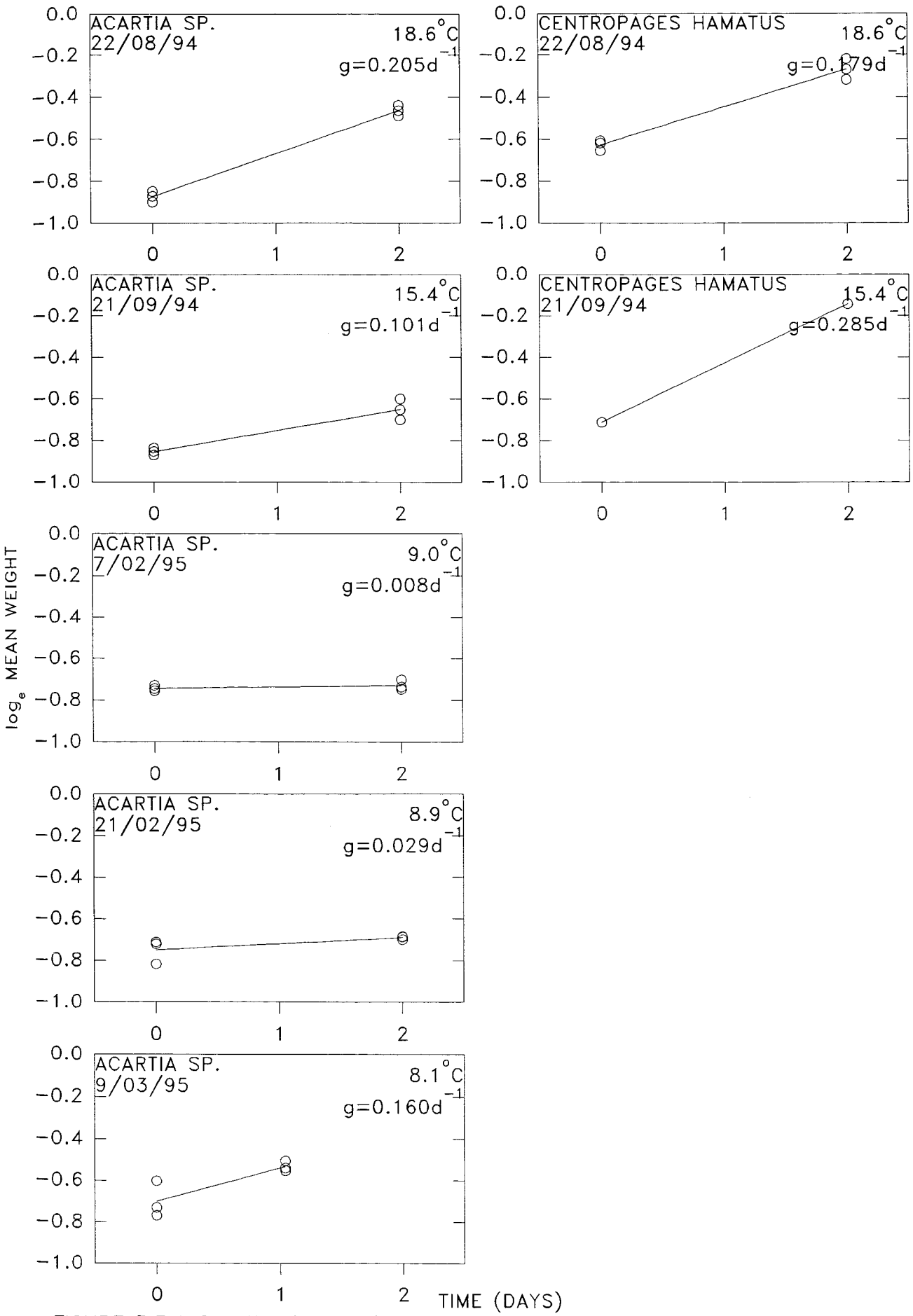


FIGURE 3.3.1 Growth of calanoid copepods during the in situ incubation experiments conducted during 1994–1995. The slope of the linear regression through data points giving weight–specific growth rates (g). Individual data points represent mean weight of copepods in each replicate.

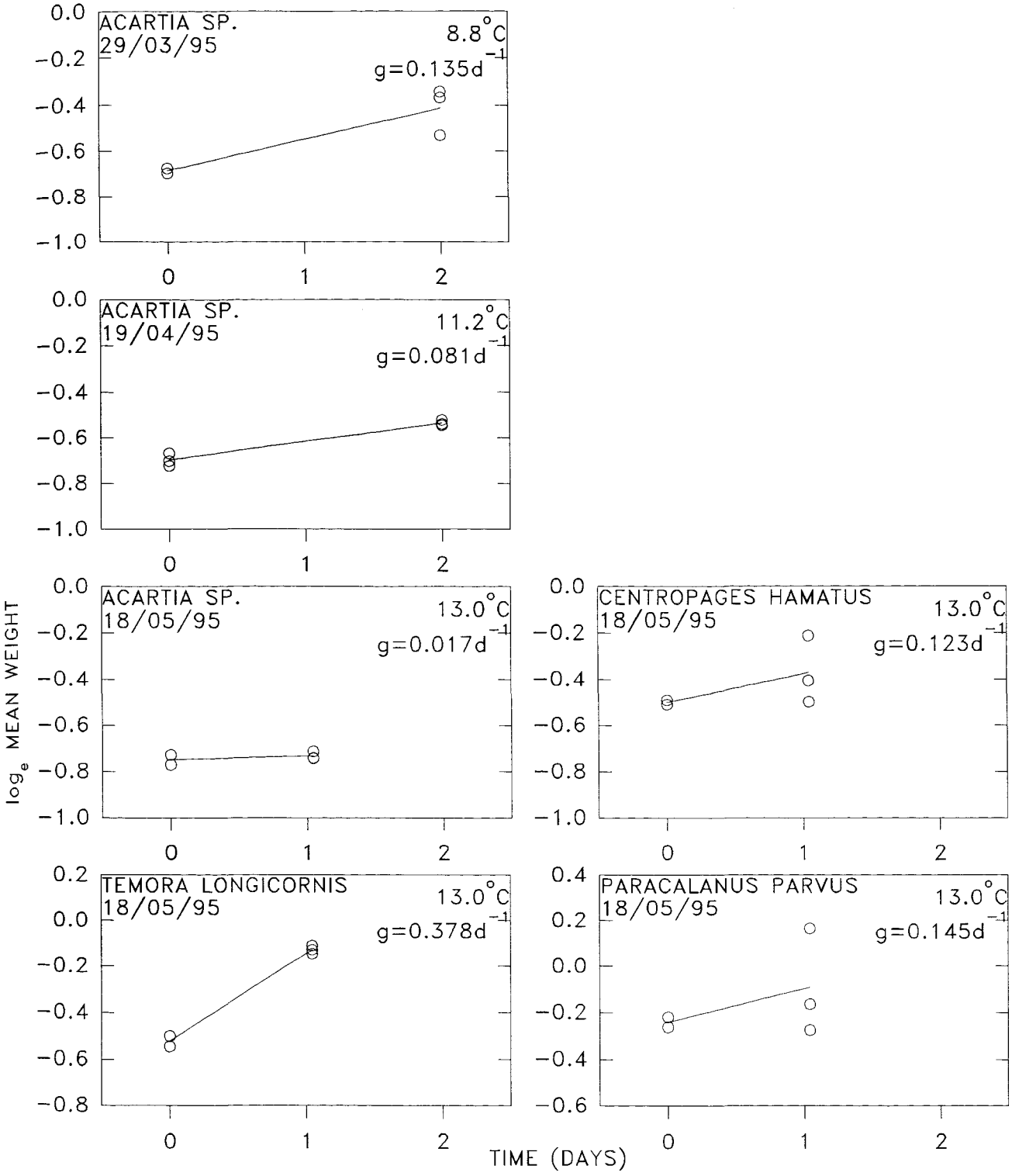


FIGURE 3.3.1 (cont.) Growth of calanoid copepods during the in situ incubation experiments conducted during 1994–1995. (Note Scale Change). The slope of the linear regression through data points giving weight–specific growth rates (g). Individual data points represent mean weight of copepods in each replicate.

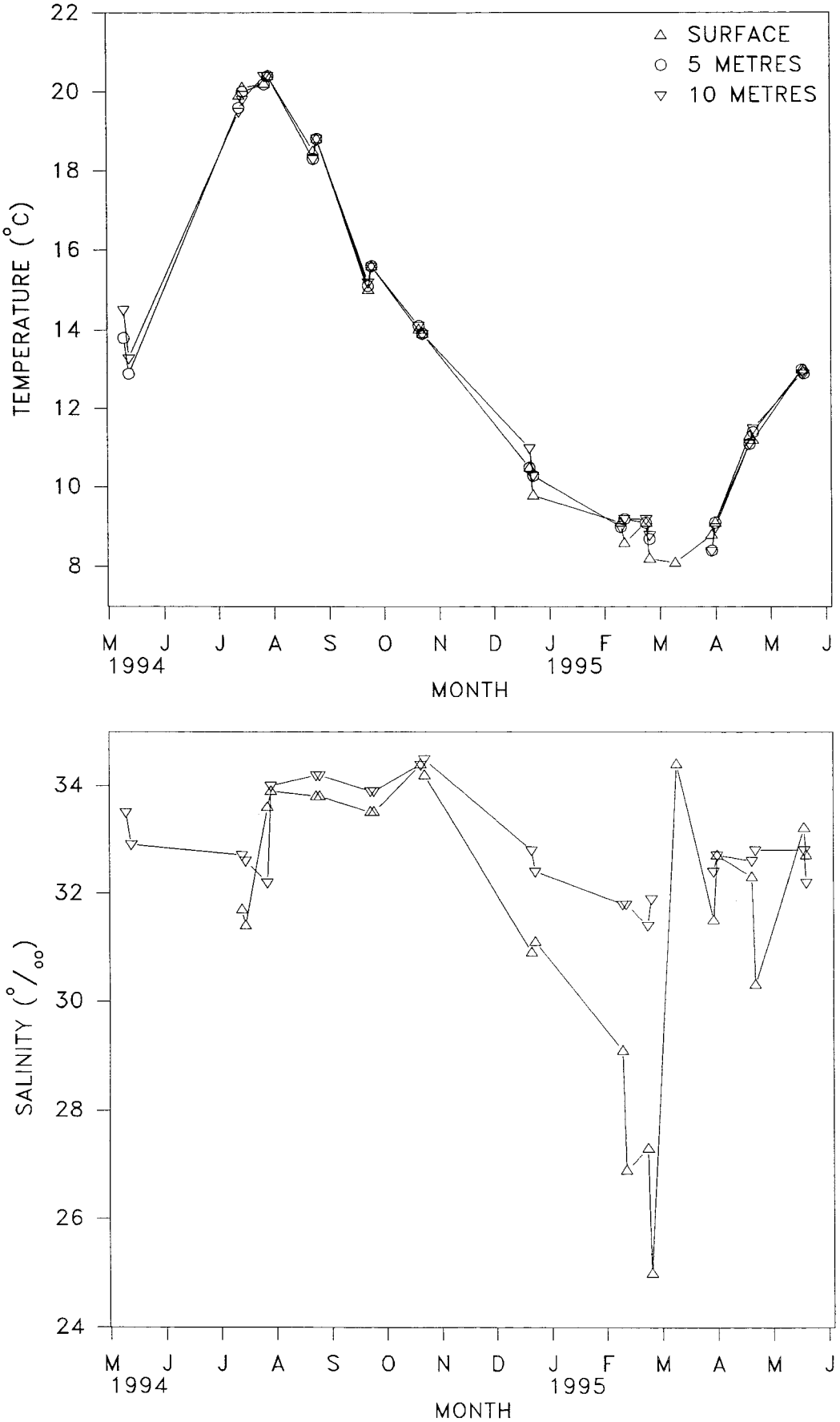


FIGURE 3.3.2 Temperature and salinity off Calshot Pier during the development rate investigation.

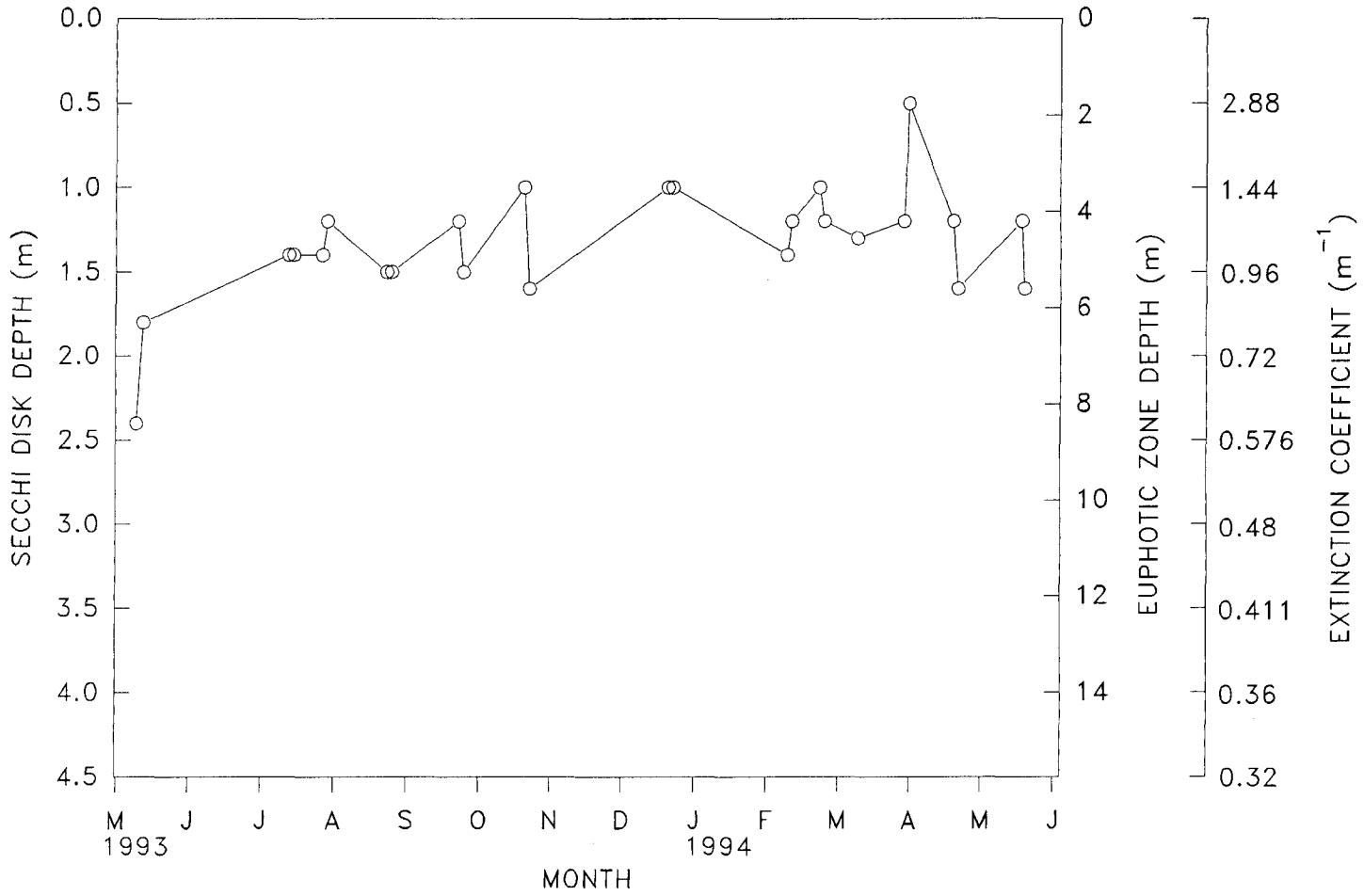


FIGURE 3.3.3 Secchi Disk Depths with associated calculated Euphotic Zone Depths and Extinction Coefficients off Calshot Pier during the development rate investigation.

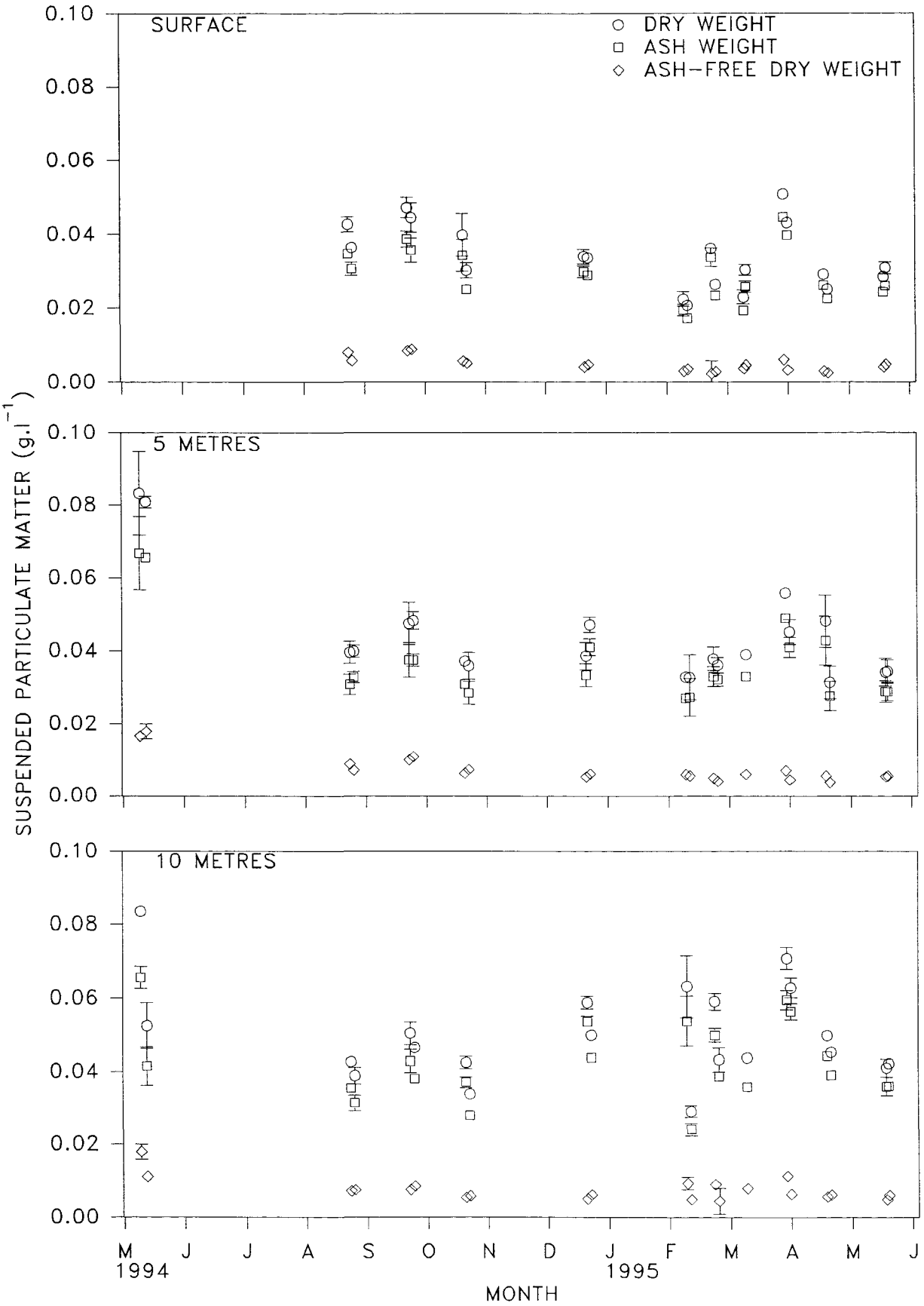


FIGURE 3.3.4 Concentration of suspended particulate matter off Calshot Pier during the development rate investigation. Error bars represent standard deviation of replicate measures.

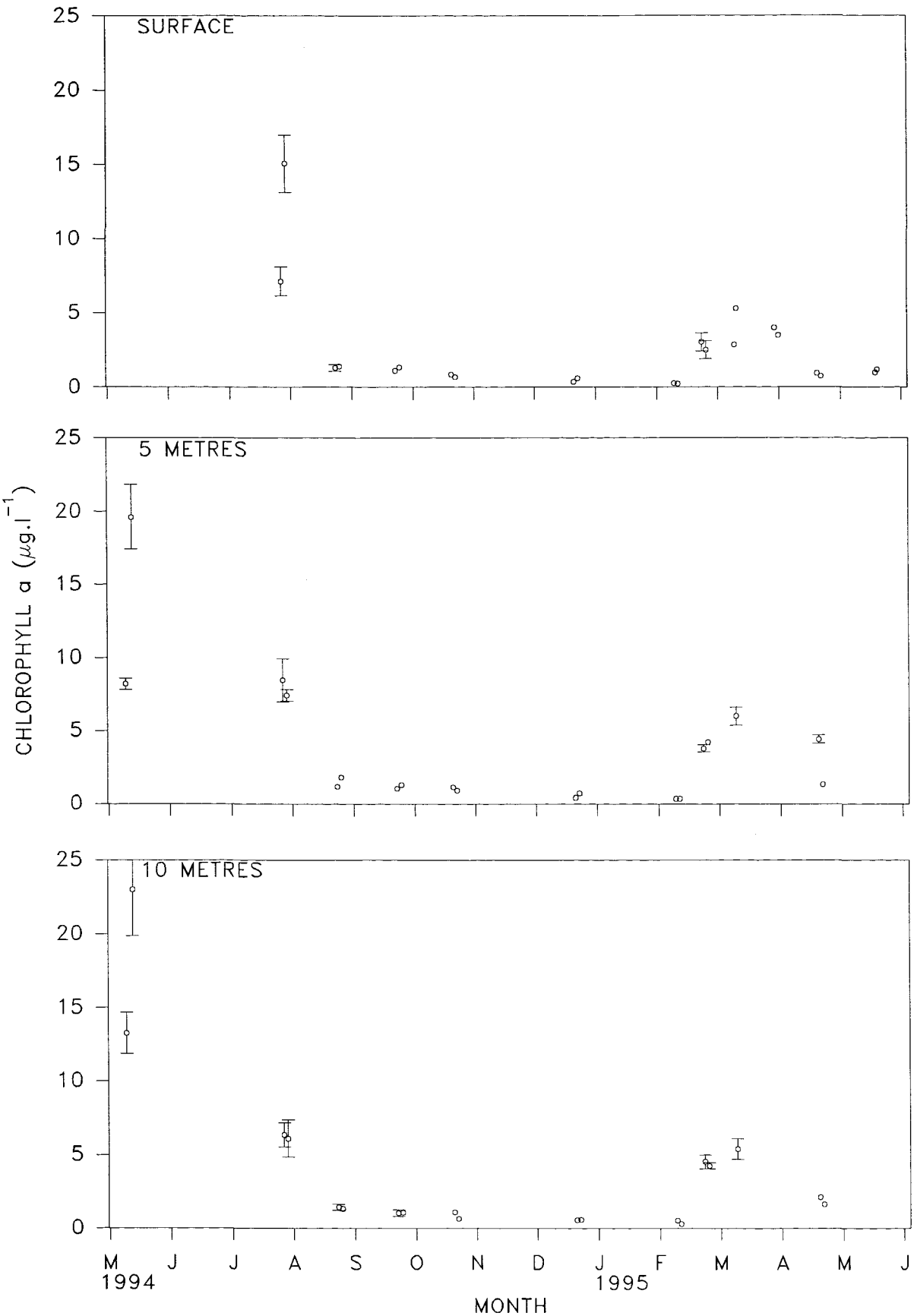


FIGURE 3.3.5 Chlorophyll a concentrations (<45μm) off Calshot Pier during the growth rate study. Error bars represent standard deviation of repicate measures.

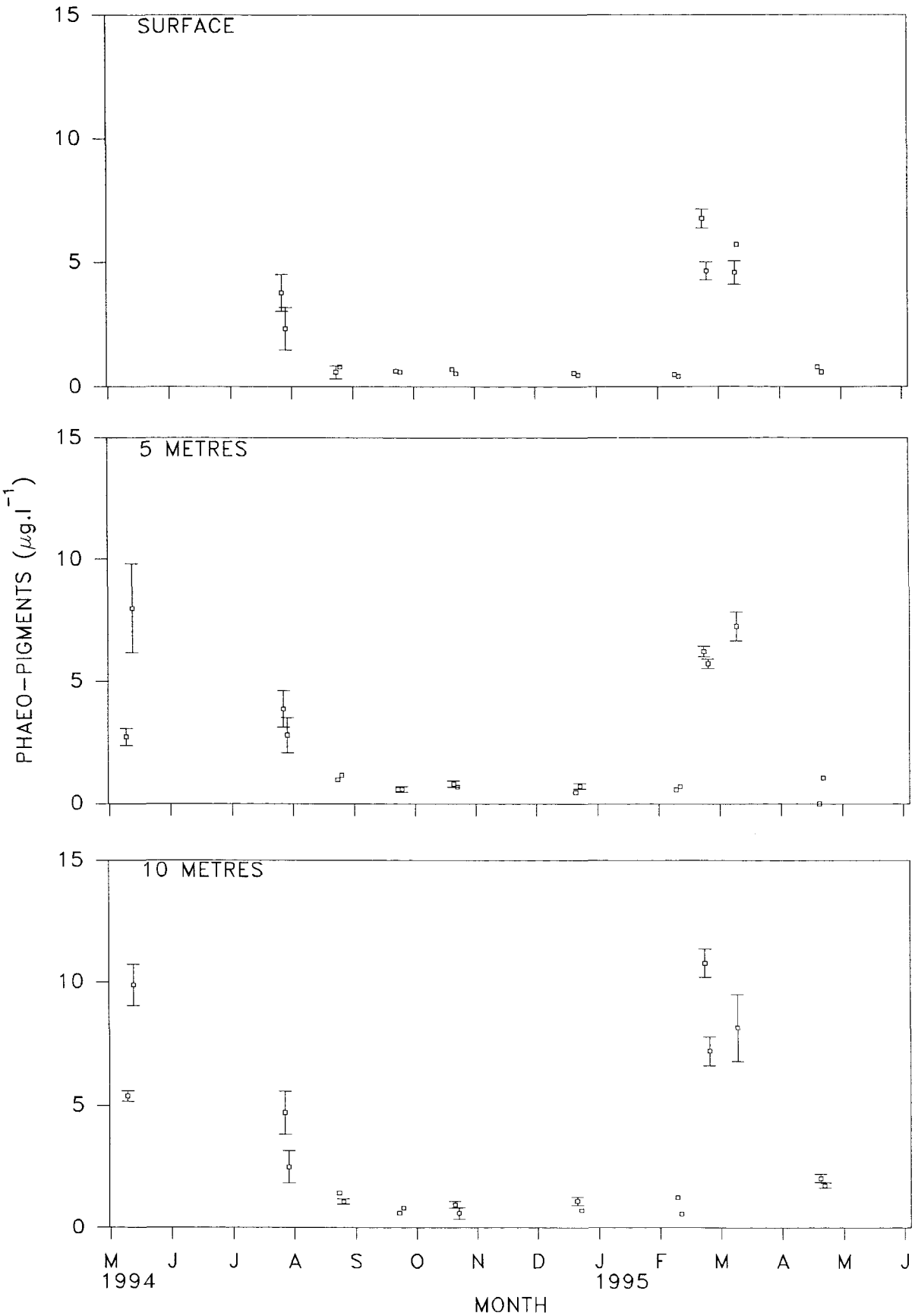


FIGURE 3.3.6 Phaeo-pigment concentrations (<45μm) off Calshot Pier during the growth rate study. Error bars represent standard deviation of replicate measures.

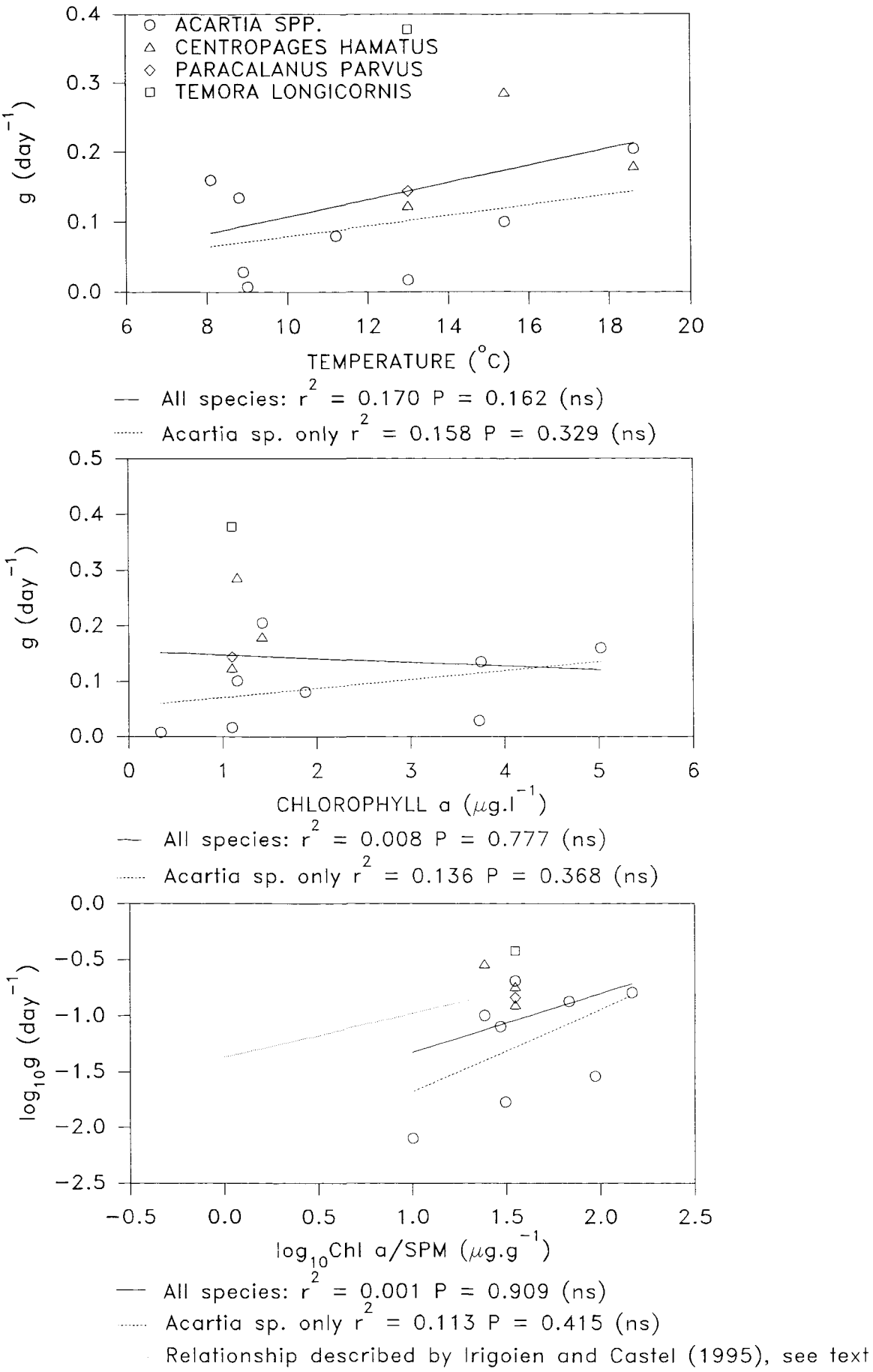


FIGURE 3.3.7 Comparisons of growth rates against temperature, chlorophyll a and Chl a to SPM (DW) ratio. Regressions for all species combined, and Acartia spp. singularly.

Secchi disk depths ranged between 2.4 and 0.5 metres, with no apparent pronounced seasonal pattern at this site. Figure 3.3.4 gives the measurements of suspended particulate matter made on the same days as establishment and retrieval of incubation containers. There were no strong seasonal trends in any of the suspended matter measures. Measures at the start and end of each incubation (ie. typically less than 48 hours apart) of AFDW and DW often varied considerably, although AFDW varied less. Chlorophyll a and phaeo-pigment measurements are given in Figure 3.3.5 and 3.3.6 respectively. There is an apparent seasonal trend, with highest values in March-May to August, and low values through the autumn and winter. Phaeo-pigment concentration trends are also similar to those of chlorophyll, with low values in autumn-winter, and high values in March-May to August. Growth rate estimates for *Acartia* spp. alone and all species combined are regressed against temperature, chlorophyll a, and $\log_{10}$ growth against $\log_{10}$ Chl a/SPM (in DW) in Figure 3.3.7. Growth rate estimates for *Acartia* spp. over the 10 month investigation, varied from a maximum rate of $0.205d^{-1}$ on the 22nd August 1994, to a minimum of $0.008d^{-1}$ on the 7th of February 1995. On a few occasions that numbers were deemed sufficient to estimate growth in other species except *Acartia*. Growth varied dramatically between species during a single individual experimental incubation. For example in May 1995 growth of *Acartia* spp. was $0.017d^{-1}$, while growth of *Temora longicornis* was over 20 times greater at $0.378d^{-1}$. Growth was apparently not significantly related to temperature for either all species (P=0.162) or *Acartia* spp. alone (P=0.329), neither was it related to chlorophyll a for all species (P=0.777) or *Acartia* spp. (P=0.368). The relationship between $\log_{10}$ growth and $\log_{10}$ Chl a/SPM (DW) is also not significantly related for all species (P=0.909) or *Acartia* spp. alone (P=0.415).

3.4 DISCUSSION

Laboratory studies have shown that food and temperature are the key factors controlling fecundity, growth and development of marine copepods (Durbin *et al.*, 1983; Peterson *et al.*, 1991). The question of whether herbivorous zooplankton experience food-limited growth and production in their natural habitat has been at the centre of much controversy, which laboratory and field studies have failed to fully resolve (Huntley and Boyd, 1984). One extreme of the limiting argument is supported by the observations of McLaren (1978), McLaren and Corkett (1981) and McLaren *et al.* (1989), who showed that, based on cohort analysis, juvenile copepods in coastal environments had development times equal to those found in the laboratory under conditions of unlimited food. Given that growth is dependent not only upon development rates, but also increase in weight, this should be considered. The growth rates of *Acartia* spp. over this study would certainly appear to be much lower at times than those under food saturated

conditions, and lower than those found in some other areas (eg. *Acartia clausi* (*omorii*?) in Onagawa Bay, Uye 1982a). There was no significant relationship between measured growth rates and the food quality ratio of Chl a:SPM(DW) ratio, as was previously found by Irigoien and Castel (1995) for *Acartia bifilosa* in an estuarine region. Nonetheless, given that *Acartia bifilosa* is dominant at some sites within Southampton Water (see Chapter 2), and that the ratio estimated for Southampton Water is at times within the range found by Irigoien and Castel (1995) to be associated with sub-optimal growth, then it would appear likely that SPM should have an inhibitory effect upon growth. The growth rates of *Acartia tranteri* in Westernport Bay, Australia, measured by Kimmerer and McKinnon (1987) using an *in situ* incubation technique, which was the basis of the method in this investigation, were found to be much lower than those in the laboratory under food saturated conditions. They had, infact, a very similar range to those in the present investigation, 0.025-0.26d^{-1} in their study, when temperatures ranged from ~11 to ~22°C, as compared to 0.008-0.205d^{-1} in this study, when temperature ranged between 8.1 and 18.6°C. In their study, the time weighted mean weight-specific growth rate was given as 0.11d^{-1}, while the time weighted mean for *Acartia* spp. is 0.08d^{-1} in the 10 month period of this investigation. Considering that temperatures in Southampton Water are slightly lower, the annual average growth rates are remarkably similar. Growth rates of *Acartia* spp. in Southampton Water were found to fall as low as 0.008d^{-1}, when temperatures were 9°C. This appears very low, although is similar to the lowest growth rates recorded by Burkill and Kendall (1982) for *Eurytemora affinis* in the Bristol Channel, U.K, where for some stages rates fell to 0.012d^{-1}. Kiørboe and Nielsen (1994) also report weight specific growth of adult females (specific egg production of *Acartia Centropages* and *Temora*) in the Southern Kattegat to fall to around 0.005d^{-1} at times, although values below 0.01d^{-1} were rare. *Centropages hamatus* growth in Southampton Water was found to range between 0.123d^{-1} to 0.285d^{-1}, at temperatures of 13.0°C and 18.6°C respectively (although only three measurements were made). Growth of *Paracalanus parvus* was measured once during the course of this investigation, when it was estimated as being 0.145d^{-1}, at a temperature of 13°C. *Temora longicornis* growth was also measured only once, at a temperature of 13°C, and growth was estimated to be 0.378d^{-1}. These results can be compared to the growth rates found by Klein Breteler *et al.* (1982) in laboratory culture, under food concentrations typically higher than in the North Sea, and at a temperature of 15°C. Copepodite stages C1 to CV had growth rates of 0.19 to 0.42d^{-1} in *Acartia clausi*, 0.28 to 0.40d^{-1} in *Centropages hamatus*, and 0.21 to 0.43d^{-1} in *Temora longicornis*. The growth of *Temora longicornis* was therefore within the laboratory culture measurements. For *Centropages hamatus*, *in situ* growth was close but usually below the growth in the laboratory, while *Acartia* spp. growth in Southampton Water was at times as great as the laboratory measure.

A comparison of the *in situ* rates of growth of copepods against temperature, including the values found in the present investigation, are given in Figure 3.4.1c. The results produced in the present investigation appear to fall close to the range of weight-specific growth under *in situ* conditions compiled from the literature. P:B ratios are also compiled for comparative purposes, with both individual data point (3.4.1a), and described relationships for individual species (3.4.1b). P:B ratios were not estimated from the present growth rate results, as no abundance/biomass data were available.

Uye *et al.* (1982) found that temperature was the only factor affecting growth rates of adult females *Pseudodiaptomus marinus* in a neritic area, when food was saturating. Johnson (1981) and Peterson (1980) also found for *Acartia californiensis* and *Calanus marshallae*, that food supplies in Oregon coastal waters were adequate to maintain maximum development rates. Under these situations temperature is generally commonly considered to limit development (eg. McLaren and Corkett, 1981). The examination of Huntley and Boyd (1984) suggests food saturated growth in neritic ares, but not offshore areas. While the study of Huntley and Lopez (1992) suggest food saturation of growth in copepods in both neritic and offshore areas. However, Klein Breteler *et al.* (1982), Durbin *et al.*, (1983), Daan *et al.* (1988), Kimmerer and McKinnon (1987) and Burkill and Kendall (1982) have shown for neritic waters that growth and/or development rates may be lower than under increased food conditions. For adult female copepods, egg production (which may be their only growth) may often be food-limited in nature (eg. Durbin *et al.*, 1983; Frost, 1985; Runge, 1985; Beckman and Peterson, 1986; Kiørboe and Johansen, 1986; Bellantoni and Peterson, 1987; Kiørboe *et al.*, 1988; Kiørboe and Nielsen, 1994; Liang *et al.*, 1994). Juvenile growth may also often be food-limited, even in estuarine and coastal areas which have extremely high rates of phytoplankton production or high chlorophyll concentrations (Burkill and Kendall, 1982; Grigg and Barnwell, 1982; Fransz and Diel, 1985; Runge *et al.*, 1985; Kimmerer and McKinnon, 1987). Rates of growth within Southampton Water are certainly well below those that would be expected at similar temperatures but under food saturated conditions.

In turbid neritic areas with high suspended particulate loading, growth rates have been shown to be significantly related to the ratio of Chl a:SPM(DW), while not being significantly related to temperature (Irigoien and Castel, 1995). Although the lack of a relationship between growth and temperature found in this study is unusual, it is therefore not entirely undescribed. Observations on the gut content of copepods in the Eastern Bristol Channel demonstrated that fine particulate material such as silt constituted their predominate dietary component (Burkill and Kendall, 1982).

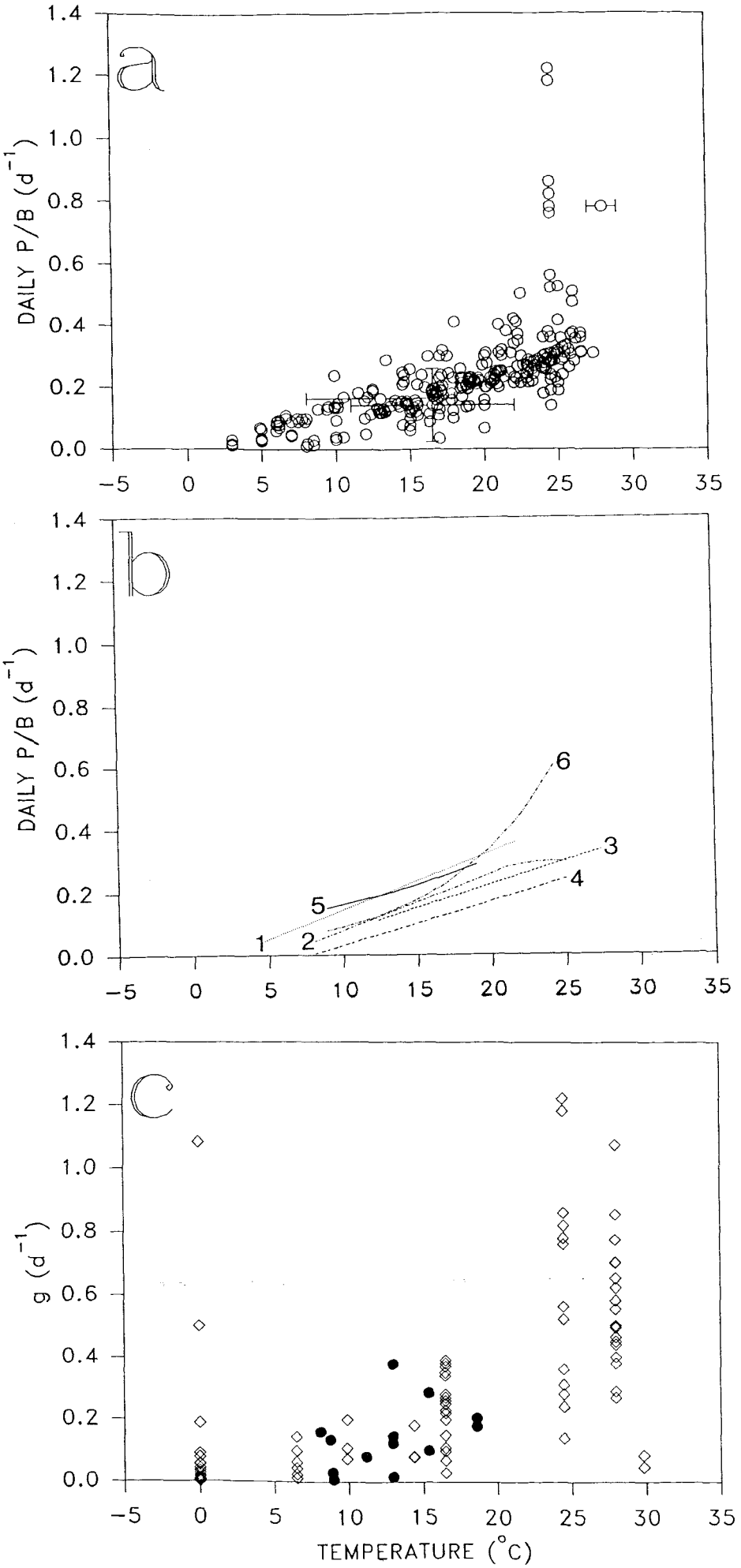


FIGURE 3.4.1 a. Compilation of daily P/B individual data points, b. Compilation of published daily P/B to temperature relationships, c. Compilation of daily weight–specific growth rates (g), together with those measured in Southampton Water in this study.

a

P/B COHORT ANALYSIS OF NATURAL POPULATIONS
ACARTIA CLAUSI (HUDSONICA?) –WASHINGTON LAGOON (LANDRY, 1978)
EURYTEMORA HERDMANI –HALIFAX HARBOUR (McLAREN ET AL., 1981 –FROM BURKILL ET AL., 1982)

P/B INCUBATION OF INDIVIDUALS UNDER QUASI IN SITU CONDITIONS
PSEUDODIAPTOMUS HESSEI –SUNDAYS RIVER ESTUARY (JERLING ET AL., 1981)
ACARTIA TRANTERI –WESTERNPORT BAY (KIMMERER ET AL., 1987)
ACARTIA TONSA –PATUXENT RIVER (HEINLE, 1966 –CALCULATED FROM AUTHORS' DATA EXCLUDES NAUPLII[b])
PARACALANIDAE –KANEOHE BAY (NEWBURY ET AL., 1976)
PSEUDOCALANUS ELONGATUS –GDANSK BAY (CISZEWSKI ET AL., 1977)
ACARTIA BIFILOSA –GDANSK BAY (CISZEWSKI ET AL.,1977)
ACROCALANUS INERMIS –KANEOHE BAY (KIMMERER, 1980)

P/B INCUBATION OF INDIVIDUALS UNDER 'FOOD SATURATED' OR CONTROLLED CONDITIONS
ACARTIA CLAUSI (OMORII?) –ONAGAWA BAY (UYE, 1982a)[a]
PSEUDODIAPTOMUS MARINUS –INLAND SEA OF JAPAN (UYE ET AL., 1983)[a]

a. Data points taken from authors' graphs due to unavailable results (pers. comm.)
b. Nauplii weights incorrect so production by this component not included in P/B data set

b

1 ACARTIA CLAUSI (OMORII?) –ONAGAWA BAY (UYE, 1982a).
$P/B = -0.0397+0.0185T$

2 CALANUS SINICUS –KII CHANNEL, INLAND SEA OF JAPAN (HUANG ET AL., 1993).
$P/B = -0.1+0.018T$

3 PSEUDODIAPTOMUS HESSEI –SUNDAYS RIVER ESTUARY (JERLING ET AL., 1981).
$P/B = -0.0716+0.0149T$

4 PSEUDODIAPTOMUS MARINUS –INLAND SEA JAPAN (UYE ET AL., 1983).
$P/B = -0.108+0.014T$

5 CENTROPAGES ABDOMINALIS –FUKUYAMA, INLAND SEA OF JAPAN (LIANG ET AL., 1996).
$P/B = 0.086e^{0.064T}$

6 ACARTIA OMORII –FUKUYAMA, INLAND SEA OF JAPAN (LIANG AND UYE, 1996).
$P/B = 0.024e^{0.133T}$

c

◇ IN SITU COPEPOD GROWTH DATA, AS COMPILED IN CHAPTER 4
• ACARTIA SPP., TEMORA LONGICORNIS, CENTROPAGES HAMATUS, PARA/PSEUDOCALANUS– SOUTHAMPTON WATER (THIS STUDY)

Examination of the gut content of copepods in winter samples taken within Southampton Water have also shown that sediment particles are common (Lucas, 1993). Often, non-algal material is a major component of the natural particulate regime found in the estuarine environment. However, there is very little information on its effects upon feeding or production in copepods. Burkill and Kendall (1982) and later Kimmerer and McKinnon (1987) suggested that suspended seston of low food value could disrupt feeding, or reduce the feeding or digestion efficiency in some manner. Burkill and Kendall (1982) suggested that the phytoplankton to seston ratio may be related to development time in *Eurytemora affinis* in the Bristol Channel. Seston or Suspended Particulate Matter (SPM) could influence the production of a species in two fundamental ways. Firstly it could reduce the rate at which algae are filtered from the environment by blocking filtering mechanisms, or through the time wasted during the manipulation of such particles. Secondly, if ingested, then their presence in the gut may consequently reduce the proportion of energy rich algal material. High suspended sediment concentrations have been shown to reduce the total survival of *Acartia tonsa* nauplii, as well as inhibiting development rate and fecundity of survivors (Sellner *et al.*, 1987). *Calanus helgolandicus* has also been shown to have reduced growth and survival, in addition to reduced stage weights and decreased ovary development, under conditions of high sediment concentrations (Paffenhöfer, 1972).

In the next chapter a multiple linear regression of copepod growth against temperature and individual body size is constructed, and compared against two of the more contemporary models of copepod growth. The results from the two models and the new equation are compared against the values found in this investigation in Table 3.4.1. The three models more commonly overestimate growth rates than underestimate it. Although the Ikeda-Motoda and Multiple Linear Regression models produce results which are closer to the real values more often than the Huntley-Lopez model, paired t-test comparisons between measured and predicted data reveal that the differences are not great enough to exclude the possibility that the differences are due to chance (Measured and Huntley-Lopez comparison, P=0.083; Measured and Ikeda-Motoda comparison, P=0.388; Measured and Multiple Linear Regression comparison, P=0.182).

Tidal state may influence the feeding environment with respect to concentrations of suspended particulate matter, as higher tides are likely to result in greater concentrations of S.P.M., both inorganic and organic forms. High concentrations of suspended sediments have been shown to result in decreased reproductive success and the development of fewer adults in the copepod *Eurytemora affinis* (Sellner and Bundy, 1987), in particular with suppression of the number of females surviving to adulthood, and retarded development.

Species	Measured g	Temperature	Mean Ind. weight	Predicted g [d^{-1}] (Measured-Predicted/Measured)		
	(d^{-1})	(°C)	(µgC)	**Huntley-Lopez**	**Ikeda-Motoda**	**MLR**
Acartia spp.	0.205	18.6	0.512	0.351 (-0.71)	0.339 (-0.65)	*0.259 (-0.26)
	0.101	15.4	0.471	0.246 (-1.44)	0.228 (-1.26)	*0.221 (-1.19)
	0.008	9.0	0.478	0.121 (-14.13)	*0.098 (-11.25)	0.153 (-18.13)
	0.029	8.9	0.487	0.120 (-3.14)	*0.096 (-2.31)	0.151 (-4.21)
	0.160	8.1	0.539	0.109 (+0.32)	0.085 (+0.47)	*0.140 (+0.13)
	0.135	8.8	0.577	0.118 (+0.13)	0.092 (+0.32)	*0.143 (-0.06)
	0.081	11.2	0.540	0.154 (-0.90)	*0.127 (-0.57)	0.167 (-1.06)
	0.017	13.0	0.478	0.188 (-10.06)	*0.166 (-8.76)	0.192 (-10.29)
Centropages hamatus	0.179	18.6	0.638	0.351 (-0.96)	0.317 (-0.77)	*0.242 (-0.35)
	0.285	15.4	0.652	*0.246 (+0.14)	0.209 (+0.27)	0.200 (+0.30)
	0.123	13.0	0.646	0.188 (-0.53)	*0.154 (-0.25)	0.175 (-0.42)
Temora longicornis	0.378	13.0	0.723	*0.188 (+0.50)	0.149 (+0.61)	0.169 (+0.55)
Paracalanus parvus	0.145	13.0	0.846	0.188 (-0.30)	*0.144 (+0.01)	0.162 (-0.12)
(*) Number of Times Prediction Closest to Measured Value / Total				2/13	6/13	5/13

TABLE 3.4.1 Comparison of measured growth rates with those predicted using the three models examined in Chapter 4. Number of times each model gives the closest prediction is also given.

Acartia tonsa has also been shown to have reduced naupliar survival and inhibited development and fecundity at high suspended sediment concentrations (Sellner *et al.*, 1987). Levels of suspended sediment below around 350mg.l^{-1} may not, however, be significant in species such as *Eurytemora affinis* (Sellner and Bundy, 1987). Levels recorded over the present growth rate programme were not found to exceed 80 mgDW l^{-1} (see Figure 3.3.4). However, the values for the Gironde estuary, S.W. France were >1000 mgDW l^{-1} (Irigoien and Castel, 1995). In this same area growth rates were positively related to the ratio of Chl a:SPM(DW). Although the levels of SPM were lower in Southampton Water and the ratio of Chl a:SPM(DW)was greater, growth rates were lower. Growth rates were not significantly related to suspended particulate matter in terms of DW alone either ($P>0.05$).

Generation times of *Acartia clausi* are compiled in Christou and Verriopoulos (1993b), and this allows a convenient comparison to the growth rates for *Acartia* spp. found within Southampton Water. In laboratory conditions with food supplied in excess, *Acartia clausi*, *A.hudsonica* and *A.omori* had generation times of; 25 days at 14-16° (Corkett, 1968), 19.4 days at 15°C, 16.7 days at 20°C (Iwasaki *et al.*, 1977), 21 days at 15°C (Landry, 1978a), and 27 to 14.2 days at 13-20°C (Uye, 1980). For field observations, 29.5 days at 15 to 20°C (Gaudy, 1976), 28 to 42 days at 13.5-8.5°C (McLaren, 1978). Ueda (1978) also compiled *in situ* generation time data from the literature. From this work it would appear that *Acartia clausi* (*hudsonica*?) had a generation time of ~56-76 days at temperatures from 0-24°C in Tisbury Great Pond, U.S.A. (from Deevey, 1948). *Acartia clausi* had generation times between ~31 and 62 days in Loch Striven, U.K. (Marshall, 1949). *Acartia clausi* had generation times between ~46-62 days at 6-18°C off Plymouth, U.K. (Digby, 1950). *Acartia clausi* (*hudsonica*?) had generation times of ~70 days in Charlestone and Green Hill ponds, U.S.A. (cited in Jeffries, 1962) and between ~63-70 days in Narragansett Bay, U.S.A. (cited in Jeffries, 1962). *Acartia clausi* (*hudsonica*?) is also reported with a generation time between ~46-62 days in Long Island Sound, U.S.A., at temperatures of 2-20°C (Conover, 1956), and between ~46-63 days in Raritan Bay, U.S.A., at temperatures of 4-18°C (Jeffries, 1962). *Acartia clausi* had generation times between ~31-93 days in the Black Sea, at temperatures between 6.8-23.5°C (Greze and Baldina, 1964). Assuming an egg weight (W_e) of 0.035µgC, and an adult weight (W_a) of 2.2µgC for the *Acartia* spp. in Southampton Water (adult weight typical for Southampton Water during abundance investigation; while egg weight is taken from Huntley and Lopez, 1992 for *Acartia clausi*), then it is possible, assuming exponential growth of individuals, and that the weight-specific growth rates (g) measured in the area are representative of growth rates throughout the life cycle of the individuals, to estimate generation times (G) using the equation:

$$G = \frac{(\log_e [W_a / W_e])}{g} \qquad (1)$$

This equation gives results for generation times in Southampton Water which vary between 20.2 and 518 days, at temperature of 18.6 and 9.0°C respectively. At the lowest temperature at which growth of *Acartia* spp. was estimated eg. 8.1°C however, the generation time was estimated as 31 days. The lowest growth rates in this study would appear to give generation times which are very long. The greatest generation time found previously was around 93 days (From Ueda, 1978: for Greze and Baldina, 1964). The growth rate results for Southampton Water do not, however, necessarily mean that generations were in fact this long, rather there were periods when growth was very low. There were also periods when growth was remarkably high, in fact very similar to those found at the same temperature, but at food saturating conditions.

The results of this study do not show any of the typical factors, upon which growth is commonly dependent, to be significantly related to the growth of *Acartia* spp. or all species together, throughout the sampling program. The lack of dependence in the case of *Acartia* spp. may in part be due to the fact that growth was not measured species specifically, rather genera specifically. Although the environmental measures were not related for all measurements, growth could nonetheless be dependent upon these, but vary over season. Thus at times growth was apparently optimal (ie. similar to food saturation rates at the same temperature), and therefore probably simply temperature dependent, while at other times growth was very low, and probably dependent upon the food quantity or quality. Significant relationships between growth and single factors may therefore not arise. Food quality was not examined closely in this investigation, high chlorophyll a concentrations will not necessarily be associated with abundant, copepod accessible, food.

The method used here has several advantages over many others commonly used. Temperature, the feeding environment and light conditions, diurnal changes in these, should reflect natural conditions, this may not be the case for laboratory incubations. Handling is also minimal, and staging and microscopy on individuals, prior to incubation, does not occur, as in some other incubation procedures. The method may also give highly spatial and temporal resolution of growth rates, with generally lower effort than needed for cohort/development identification methods. The method may also be used in highly dynamic areas, where such identification proceedures may be difficult or impossible.

There are potentially several problems with the growth method in this work. Firstly it is

assumed that incubation does not change the growth rates of the individuals examined. Although the growth rates were not directly utilised to determine production, it may also be assumed that these rates are representative of the entire size/development stages of the species. Such constant weight-specific growth rates are commonly assumed, although these are not always found in nature (see Burkill and Kendall, 1982; Peterson *et al.*, 1995). Containerisation does have the potential to change growth rates of zooplankton, and these effects unfortunately could not be examined in this study because of time limitations. Non-algal sources may be important as food for estuarine copepods. These sources went unexamined in this study, as in many other studies. As already detailed, copepods may clear sediment particles, these may have associated surface food, and they may also prey upon microbial components such as ciliates (Berk *et al.*, 1977; Stoecker and Sanders, 1985; Fessenden and Cowles, 1994), and detritus. However, changes in these during incubation were not examined here, nor have they been in other *in situ* containerisation studies (eg. Kimmerer and McKinnon, 1987).

One potential problem not mentioned by Kimmerer and McKinnon (1987), but encountered in the present investigation, was the possible contamination of samples with other species and also detritus. Barnacle nauplii were found to be very abundant at times in the incubation containers. As density assessment was based upon copepod numbers, then the variation in barnacle numbers could have a potential interfering effect. In the present investigation it was also found that barnacle nauplii tended not to survive the incubation (assessed by their lack of staining). Although the effect of addition of food was not assessed it is clear from the growth rate data, that the population was probably limited by the quality or quantity of food though large parts of the year. The control of densities of studied organisms is also problematic on board the small research vessel in these dynamic waters. Additionally, densities can not be exactly matched to those in the environment, indeed it is questionable what density they should be made up to, presumably a density where feeding rates and digestion efficiencies are the same as in nature. Although the feeding environment in terms of chlorophyll and phaeo-pigments were exanined in this study, there were no measurements of the species composition of this food source. While chlorophyll a and phaeo-pigment concentration did not significantly change during incubation, the species composition may have. Although there are therefore problems with this method, it is still likely that it is better than extrapolation of laboratory measures to the natural environment. Despite criticisms of container effects, these are probably minor provided that food does not become depleted (Kimmerer and McKinnon, 1987). The effects of incubation do however, need further investigation. Turbulence for example may have profound effects on feeding of copepods. Presumably containerisation will effect turbulence and therefore may also have an impact upon the feeding and growth processes of copepods, this

has apparently never been examined.

FUTURE IMPROVEMENTS

The spatial and temporal coverage of growth rates in Southampton Water needs to be extended to allow a better descriptions of growth throughout the estuary. Growth rates may also be augmented by growth rate estimated through the egg production method, and investigation of growth of different size classes or stages needs to be studied. Although growth rates for *Acartia* have previously been shown to be fairly constant with size (Kimmerer and McKinnon, 1987). Further examination of growth and the effects of increasing food concentrations in incubation containers, and laboratory incubation (as in Kimmerer and McKinnon, 1987) would help to elucidate the extent of food limitation. Work to explore the effects of SPM upon growth would also be of great value, and a fuller description of diet may aid in determining the factors actually controlling growth rates. As no length-weight equations were completed in this investigation, these should be completed to allow better growth prediction, given the dependency upon accurate weight determination. As the methods used are only applicable if growth is log-linear during incubation, then this should be confirmed by removing samples part way through the incubation course. Log-transformed data could then be tested for departure from linearity using ANOVA in a regression model with multiple y values for each x value (Kimmerer and McKinnon, 1987). Under similar incubation conditions, growth has been shown to be constant for up to at least 50 hours (Kimmerer and McKinnon, 1987). Incubation in this work never exceeded ~49 hours, even so these assumptions should be tested.

CHAPTER 4

ARE WEIGHT-SPECIFIC GROWTH RATES BODY WEIGHT INDEPENDENT IN MARINE COPEPODS? A RE-ANALYSIS OF THE GLOBAL SYNTHESIS AND A NEW EMPIRICAL MODEL.

4.1 INTRODUCTION

Copepods are important grazers and nutrient recyclers in the marine environment, they are the dominant trophic link between primary producers and higher trophic levels such as fish. Measuring and gaining an understanding of zooplankton grazing, processing and production is essential in fully appreciating their role in energy and nutrient flow and transformation. Estimating copepod growth rates in nature is generally time consuming and effort intensive, even when cohorts are identifiable. When such methods for distinguishing natural growth rates without manipulation are not possible, then incubation techniques can be used. Difficulties may arise however, in incubating individuals under conditions that are deemed to be representative of those in nature. Alternative techniques, which allow estimation of growth without incubation, including biochemical measurement have been developed (eg. enzyme activities, RNA concentrations) but in some cases have also been criticised (Dagg and Littlepage, 1972). Recently a radiochemical method has been introduced to measure growth in aquatic crustacea (Roff *et al.*, 1994b). Once again incubation is necessary, as is the labelling of food with ^{14}C, which may also prove to be problematic with respect to *in situ* study. Models which allow faster and less effort expensive estimation of growth and production, without the need of incubation, have been constructed and applied. These typically utilise a few easily measurable parameters and may allow prediction of zooplankton growth and production (eg. Ikeda and Motoda, 1978; Huntley and Boyd, 1984; Huntley and Lopez, 1994). Such models have often gone without rigorous testing however. A number of the more recently produced methods are outlined below.

Model: Ikeda and Motoda (1975).

Parameters measured: Zooplankton size distributed biomass, Temperature.

Application: Ikeda and Motoda (1975; 1978), Joh and Uno (1983), Koga (1986), Uye *et al.* (1987).

Problems: Many assumptions are made in achieving a final temperature and weight dependent growth rate, including the use of a single assimilation efficiency of 0.7 and gross growth

efficiency of 0.3. These efficiencies however, may change as a function of body size and temperature (eg. Ross, 1982b). Assimilation efficiencies for herbivorous zooplankton may be particularly variable, ranging from ~30% to >90% (Alldredge, 1984; Omori and Ikeda, 1984).

Model: Banse and Mosher (1980), as applied by Tremblay and Roff (1983).
Parameters measured: Annual average temperature, Zooplankton speciated biomass, and Adult weights for each species.
Application: Tremblay and Roff (1983).
Problems: Criticised on the grounds that the equation relating annual P/B to adult body mass should not be used for specific groups and circumstances (Banse and Mosher, 1980; Banse, 1984). Furthermore, the equation itself was deemed to produce results contrary to measured values (McLaren and Corkett, 1984). A rebuttle of criticisms was made by Roff and Tremblay (1984), although it was accepted that 'prediction using such equations should be cautiously interpreted'. This method also has drawbacks in that it allows prediction of only annual production rates.

Model: Huntley and Boyd (1984).
Parameters measured: Temperature, Food concentration (algae biomass/chlorophyll).
Application: Huntley (1985); Boyd (1985); comparison was made to real data by Kimmerer and McKinnon (1987); used for modelling purposes by Davis (1987).
Problems: Limited range of body sizes over which it may be applied ie. 0.01mgDW ind.$^{-1}$ to 1.0mgDW ind.$^{-1}$, indeed, relationships appear to break down outside these body weights ranges (*personal observation*). Incorrectly applied with regard to these body weight limits (ie. outside) by both Kimmerer and McKinnon (1987) and Davis (1987). The model is therefore very restricted in application given the weight ranges of copepods in most pelagic community (for example see results of Uye *et al.*, 1990). Model also assumes that food is adequately represented by chlorophyll or particulate algal carbon measurements, even though copepods may be highly selective autotrophs, heterotrophs or detritivores (see Hay, 1995). Measuring food concentrations actually experienced by copepods is difficult, prey and predator patchiness on micro-scale usually ignored, the ability of zooplankton to find small scale patches is also typically unknown.

Model: Huntley and Lopez (1992).
Parameters measured: Zooplankton biomass, Temperature.
Application: Comparisons made to real data by Hay (1995).
Problems: Empirically derived from adult and egg weight and generation time, and assuming that weight-specific growth is exponential, ie. body weight independent for each measurement.

Appears to predict that growth is just temperature dependent and body size independent, and to demonstrate that growth is body size independent in marine copepods. Results from model are believed to predict that growth is always food saturated in nature, however, much evidence suggests that growth of adults (egg production) and juveniles may be severely food limited at times (eg. Burkill and Kendall, 1982; Kimmerer and McKinnon, 1987; Peterson *et al.*, 1991).

In the present investigation comparisons of two of these reductionist methods, namely those presented in; Huntley and Lopez (1992) and Ikeda and Motoda (1978), are made by examining growth rates and generation times predicted by the models with actual measurements. The two models differ in their application in one major respect; with the Ikeda-Motoda model growth rate is a function of temperature and body size, whereas in the Huntley-Lopez model only temperature is the dependent function. The other models are not included in the comparisons as they have either been severely criticised (ie. application by Tremblay and Roff (1983) of the annual P/B to adult body mass relationship given by Banse and Mosher (1980)), or are often not applicable to real populations as a result of their restrictive size range (ie. Huntley and Boyd, 1984).

The importance of temperature upon growth rates in invertebrates is widely accepted (although see Banse and Mosher, 1980). Weight-specific growth rates in marine copepod species have been shown to increase as a function of temperature, both linear (*Acartia tranteri*: Kimmerer and McKinnon, 1987; *Pseudodiaptomus marinus*: Uye *et al.*, 1982) and power functions (*Sinocalanus tenellus*: Kimoto *et al.*, 1986; *Calanus sinicus*: Uye, 1988; *Paracalanus* sp.: Uye, 1991; *Centropages abdominalis*: Liang *et al.*, 1996; *Acartia omorii*: Liang and Uye, 1996) being chosen to describe the relationship between weight-specific growth rate and temperature. Relationships where weight-specific growth rates reach maxima and then decline have also been found (*Acartia clausi* and *Acartia steueri*: Uye, 1981; *Paracalanus* sp.: Uye and Shibuno, 1992), such a pattern probably being the result of temperature exceeding the optimal range for the species. Both the Ikeda-Motoda model and Huntley-Lopez model are temperature dependent, relating growth to temperature through logarithmic functions. What is controversial with respect to the content of these two models however, is whether weight-specific growth is body weight dependent. The Ikeda-Motoda model predicts growth to decline with body size, whereas the Huntley-Lopez model predicts weight independence. For individual species there is certainly variability in weight-specific growth rate with development stage (Huntley and Lopez, 1992). This rate has been reported to decrease during the later developmental stages of large copepods such as *Calanus pacificus* and *Rhincalanus nasutus* (Mullin and Brooks, 1970a; Paffenhöfer, 1976a). While maximum growth rates have also been shown to decrease with

increasing body weight in *Calanus agulhensis* and *Calanus pacificus* (Peterson and Hutchings, 1995). In other species the rate may be highest during young copepodite stages (CI-CIII), with lower rates in nauplii and later copepodite stages, eg. in *Pseudocalanus elongatus* (Paffenhöfer and Harris, 1976), *Temora longicornis* (Harris and Paffenhöfer, 1976; Klein-Breteler *et al.*, 1982), *Centropages hamatus* (Klein-Breteler *et al.*, 1982), *Pseudodiaptomus marinus* (Uye *et al.*, 1983) and *Calanus sinicus* (Uye, 1988). Weight-specific growth has also been shown to increase from early stage copepodites, late copepodite stages and nauplii respectively eg. in *Temora stylifera* and *Centropages typicus* (Razouls and Razouls, 1976). While some have split growth estimates for the nauplii and copepodite periods, and reported that the nauplii have lower specific growth rates than the copepodites (see Table 1 in Uye, 1988; Kimoto *et al.*, 1986; Uye, 1991; Liang *et al.*, 1996), or vice-versa (eg. *Microsetella norvegica*, Table 1 in Uye, 1988; *Acartia omorii*: Liang and Uye, 1996).

Huntley and Lopez (1992) proposed that copepod weight-specific growth rates were independent of species and body size in marine copepods, indeed apparent weight independence in the specific growth rate has been found in some species. McLaren (1978) suggested that if copepods increase weight between moults by a constant fraction, together with isochronal development, then growth would be exponential (at constant temperatures) and the 'P/B ratios would be the same for all stages [of a single species]'. Specific growth rates were reported to be equal in *Acartia clausi* (*hudsonica*?) (Landry, 1978a). The maximum specific growth rate of pre-adults of *Acartia hudsonica* were shown to be similar to maximum specific egg production in adult females when cultured in the laboratory (Sekiguchi *et al.*, 1980). This has also been demonstrated in *Eurytemora herdmani* (McLaren and Corkett, 1981), *Pseudocalanus* sp. (Corkett and McLaren, 1978; Sekiguchi *et al.*, 1980) and also possibly *Calanus pacificus* (Runge, 1984). Furthermore, the weight specific-growth of adult females of *Acartia tonsa* have been shown to be very similar to the weight-specific growth rates of its juvenile stages, at a variety of food concentrations (Berggreen *et al.*, 1988). Results of this nature can be used in justifying the application of weight-specific growth rates of adult females (egg production) directly to non-adults in the estimation of total copepod production. Conversely weight-specific growth rates of pre-adult size classes may also be applied to adult and other pre-adults. However, as already mentioned, intra-specific growth may decrease with increasing body weight, with larger individuals growing more slowly than smaller individuals (Zaika, 1968; Zaika and Malowitzkaja, 1967; Asknes and Magnesen, 1988; Hutchinson *et al.*, 1995; Peterson and Hutchings, 1995).

Individual body weight would certainly appear to effect many physiological processes, indeed body size is an integral component of the physiological method of Ikeda and Motoda

(1978) because of the apparent body weight dependence of weight-specific respiration. Weight-specific respiration rates decreasing with body weight in offshore boreal, temperate, sub-tropical, tropical regions (Ikeda, 1970), and eutrophic coastal environments (Uye and Yashiro, 1988). Huntley and Boyd (1984) also found that for boreal, temperate and subtropical zooplankton, weight-specific clearance rate decreased with increasing body weight (although for tropical zooplankton the reverse appeared to be true). Daily ration, in terms of % body weight ingested per day, has also been shown to decrease with increasing body weight in marine copepods (Ikeda, 1977b). While weight-specific ingestion rates were shown by Schnack (1985) to decrease with increasing body weight in a data set including Antarctic copepods and a euphausiid. Weight-specific excretion rates have also been shown to decrease with increasing body weight, both for single species and combined species groups (Corkett and McLaren, 1978; see Raymont, 1983; Uye *et al.*, 1990). Further, weight-specific growth rates of natural assemblages consisting of more than a single copepod species have themselves also been demonstrated to decline with body weight (Peterson *et al.*, 1991; see comments in Hopcroft and Roff, 1995). Hopcroft and Roff (1995) found that 'the growth rates obtained for *Paracalanus* are in good agreement with other growth rates obtained in Jamaica...and an emerging picture relating growth rate to copepod size (J.C.Roff *et al.*, unpublished), which suggest that *P.crassirostris*, by the virtue of it being the smallest calanoid copepod in this ecosystem, also has the highest growth rates'. Maximum weight specific growth rates may also be weight dependent but apparently species independent (ie. Peterson and Hutchings, 1995). The maximum weight-specific growth rates of adult females was shown to decrease with increasing body weight in the compilation work of Kiørboe and Sabatini (1995). Not only have physiological processes been shown to be weight dependent, but there is also controversy about whether population process other than growth are weight dependent. Mortality was described as being body weight independent in marine copepods (Kiørboe and Sabatini, 1995), however, this view was criticised, with Asknes (1996) suggesting that mortality in nature could indeed be dependent upon individual body size, with smaller individuals having greater mortality than larger individuals.

There is clear controversy as to whether models of weight-specific growth (and other population parameters) need to be body weight sensitive. The aim of this study is to determine whether copepod weight-specific growth rates are body size independent, and to determine which model is the better predictor of measured copepod growth rates. A new, empirically derived equation relating growth in marine zooplankton to temperature and body weight is also derived in this chapter, and compared with the published models.

4.2 METHODS

The two models examined are outlined below. The first, and the more simple to apply, is the Huntley-Lopez growth model, which is described by the equation:

$$g = 0.0445e^{0.111T} \qquad (1)$$

Where g is individual weight-specific growth rate per day
and T is the temperature (°C)

The second method is that given by Ikeda and Motoda (1975; 1978) and later applied in the determination of production by Uye *et al.* (1987). In this method, growth is estimated from respiration, which is described by an equation relating respiration to body weight and temperature. The relationship between respiration rate (R, µl O_2 individual^{-1} hr^{-1}), habitat temperature (T, °C) and individual animal dry weight (W, mg) as determined by Ikeda (1974) is:

$$R = aW^b \qquad (2)$$

Where $a=10^{(0.02538T-0.1259)}$
$b=-0.01089T+0.8918$

Oxygen respired is then converted to carbon by adopting a respiratory quotient of 0.8. Daily respiration being given as:

$$Rc = 0.8 \times \frac{12}{22.4} \times 24 \times aW^b$$

$$=10.286 \times aW^b \qquad (3)$$

Assuming an assimilation efficiency of 0.7 and a gross growth efficiency of 0.3, daily net production (P, µg C animal^{-1} d^{-1}) may then be calculated as:

$$P = 0.3 \times \frac{Rc}{(0.7-0.3)} \qquad (4)$$

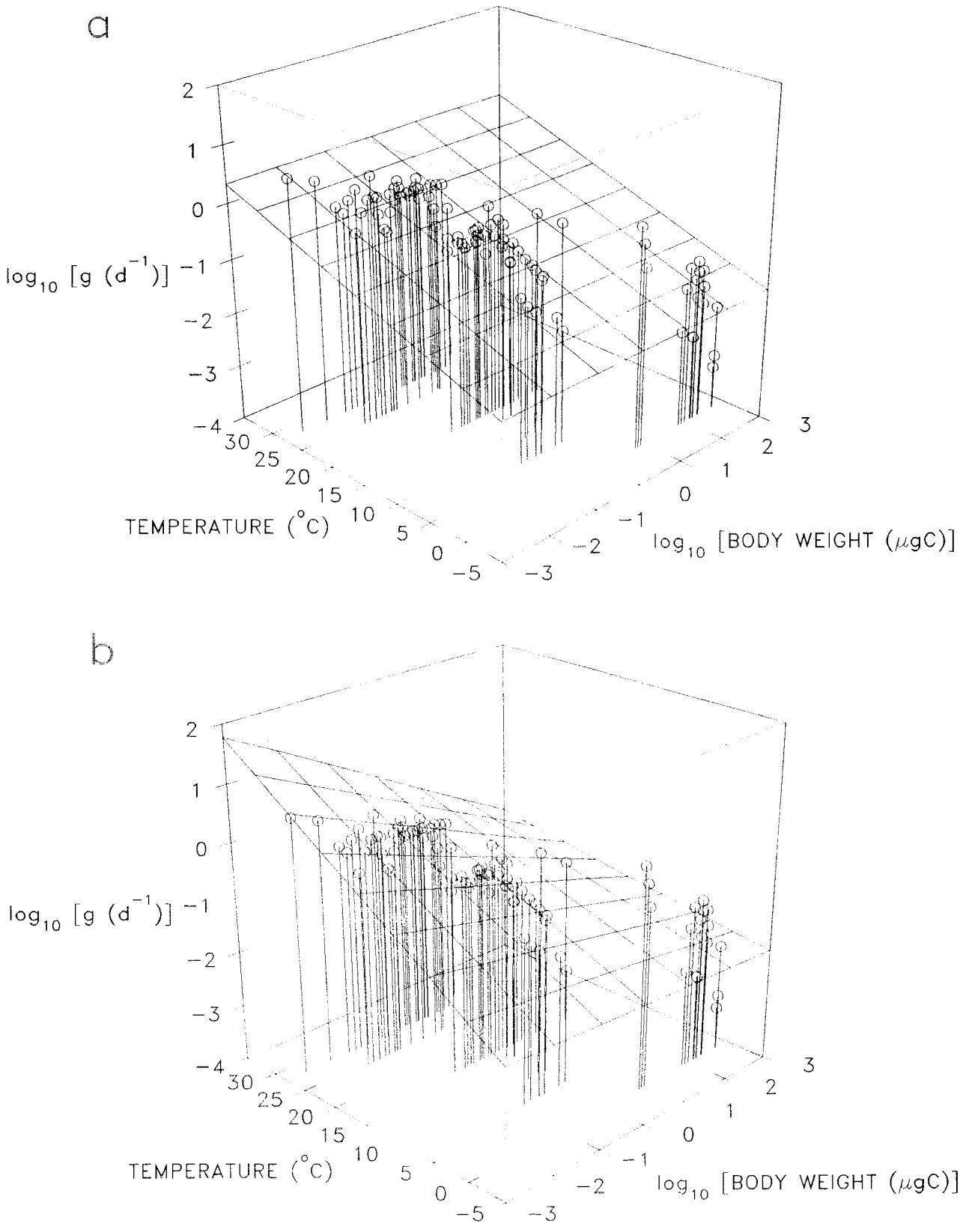


FIGURE 4.2.1 Predictive relationships between weight-specific growth rates of copepods, temperature and individual body weights, as given by the models of a. Huntley and Lopez (1992), and b. Ikeda and Motoda (1978), c. and by Multiple Linear Regression of the actual data, represented by grids. Measured copepod growth rates as detailed in Appendix 4 are represented by ball and stick points.

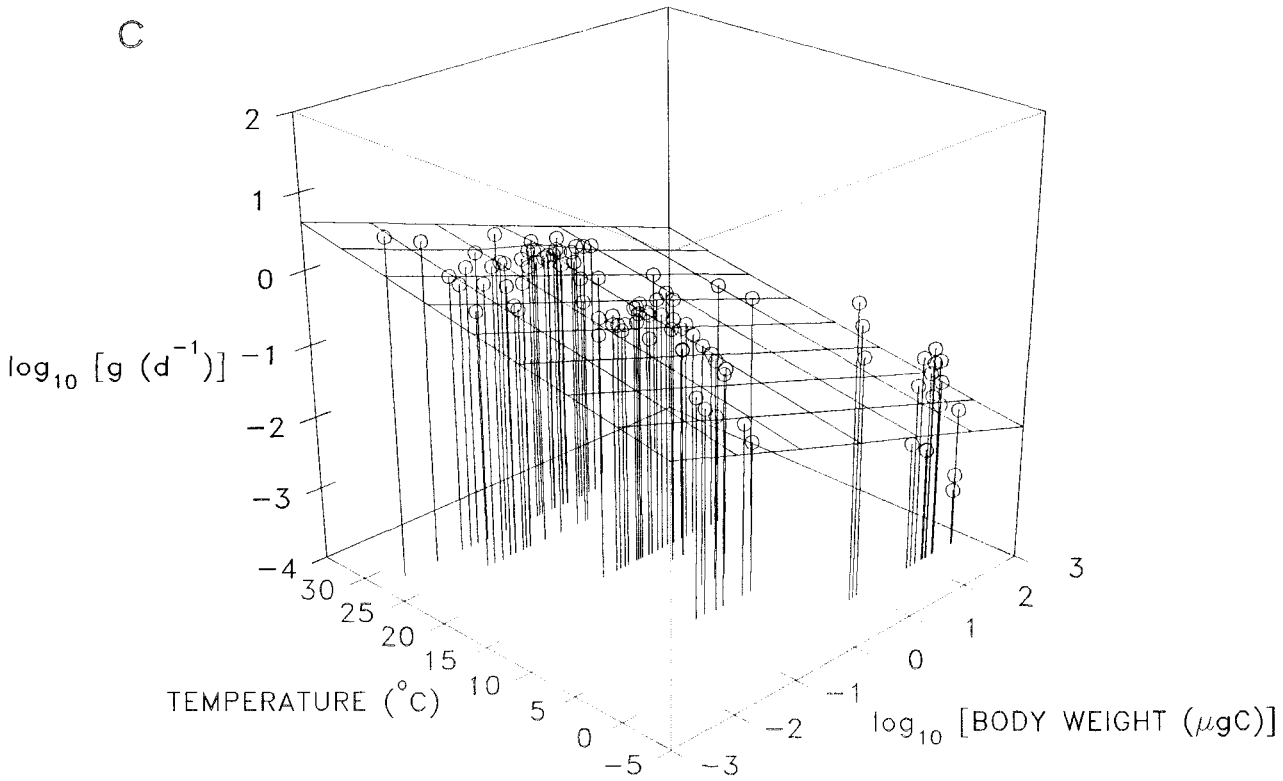


FIGURE 4.2.1 Predictive relationships between weight–specific growth rates of copepods, temperature and individual body weights, as given by the models of a. Huntley and Lopez (1992), and b. Ikeda and Motoda (1978), c. and by Multiple Linear Regression of the actual data, represented by grids. Measured copepod growth rates as detailed in Appendix 4 are represented by ball and stick points.

One may therefore produce an equation for daily weight-specific growth rate of an animal as follows:

$$g = \frac{7.714 \times 10^{0.02538T-0.1259} \times W^{-0.01089T+0.8918}}{W_c} \quad (5)$$

Where W_c is individual animal weight in μgC

Weight-specific growth rates, comparing the models:

Data for this analysis were taken from published studies where weight-specific growth rate (d^{-1}), temperature (°C) and the body weights were all available for individual stages or very short periods of life-history. Studies were differentiated into those in which growth was measured under: 1. *In situ* incubation or *quasi-in situ* conditions ie. conditions as close to natural feeding conditions as current methods allow, typically including incubation in natural seawater and temperature, but with the removal of predators, and 2. Food saturated conditions. Such distinctions meant that the study of Petipa *et al.* (1975b) for example, where detritus and humus were supplied to *Undinula darwini*, was not accepted as this fell into neither group. The estimates of growth in *Euchaeta elongata* given by Dagg and Littlepage (1972) were not used because of the relative uncertainty in temperature. The results of Petipa *et al.*, (1975a) were deemed to be derived under food saturated conditions in the 'mixed food cases', but the monoculture results were rejected. When individual body weights were not given in units of carbon, conversion from dry weight was carried out assuming a factor of 0.4 (Omori and Ikeda, 1984; Båmstedt, 1986). It should be noted here that carbon as a percentage of dry weight is apparently unaffected by individual size (see Uye, 1982b), and the results are therefore not biased by a single conversion. Conversions were also necessary in several instances where body weights were quoted in terms of calories, under these circumstances a conversion factor of 1g dry weight = 6kcal (Tremblay and Roff, 1983) was used prior to conversion to carbon. In the case of growth rate data presented by Chisholm and Roff (1990b), stages were given but weights were not, however, weights for stages were given in their accompanying paper (Chisholm and Roff, 1990a). Copepod body weights (geometric mean over period) were therefore derived from the length-weight and mean lengths given Table 1 and 3 of Chisholm and Roff (1990a). As the data were from a tropical region in which mean prosome lengths were in almost all cases not found to change significantly seasonally, then such assumption may be justified. No attempt was made to separate the species into broadcast or sac spawners (as in the compilation of Kiorboe and Sabatini, 1995).

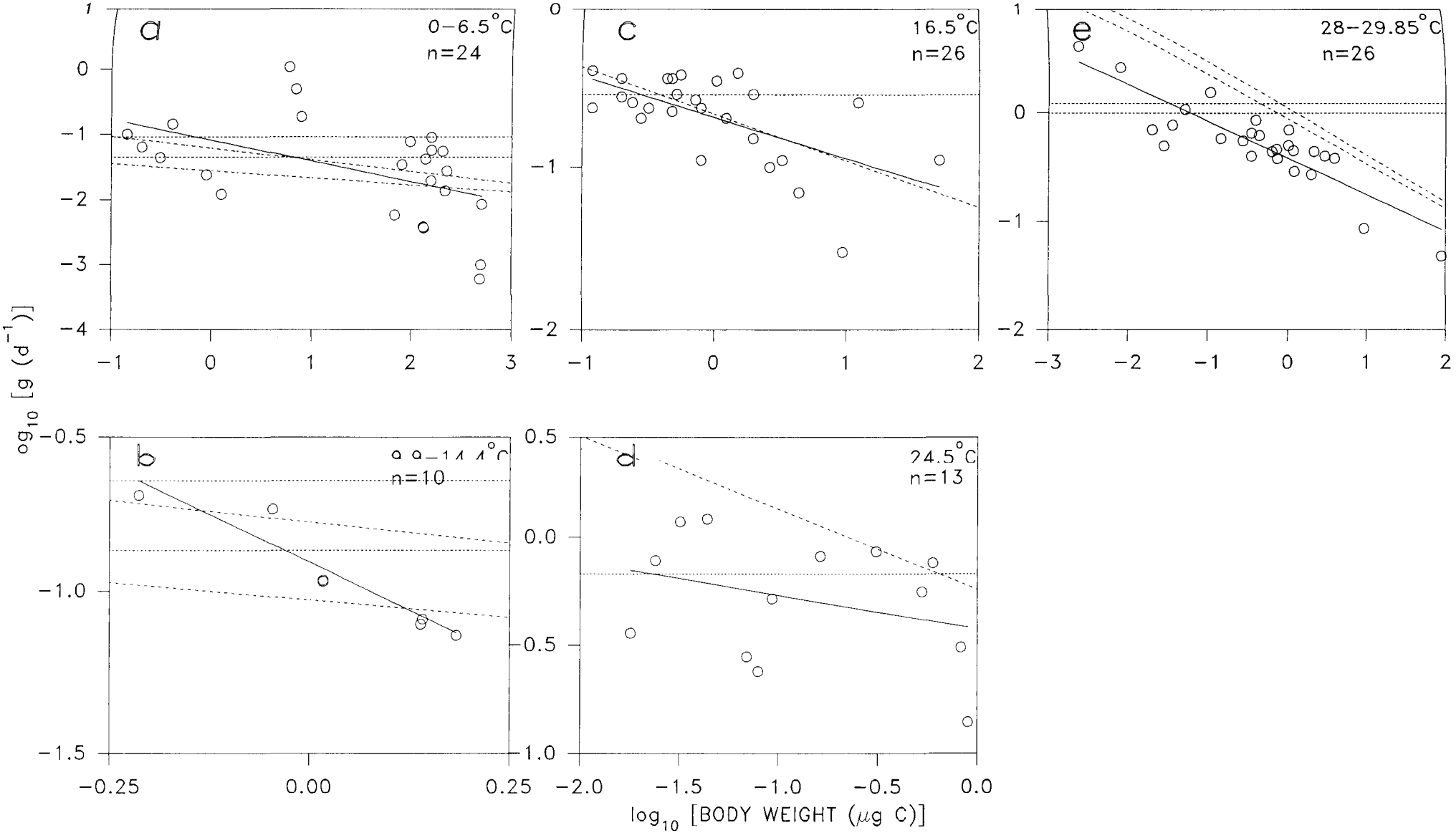
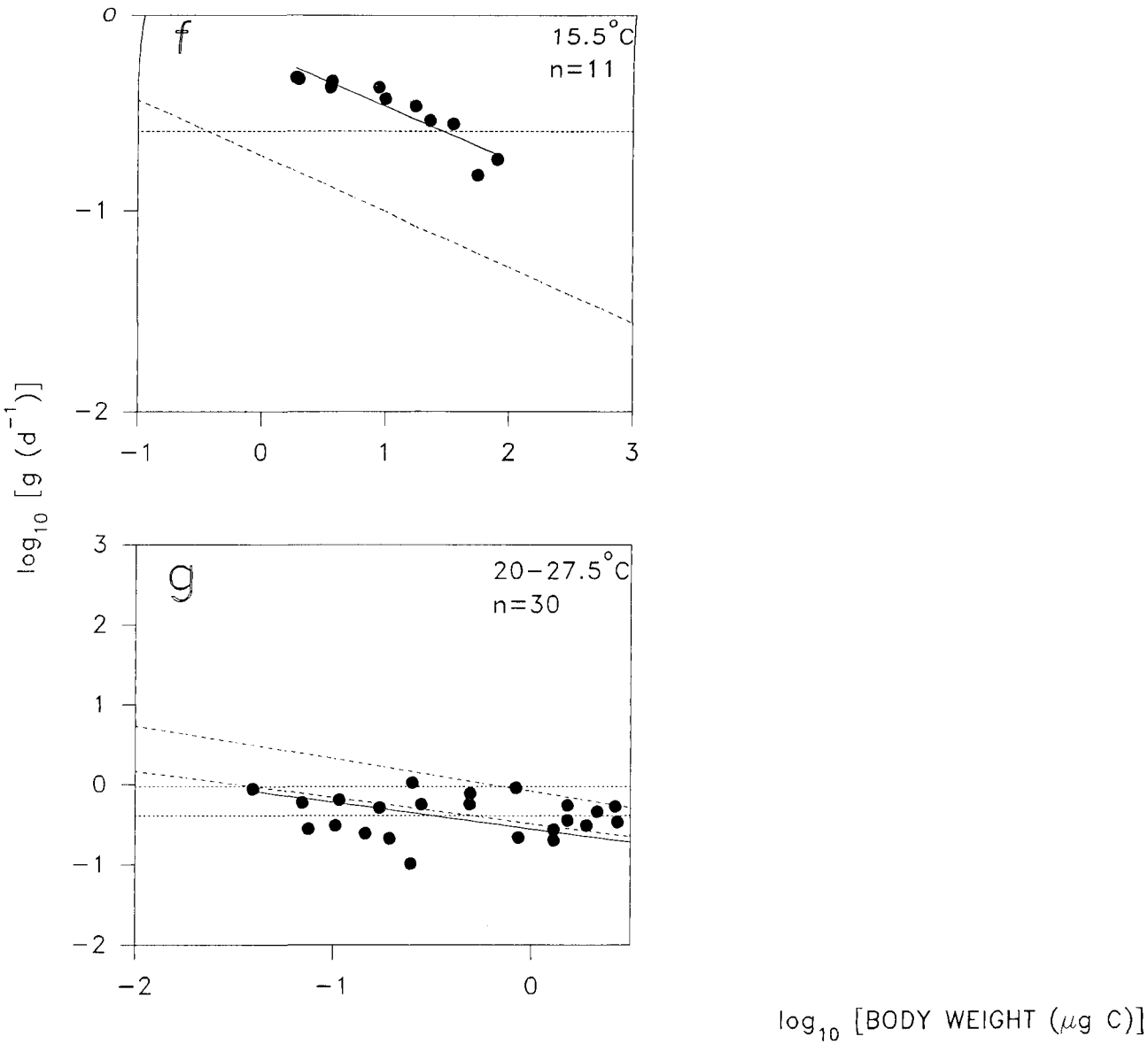


FIGURE 4.2.2 Measured growth rate versus individual body weight, data given in Appendix 4. Data divided into small temperature ranges to reduce the effect which this factor has upon growth rates in each graph. Short dash lines give predicited weight-specific growth rates at temperature extremes calculated using the Huntley–Lopez model. Long dash lines give predicted weight–specific growth rates at temperature extremes calculated using the Ikeda–Motoda model. Type I least squares regression through data shown by unbroken line. Graphs a–e: Natural food conditions/in situ incubation (o). Graph f–g: Food saturated laboratory work/saturated rate (●).



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Temperature (°C)	No. data points	No. Species	Wt. Range (µg C.ind.$^{-1}$)	log[g] vs. log[BW] Interc.	Slope	Significance r^2	P
Natural conditions:							
0-6.5	24	~6	0.144 - 511	-1.0882	-0.3182	0.242	$\log_{10}$ [g] tends to decrease as $\log_{10}$ [BW] increases (P=0.015)
9.9-14.4	10	1	0.612 - 1.528	-0.9098	-1.1839	0.896	$\log_{10}$ [g] tends to decrease as $\log_{10}$ [BW] increases (P<0.001)*
16.5	26	6	0.12 - 50.0	-0.6939	-0.2529	0.371	$\log_{10}$ [g] tends to decrease as $\log_{10}$ [BW] increases (P<0.001)
24.5	13	1	0.018 - 0.9	-0.4235	-0.1549	0.104	There is no detectable relationship (P=0.283)
28-29.85	26	~6	0.0024 - 88.4	-0.4141	-0.3381	0.760	$\log_{10}$ [g] tends to decrease as $\log_{10}$ [BW] increases (P<0.001)
Food Saturated:							
15.5	11	2	1.88 - 80.8	-0.2178	-0.2646	0.841	$\log_{10}$ [g] tends to decrease as $\log_{10}$ [BW] increases (P<0.001)
20-27.5	30	8	0.039 - 94.467	-0.5504	-0.3322	0.482	$\log_{10}$ [g] tends to decrease as $\log_{10}$ [BW] increases (P<0.001)

TABLE 4.2.1 Summary of compiled data set with results of analysis for determining whether weight-specific growth rates in marine copepods are body size dependent. (*Fails normality test (P<0.001)).

No distinctions were made because the eventual model produced was intended for wide application, regardless of copepod type. When growth was given in units of finite weight-specific growth ie. G (eg. see Chisholm and Roff, 1990b) it was converted to weight-specific growth (g) using the formula:

$$g = \log_e (G + 1) \qquad (6)$$

The compiled data set includes growth data collected at temperatures ranging from 0 to 29.85°C, for individuals ranging in size from 0.0024 to 511μgC, and from polar, tropical and temperate regions. Figure 4.2.1 (a and b) shows plots of $\log_{10}$ transformed body weight, $\log_{10}$ transformed growth rate and temperature, from the compiled studies. Predictions for the two models are given by the grid surface plots. Backwards Step-Wise Regression analysis was completed upon the compiled data set with the dependent variable $\log_{10}$ weight-specific growth and the independent variables temperature and $\log_{10}$ body weight, with F-to-enter being set at 4.0 and F-to-remove at 3.9. The results of this analysis show that both temperature and $\log_{10}$ body weight should be included in the prediction. The *in situ* and *quasi-in situ* growth rates (group 1) were therefore combined into a multiple linear regression equation, relating $\log_{10}$ [growth] to temperature and $\log_{10}$ [body weight]. Although food saturated growth rates (group 2) have been completed, and are analyzed with respect to the effect of body weight, these were not included in the multiple linear regression analysis. A multiple linear regression (MLR) fit gave the expression:

$$\log_{10} [g] = -1.1352 + 0.0248 [T] - 0.2976 \log_{10} [BW] \qquad (7)$$

Where g is the growth rate (d^{-1})
T is the temperature (°C)
and BW is individual body weight (μgC $individual^{-1}$)

This relationship has an r^2=0.671. Log_{10}[g] was predicted from a linear combination of the independent variables temperature (P<0.001), and $\log_{10}$[body weight] (P<0.001). These results suggest that under natural feeding conditions weight-specific growth rate is weight dependent. The equation is shown as a grid surface plot together with the data from which it was derived in Figure 4.2.1 (c). This new empirically derived growth equation was used in the prediction of weight-specific growth rates and to drive models used in the estimation of generation time.

Although the results of the multiple linear regression clearly demonstrated decreasing

weight-specific growth with increasing body weight, this was tested using a second method. Firstly, to reduce the effect of temperature, the completed data set of *in situ* growth rates was re-organised into relatively small temperature ranges. These ranges had a minimum interval of 0°C, a maximum interval of 4.5°C and a mean interval of 1.27°C. These groups are presented in graphical form in Figure 4.2.2 (a-e). The Huntley-Lopez and Ikeda-Motoda predicted growth rates are also shown for the temperature extremes in each group. For each of the groups, a least squares regression (Type I) was completed, and tested for significance. Food saturated laboratory studies were regressed also, but separately from the natural feeding condition data, in this case data were combined into two groups, one ranging in temperature from 20 to 27.5°C, and the other at 15.5°C. Table 4.2.1 gives a summary of the data used including the range of temperatures for the compiled data, the range in body weight for the measurements, and the number of species. The results of the linear regression are also included with r^2 and probability of a significant relationship. There were significant negative relationships with $\log_{10}$ [g] declining with increasing $\log_{10}$ [body weight] for 4 of the 5 sets of data for natural feeding conditions. In the cases of the 24.5°C group, when this relationship was not significant, one species was included, and there was only a relatively narrow body size range. For the food saturated groups (Figure 4.2.2(f and g)), the relationship was also negative and significant. The regression residuals were tested for normality using the Kolmogorov-Smirnov test (P=0.05), and all cases except one, the 9.9-14.4°C group, passed. It would therefore appear that copepod weight-specific growth may be body weight dependent.

Predicting generation time using the three models:

Data for this analysis were taken from the extensive data set presented as Appendix A in Huntley and Lopez (1992). This data base reports egg weight, adult weight, generation time and temperature in 181 cases for 33 species, over a range of temperature from -1.7 to 30.7°C, and in habitats ranging from the poles to the tropics (for specific details of data set collection see original study). Comparison between the predicted generation time using the 3 models; Ikeda-Motoda, Huntley-Lopez and MLR (multiple linear regression, completed in this study) were conducted as follows. The weight on day zero was equal to the egg weight. The weight after one day could then be estimated for each of the three methods using the temperature, and where necessary individual body weight, the new weight being equal to the weight increment plus the initial weight. The second day of growth could then be calculated from the weight on day 1 and the temperature. No attempts were made to take account of loss of biomass through ecdysis. The growth process was continued in this way until the day when the body weight reached that

reported for the adult. The total growth period (in whole day units) was defined as the 'generation time'.

Determining whether generation time is body weight dependent:

Huntley and Lopez (1992) attempted to demonstrate that generation time itself was body weight independent. To normalize for the effects of temperature, analyses were restricted to considering data in small temperature intervals. In their analyses, generation time was tested against log adult body weight. Re-analysis was undertaken to allow for the range of body weight experienced by a given species at a given temperature (ie. range being from egg to adult weight), rather than simply applying the adult weight. With this in mind, tests were repeated upon the data set of Huntley and Lopez (1992) in two ways. First, $\log_{10}$ mid-weights (adult weight plus egg weight divided by 2) were regressed against generation time, temperature ranges were kept the same as in the Huntley and Lopez study, except in the case of 10-11°C group which was extended to allow temperature rounding (as undertaken by Huntley and Lopez in the original study for the other groups). Secondly, $\log_{10}$ geometric mean weights were calculated and regressed against generation time using the same temperature ranges as previously.

4.3 RESULTS

Weight specific-growth rates, comparing the models:

Results of the predicted weight-specific growth rates given by the two models are given in Appendix 4, together with the raw measurements. Paired-t tests could not be used to compare predictions with measurements as the data failed normality tests (where the probability level was set at P=0.05). The non-parametric Wilcoxon Signed Rank Test was therefore used as an alternative. The results of the tests were as follows:

Measured vs. Huntley-Lopez prediction:

There is a statistically significant difference between the two groups (P<0.001).

Measured vs. Ikeda-Motoda prediction:

There is a statistically significant difference between the two groups (P<0.001).

Measured vs. Multiple Linear Regression prediction:

There is **not** a statistically significant difference between the two groups (P=0.163).

Predicted growth rates from both the Huntley-Lopez model and the Ikeda-Motoda model are statistically significantly different from the measured values.

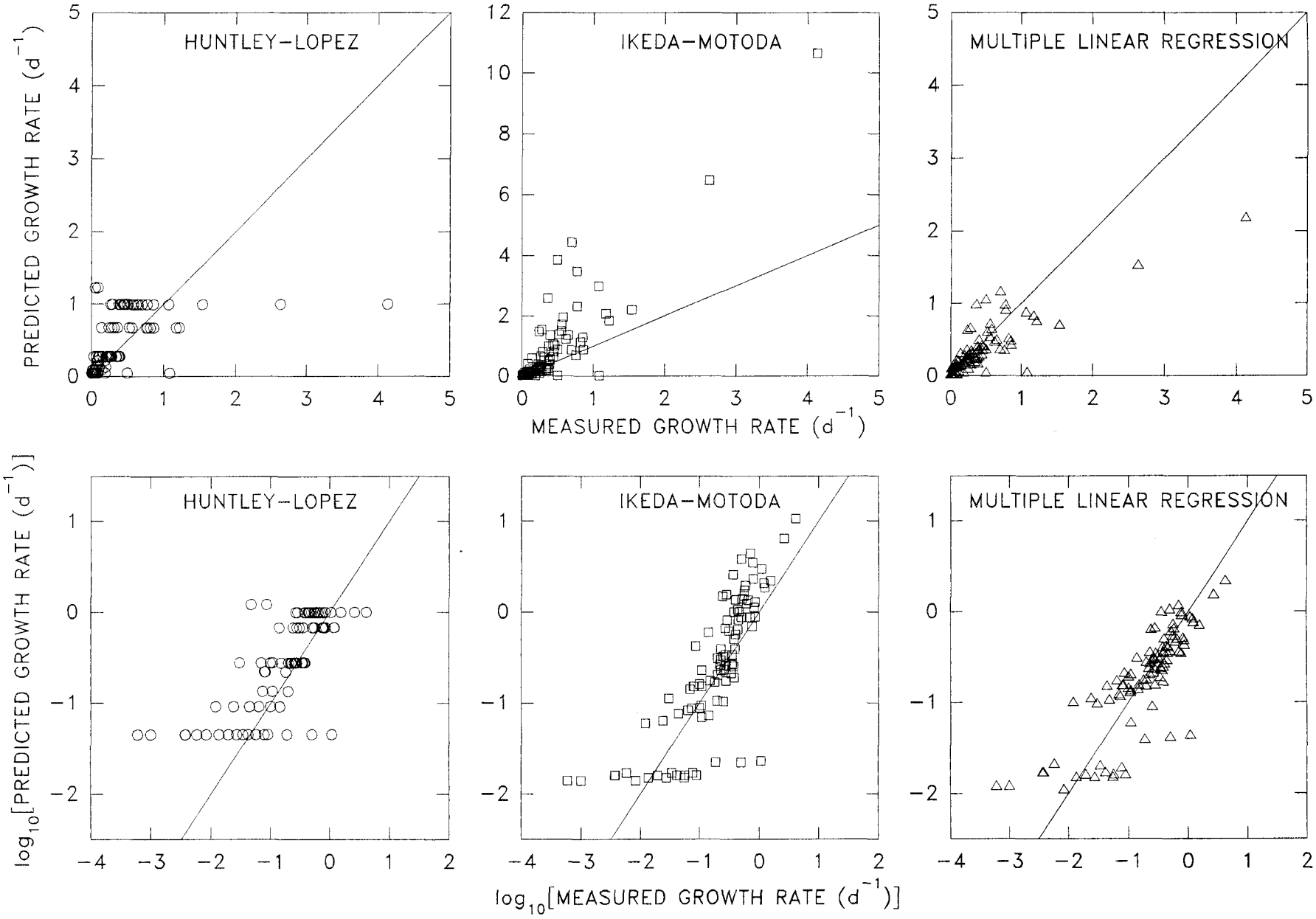


FIGURE 4.3.1 Comparisons between measured growth rates and predicted growth rates generated using the 3 models. Solid lines give 1:1 relationship.

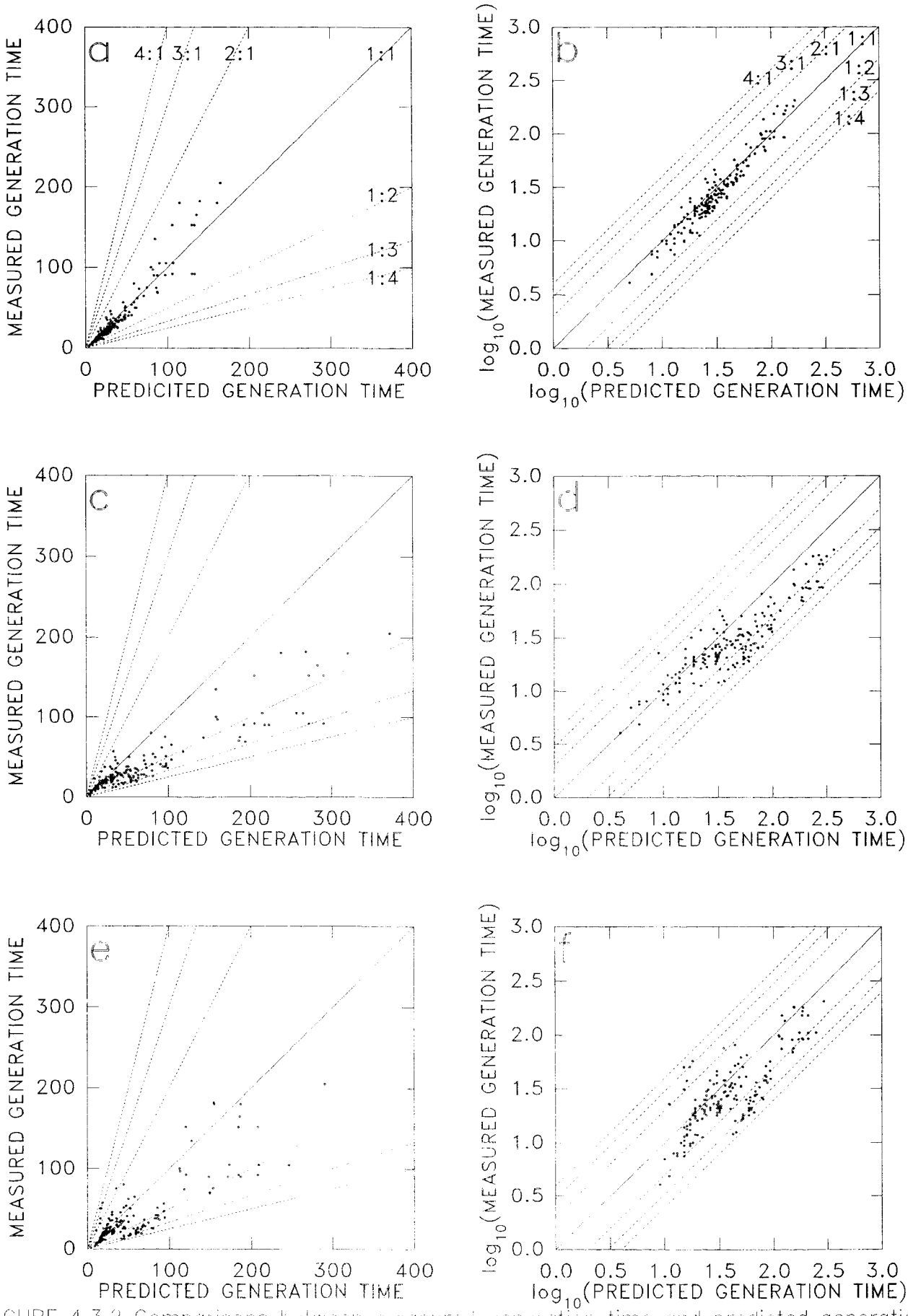


FIGURE 4.3.2 Comparisons between measured generation time and predicted generation time. a. and b. predictions made from runs using Huntley--Lopez growth model, c. and d. predictions made from runs using Ikeda--Motoda growth model, e. and f. predictions made from runs using the Multiple Linear Regression model.

Temperature Range[1] (°C)	No. data points	No. Species	Mid-BW Range (µg C.ind.$^{-1}$)	GT vs.log[mid-BW] Interc.	Slope	Significance r^2	P
3.5-6.4	13	9	0.081 - 492.70	62.394	13.63	0.355	GT tends to increase as log [mid-BW] increases (P=0.032)
9.5-11.4	21	12	0.815 - 60.125	28.970	7.852	0.541	GT tends to increase as log [mid-BW] increases (P<0.001)
14.5-15.5	48	20	0.815 - 75.05	18.096	3.091	0.239	GT tends to increase as log [mid-BW] increases (P<0.001)
19.5-21.4	10	8	1.074 - 44.125	10.810	3.182	0.282	There is no detectable relationship (P=0.114)

TABLE 4.3.1 Summary of compiled data set with results of analysis for determining whether generation time (GT) is body size dependent in marine copepods. Adult and egg weight combined by estimating mid-weight. (Data set for analysis from the Appendix A: Huntley and Lopez, 1992).

1 Overall temperature ranges include rounding to nearest whole degree. Thus ranges given are the exclusive ranges within which data were accepted.

Temperature Range[1] (°C)	No. data points	No. Species	Geometric mean BW Range (µg C.ind.$^{-1}$)	GT vs.log[Mean-BW] Interc.	Slope	Significance r^2	P
3.5-6.4	13	9	0.018 - 36.983	74.438	16.079	0.350	GT tends to increase as log [mid-BW] increases (P=0.033)
9.5-11.4	21	12	0.215 - 5.477	35.314	10.156	0.523	GT tends to increase as log [mid-BW] increases (P<0.001)
14.5-15.5	48	20	0.215 - 5.000	20.693	3.739	0.205	GT tends to increase as log [mid-BW] increases (P<0.001)
19.5-21.4	10	8	0.244 - 4.690	13.338	4.055	0.270	There is no detectable relationship (P=0.123)

TABLE 4.3.2 Summary of compiled data set with results of analysis for determining whether generation time (GT) is body size dependent in marine copepods. Adult and egg weight combined by estimating geometric mean. (Data set for analysis from the Appendix A: Huntley and Lopez, 1992).
1 Overall temperature ranges include rounding to nearest whole degree. Thus ranges given are the exclusive ranges within which data were accepted.

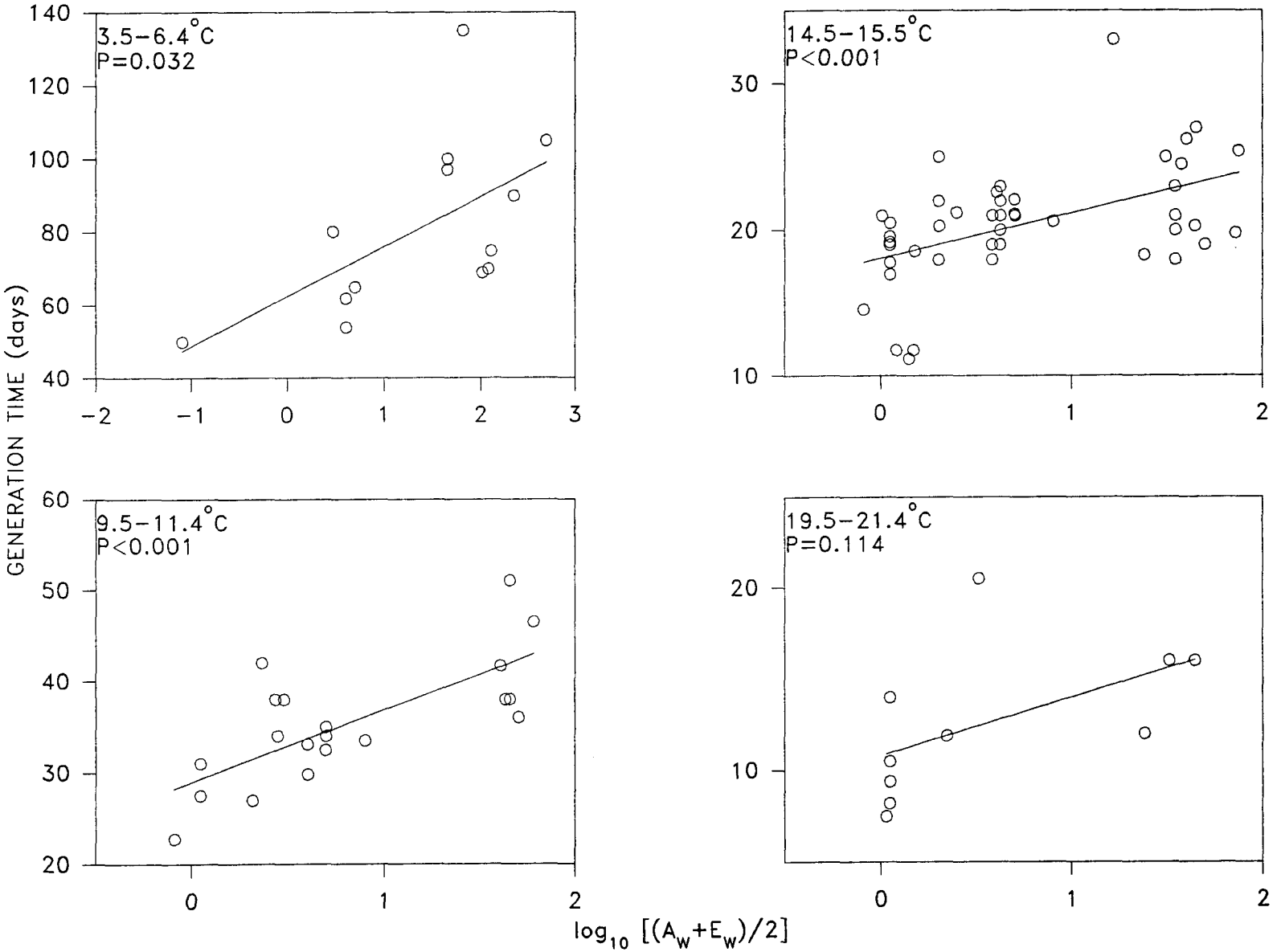


FIGURE 4.3.3 Log_{10} mid–body weight versus generation time over 4 temperature intervals (given on each graph), with least squares linear regression through data. See text for details.

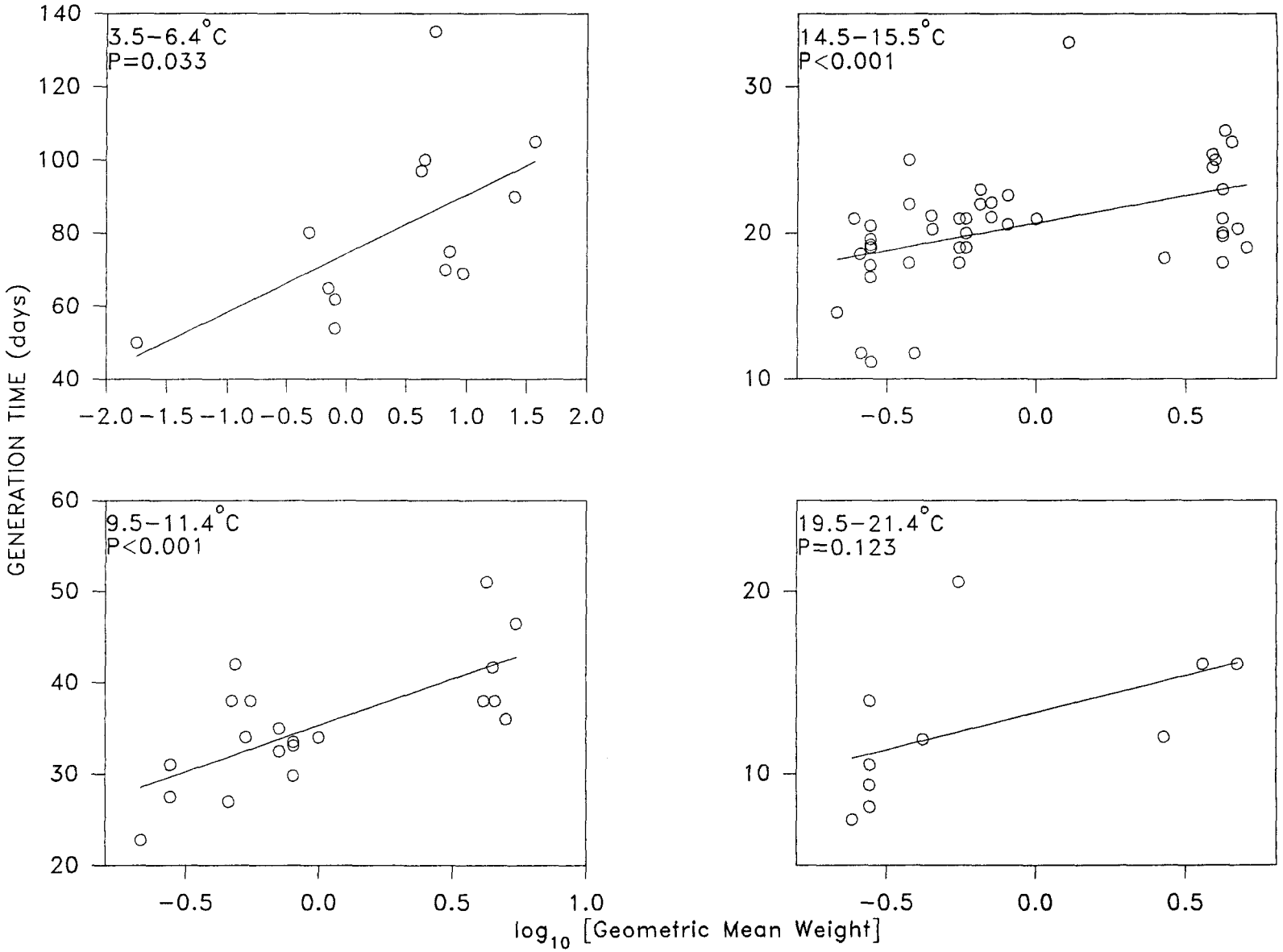


FIGURE 4.3.4 Log_{10} geometric mean body weight versus generation time over 4 temperature intervals (given on each graph), with least squares linear regressions through data. See text for details.

The empirically derived MLR model predicted results are not significantly different from the measured values, although of course the model lacks independence from the measured data. Graphical comparisons of predicted and measured growth rates are given in Figure 4.3.1.

Predicting generation time using the three models:

Once again the data sets of measured generation time and the predicted generation time failed normality tests using the Kolmogorov-Smirnov test (P=0.05), the non-parametric Wilcoxon Signed Rank Test was therefore used to compare data sets (ie. to compare measured generation times with those predicted by the three models). The results of these tests are as follows:

Measured vs. Huntley-Lopez prediction:

There is a statistically significant difference between the two groups ($P<0.001$).

Measured vs. Ikeda-Motoda prediction:

There is a statistically significant difference between the two groups ($P<0.001$).

Measured vs. Multiple Linear Regression prediction:

There is a statistically significant difference between the two groups ($P<0.001$).

Figures 4.3.2 compares the predicted generation times with the measured generation times. Although all the models produce results which are significantly different, the Huntley-Lopez model would appear to produce the most similar results.

Determining whether generation time is body weight dependent:

A summary of the data sets in this analysis are compiled in Tables 4.3.1 and 4.3.2, and shown graphically in Figures 4.3.3 and 4.3.4. For both methods of combining adult and egg weight, generation time appeared to increase as $\log_{10}$ body weight increased, except for one case in each analysis (the 19.5-21.4°C group, which had relatively few data points), this is contrary to the results of Huntley and Lopez (1992) that generation time is body size independent.

4.4 DISCUSSION

Huntley and Lopez (1992) found no detectable relationship between weight-specific growth rates and body weight, this is contrary both to the predictions from the Ikeda-Motoda model, and to the results of the present investigation. When the compiled growth rate data set was divided into small temperature ranges, in all tested cases, except one, there were significant negative relationships between weight-specific growth rate and individual body size. Multiple

linear regression also demonstrated that both temperature and body weight were significantly related to *in situ* measures of weight-specific growth. Several workers have also reported decreasing weight-specific growth with increasing body size between species (Peterson *et al.*, 1991; see comments in Hopcroft and Roff, 1995), as well as for individual species (Zaika, 1968; Zaika and Malowitzkaja, 1967; Vidal, 1980a; Hutchinson *et al.*, 1995). Huntley and Lopez (1992) found no detectable relationship between their model predicted weight-specific growth rates and corresponding weights of adults. However, to generate the predicted growth rates they assumed that rates of weight specific growth were exponential ie. weight independent for each separate determination.

Unfortunately the weight-specific growth data were non-normal distributed and therefore a non-parametric test had to be used in comparing predicted growth rates. Both the Ikeda-Motoda and Huntley-Lopez models produced weight-specific growth rates which were significantly different from the measured values. The MLR model did not produce significantly different results, though this method of course lacked independence. If the data set were normally distributed then parametric tests could be completed which would have allowed better tests upon the similarity of predictions to the actual measures. Although no adequate independent test was completed to determine which model was the best description of copepod growth rates, the empirical relationship gives a better description of the data itself than either of the other models.

Prediction of generation time using the three models all produced results which were statistically different to the measured values. Visual comparisons tend to suggest that the Huntley-Lopez model was the best predictor, however, this may be expected as this model was constructed from the same generation time data. The two weight dependent models were generation time independent in their construction, even so, their predictions were similar to the measured values, although generally the predicted generation times were longer (see prediction accuracy bars on Figure 4.3.2). This may, in part, be the result of Huntley and Lopez's pooling generation times of natural individuals with those derived under food saturated laboratory conditions. Indeed the empirically derived MLR model cannot be expected to reproduce growth for all species at all temperatures exactly. There is another important reason which may help to explain the general overestimation of generation time by the two weight dependent models. Cohorts of copepods may grow asynchronously, and slower growing individuals may have greater rates of mortality (Lopez, 1991). Generation times derived under both laboratory and field conditions may be biased by this effect, since these estimates will reflect the growth of only the faster growing individuals.

			Measured-Predicted/Measured (predicted g d^{-1} in brackets)			
Group	**Weight**	**Measured Weight-**	**MLR**	**Ikeda-Motoda**	**Huntley-Lopez**	**Source**
(Temperature °C)	**(µgC)**	**Specific Growth**				
Natural or laboratory conditions described by author/s as similar to natural:						
Thaliaceans	3.0-5.0	0.088 (mean)	*-0.73 (0.152)	-12.0 (1.144[1])	-3.66 (0.410)	Deibel, 1982
20°C	5.0-7.0	0.188 (mean)	*+0.28 (0.135)	-4.33 (1.002[1])	-1.18 (0.410)	
	7.0-9.0	0.203 (mean)	*+0.39 (0.124)	-3.49 (0.912[1])	-1.02 (0.410)	
	9.0-11.0	0.22 (mean)	*+0.47 (0.116)	-2.85 (0.848[1])	-0.86 (0.410)	
	11-13	0.28 (mean)	+0.61 (0.110)	-1.85 (0.799[1])	*-0.46 (0.410)	
	13-15	0.23 (mean)	*+0.54 (0.105)	-2.30 (0.760[1])	-0.78 (0.410)	
	15-17	0.04 (mean)	*-1.53 (0.101)	-17.2 (0.728[1])	-9.25 (0.410)	
	17-19	----	---- (0.097)	---- (0.700[1])	---- (0.410)	
	19-21	0.08 (mean)	*-0.18 (0.094)	-7.46 (0.677[1])	-4.13 (0.410)	
	21-23	0.11 (mean)	*+0.17 (0.091)	-4.96 (0.656[1])	-2.73 (0.410)	
Cyclosalpa bakeri	4720	0.29 (mean)	+0.96 (0.011)	+0.62 (0.110[1])	*+0.48 (0.151)	Madin and Purcell, 1992
11°C (range 10-12°C)						
Aurelia aurita	11.44	0.105	+0.48 (0.055)	-0.75 (0.184)	*-0.001 (0.106)	This study (Cracknore)
7.8-15.5°C	51.96	0.056	*+0.29 (0.040)	-1.80 (0.157)	-1.39 (0.134)	
	747.60	0.314	+0.94 (0.020)	+0.66 (0.106)	*+0.46 (0.171)	
	8760.05	0.077	+0.87 (0.010)	*+0.14 (0.066)	-1.51 (0.193)	
	35490.89	0.052	+0.85 (0.008)	*+0.13 (0.045)	-3.77 (0.248)	
Ceseis acicula[8]	175.1	0.026	*-2.35 (0.087)	-6.38 (0.192)	-46.04 (1.223)	Gerber and Gerber, 1979
29.85°C						
Salpa fusiformis[8] (oozooid)	3034	1.526	+0.98 (0.024)	+0.95 (0.073)	*+0.66 (0.512)	Le Borgne, 1982
22°C						

Glaucus atlanticus[8]	47100	0.160	+0.94 (0.010)	*+0.93 (0.012)	-2.2 (0.512)	Le Borgne, 1982
22°C						
Food non-saturating or not determined:						
Oikopleura dioica	0.09[2]	0.69	*+0.54 (0.315)	-3.06 (2.800[4])	+0.73 (0.188)	Paffenhöfer, 1976b
13°C	0.71[2]	0.77	+0.78 (0.170)	-1.17 (1.671[4])	*+0.76 (0.188)	
	3.60[2]	1.00	+0.90 (0.105)	*-0.11 (1.114[4])	+0.81 (0.188)	
	0.08[2]	0.65	*+0.50 (0.326)	-3.44 (2.883[4])	+0.71 (0.188)	
	0.47[2]	1.09	+0.82 (0.193)	*-0.70 (1.853[4])	+0.83 (0.188)	
	1.89[2]	0.76	+0.83 (0.127)	*-0.72 (1.309[4])	+0.75 (0.188)	
	3.77[2]	0.74	+0.86 (0.104)	*-0.49 (1.101[4])	+0.75 (0.188)	
	0.10[2]	0.64	*+0.52 (0.305)	-3.26 (2.727[4])	+0.71 (0.188)	
	0.37[2]	0.96	*+0.78 (0.207)	-1.05 (1.967[4])	+0.80 (0.188)	
	1.41[2]	0.59	+0.76 (0.139)	-1.39 (1.408[4])	*+0.68 (0.188)	
	2.66[2]	0.57	+0.80 (0.115)	-1.11 (1.202[4])	*+0.67 (0.188)	
Pleurobrachia bachei	0.1	0.67	*+0.54 (0.305)	-0.90 (1.272)	+0.72 (0.188)	calculated from Table 1 in
13°C	4.1	0.56	+0.82 (0.101)	*+0.10 (0.503)	+0.66 (0.188)	Reeve and Walter, 1976
	63	0.50	+0.91 (0.045)	*+0.49 (0.254)	+0.62 (0.188)	
	209	0.08	*+0.61 (0.031)	-1.35 (0.188)	-1.35 (0.188)	
	364	0.08	*+0.66 (0.027)	-1.05 (0.164)	-1.35 (0.188)	
Mnemiopsis mccradyi	1.72[7]	0.50	+0.59 (0.207)	-3.62 (2.312)	*+0.08 (0.458)	Reeve and Baker, 1975
21°C	44.21[7]	0.50	+0.84 (0.079)	-0.55 (0.775)	*+0.08 (0.458)	
	1055.12[7]	0.21	+0.85 (0.031)	*-0.27 (0.266)	-1.18 (0.458)	
	12208.00[7]	0.069	+0.78 (0.015)	*-0.70 (0.117)	-5.64 (0.458)	
	24241.60[7]	0.069	+0.83 (0.012)	*-0.35 (0.093)	-5.64 (0.458)	

26°C	1.72[7]	0.78	+0.65 (0.275)	-3.53 (3.532)	*-0.02 (0.798)	
	44.21[7]	0.78	+0.87 (0.105)	-0.27 (0.991)	*-0.02 (0.798)	
	1055.12[7]	0.23	+0.82 (0.041)	*-0.24 (0.286)	-2.47 (0.798)	
	12208.00[7]	0.071	+0.72 (0.020)	*-0.55 (0.110)	-10.24 (0.798)	
	24241.60[7]	0.071	+0.77 (0.016)	*-0.18 (0.084)	-10.24 (0.798)	
31°C	1.72[7]	0.65	*+0.44 (0.366)	-7.30 (5.394)	-1.14 (1.389)	
	44.21[7]	0.65	*+0.79 (0.139)	-0.95 (1.269)	-1.14 (1.389)	
	1055.12[7]	0.23	+0.77 (0.054)	*-0.34 (0.308)	-5.04 (1.389)	
	12208.00[7]	0.069	+0.62 (0.026)	*-0.51 (0.104)	-10.13 (1.389)	
	24241.60[7]	0.069	+0.70 (0.021)	*-0.10 (0.076)	-19.13 (1.389)	
Sagitta hispida	0.98[6]	0.25	*+0.02 (0.244)	-0.48 (0.369[6])	-0.83 (0.458)	Reeve and Baker, 1975
21°C	4.53[6]	0.25	+0.38 (0.155)	*+0.12 (0.220[6])	-0.83 (0.458)	
	13.25[6]	0.25	+0.55 (0.113)	*+0.39 (0.153[6])	-0.83 (0.458)	
	31.97[6]	0.25	+0.65 (0.087)	*+0.54 (0.114[6])	-0.83 (0.458)	
	59.27[6]	0.25	+0.71 (0.072)	*+0.63 (0.093[6])	-0.83 (0.458)	
	97.88[6]	0.25	+0.75 (0.062)	*+0.69 (0.078[6])	-0.83 (0.458)	
	156.70[6]	0.083	+0.35 (0.054)	*+0.19 (0.067[6])	-4.52 (0.458)	
	238.42[6]	0.044	*-0.09 (0.048)	-0.32 (0.058[6])	-9.41 (0.458)	
26°C	0.98[6]	0.35	*+0.07 (0.325)	-0.96 (0.686[6])	-1.28 (0.798)	
	4.53[6]	0.35	+0.41 (0.206)	*-0.08 (0.377[6])	-1.28 (0.798)	
	13.25[6]	0.35	+0.57 (0.150)	*+0.29 (0.248[6])	-1.28 (0.798)	
	31.97[6]	0.35	+0.67 (0.115)	*+0.50 (0.175[6])	-1.28 (0.798)	
	59.27[6]	0.35	+0.73 (0.096)	*+0.61 (0.138[6])	-1.28 (0.798)	
	97.88[6]	0.35	+0.76 (0.083)	*+0.68 (0.113[6])	-1.28 (0.798)	
	156.70[6]	0.074	*+0.03 (0.072)	-0.27 (0.094[6])	-9.78 (0.798)	

	238.42[6]	0.007	*-8.00 (0.063)	-10.43 (0.080[6])	-113.00 (0.798)	
31°C	0.98[6]	0.41	*-0.06 (0.433)	-2.11 (1.277[6])	-2.39 (1.389)	
	4.53[6]	0.41	*+0.33 (0.274)	-0.57 (0.644[6])	-2.39 (1.389)	
	13.25[6]	0.41	+0.51 (0.199)	*+0.02 (0.400[6])	-2.39 (1.389)	
	31.97[6]	0.41	+0.63 (0.153)	*+0.34 (0.270[6])	-2.39 (1.389)	
	59.27[6]	0.41	+0.69 (0.128)	*+0.50 (0.205[6])	-2.39 (1.389)	
	97.88[6]	0.11	*0.00 (0.110)	-0.49 (0.164[6])	-11.63 (1.389)	
	156.70[6]	0.041	*-1.34 (0.096)	-2.24 (0.133[6])	-32.88 (1.389)	
Euphausia pacifica	2.78	0.1079	+0.21 (0.085)	+0.13 (0.094[3])	*-0.001 (0.108)	Ross (1982a; 1982b)
8°C	11.06	0.1275	+0.55 (0.057)	+0.58 (0.053[3])	*+0.15 (0.108)	
	33.91	0.0469	*+0.13 (0.041)	+0.17 (0.039[3])	-1.30 (0.108)	
	124.29	0.0300	+0.07 (0.028)	*+0.03 (0.029[3])	-2.6 (0.108)	
	198.55	0.0256	+0.06 (0.024)	*-0.05 (0.027[3])	-3.22 (0.108)	
	417.20	0.0200	*+0.05 (0.019)	-0.15 (0.023[3])	-4.4 (0.108)	
	565.94	0.0181	*+0.01 (0.018)	-0.22 (0.022[3])	-4.97 (0.108)	
	1469.94	0.0278	+0.53 (0.013)	*+0.35 (0.018[3])	-2.88 (0.108)	
	2954.25	0.0210	+0.48 (0.011)	*+0.24 (0.016[3])	-4.14 (0.108)	
12°C	2.78	0.0935	*-0.14 (0.107)	-0.53 (0.143[3])	-0.81 (0.169)	
	8.83	0.1699	+0.55 (0.076)	+0.51 (0.084[3])	*+0.01 (0.169)	
	33.18	0.0787	+0.35 (0.051)	*+0.30 (0.055[3])	-1.15 (0.169)	
	136.85	0.0477	+0.29 (0.034)	*+0.20 (0.038[3])	-2.54 (0.169)	
	225.29	0.0401	+0.28 (0.029)	*+0.15 (0.034[3])	-3.21 (0.169)	
	491.74	0.0306	+0.25 (0.023)	*+0.08 (0.028[3])	-4.52 (0.169)	
	675.67	0.0678	+0.69 (0.021)	*+0.62 (0.026[3])	-1.49 (0.169)	
	1462.73	0.0453	+0.62 (0.017)	*+0.54 (0.021[3])	-2.73 (0.169)	

	2654.54	0.0352	+0.60 (0.014)	*+0.49 (0.018^3)	-3.80 (0.169)
(*) Number of Times Prediction Closest to Measured Value / Total			*32/90*	*43/90*	*15/90*

TABLE 4.4.1 Comparisons between data for non-copepod plankton growth and that predicted by the MLR, Ikeda and Motoda (1975) and Huntley and Lopez (1992) equations.

1 Dry weight of thaliacean was estimated from carbon by assuming carbon was 3.2% of DW (Madin and Purcell, 1992). Weight classes as given in Deibel's Table II. 2 Geometric mean carbon weight, estimated from ash-free dry weights assuming carbon to be 45% of AFDW (see Uye and Ichino, 1995). 3 Dry weight converted from given carbon weight using the equation given in same work (Ross, 1982a). 4 Dry weight of thaliacean was estimated from carbon by assuming carbon was 1.61% of DW (Uye, 1982b). 5 Dry weight estimated from carbon assuming carbon to be 4.45% of DW (as determined in original study: Reeve and Walter, 1970). 6 Carbon weight estimated from ash-free dry weight assuming carbon weight to be 44.9% of AFDW (as determined in original study: Reeve and Baker, 1975), dry weight estimated from carbon assuming carbon to be 40.7% of DW (as determined in original study: Reeve and Baker, 1975). 7 Carbon weight estimated from ash-free dry weight assuming carbon to be 8.72% of AFDW (as determined in original study: Reeve and Baker, 1975), dry weight estimated from ash-free dry weight by assuming AFDW to be 22% of DW (taken from Baker, 1973). 8 Dry weight and carbon weights both given in original study of Le Borgne (1982).

Generation time estimates may also be biased when peaks in abundance are used to follow growth, as these peaks are made up of optimally growing individuals (Carlotti and Nival, 1991). This has implications for the Huntley-Lopez model, as when applying generation times in the determination of growth rate where there is exponential growth, mean population growth rates will be overestimated when this effect holds true. Growth measured using typical short-term incubation techniques (eg. Kimmerer and McKinnon, 1987; Peterson *et al.*, 1991), may in fact underestimate growth as a result of the removal of predators, when these prey more heavily upon slower growing individuals. However, given typical removal rates over short-term incubations, such effects may be minimal. Alternatively incubation could lead to overestimation of growth if individuals which die during incubation were slower growing, and are subsequently ignored in the final estimate of growth (eg. as applied in the method of Kimmerer and McKinnon, 1987). Mortality is however, generally very low during short-term incubations of copepodite stages (<15% in accepted growth rate measures of Kimmerer and McKinnon, 1987; and even lower using the same technique in Southampton Water, see Chapter 3), and such effect may therefore be slight. Although there are no data present here to support the argument, short-term incubations when rigorously conducted, may be expected to give results which are more accurate a representation of growth than a simple generation time method could give. When generation times are greater than growth rate incubations (as they invariably are using typical techniques), then the effects of greater mortality amongst slower growing individuals will also of course be more appreciable. Although Huntley and Lopez (1992) hypothesised that copepods may not be food-limited in nature because the slower growing individuals would die, they did not appear to appreciate that such an effect would bias the generation time data with respect to growth.

Many other groups of organisms have been shown to have some form of weight dependence in their growth. Log_{10} P:B (yr^{-1}), which is dimensionally equivalent to weight specific growth currently examined (ie. unit $time^{-1}$), has been demonstrated to decrease with increasing log_{10} mass on reaching maturity in invertebrates and fish, and increasing log_{10} adult mass in mammals (Banse and Mosher, 1980), and decreasing P:B ratios with size have also been recorded for unicells, poikilotherms and homeotherms (Fenchel, 1974). Ciliate growth is correlated with cell size (Fenchel, 1968; Fenchel and Finlay, 1983) and temperature (Fenchel, 1968; Finlay, 1978); indeed a multiple linear regression was devised by Montagues *et al.* (1988), which combined log_e intrinsic rate of increase (d^{-1}) with temperature and log_e cell volume. Higher weight-specific growth rates are often observable in smaller zooplankton forms compared to larger ones, for example, Le Borgne (1982) found that microzooplankton (50-200μm in size), had a P:B (range 34-230%) which was on average 3.8 times that of the P:B (range 15-62%) of mesozooplankton (200-5000μm in size). This is not surprising, a broad generally acknowledged

phenomenon is that there is a decrease in the turnover time (days), which is the reciprocal of growth rate (d^{-1}), with decreasing size across suites of organisms (for example see results for fresh water lake of Hansen and Christoffersen, 1995).

The Ikeda-Motoda model has not only been utilised in estimating copepod growth and production, but has also been applied to other zooplankton groups. Indeed in the study by Ikeda and Motoda (1978), it was applied to size distributed biomass data which included, in addition to copepods, *Noctiluca*, appendicularians, and chaetognaths. Joh and Uno (1983) used it to estimate the production of copepods, cladocera, other crustacea, polychaeta, appendicularia, and sagittoides, while Koga (1986) used it in the estimation of the production of copepods, cladocera, sagittidea, appendicularia and thaliacea. Huntley and Lopez (1992) proposed, as a null hypothesis, that their model would give good predictions of other zooplankton groups. As weight-specific respiration rate (Ikeda, 1970; 1974; Uye and Yashiro, 1988) and weight-specific clearance rate (Huntley and Boyd, 1984) may be apparently independent of taxonomic category, it is possible that other physiological functions such as growth rate may also be independent. As both respiration and clearance may also be weight dependent (declining with increasing body weight) across taxonomic categories, a temperature and weight dependent model may be best. Other zooplankton and non-zooplankton groups have been shown to have weight-specific growth rates which are positively related to temperature and negatively related to body size. The data of Ross (1982a,b) demonstrates a positive relationship between weight-specific growth and temperature, and a negative relationship between weight-specific growth rate and body size in *Euphausia pacifica*. Indeed Tarling *et al.*, (submitted) used the Ikeda-Motoda model to predict euphausiid growth and production on the Patagonian shelf, Southwest Atlantic Ocean. Vidal (1980a) found increasing growth rates with decreasing size in cultured *Paracalanus* sp., and also pointed out such patterns existing in an array of species including; sock eye salmon fry (Shelbourn *et al.*, 1973), a freshwater snail (Prinsloo and Eedeen, 1973), insect larvae (Sweeney, 1976), the chaetognath *Sagitta hispida* (Reeve and Walter, 1972), and the amphipod *Calliopius laeviusculus* (Dagg, 1976). From the data presented in Boyle (1987), it is evident that cephalopods throughout their life may also commonly demonstrate decreasing weight-specific growth with increasing body weight. Hopcroft and Roff (1995) suggest, from their compilation of data from the literature, that larvacean and thaliacean weight-specific growth decreases with increasing size (ie. on an inter-species level). On an intra-specific basis however, this may not always be the case. Deibel (1982) demonstrated that the daily weight-specific growth of the thaliaceans *Thalia democratica* and *Dolioletta gegenbauri*, were constant over much of their size range, although the largest and smallest individuals had reduced rates.

In Table 4.4.1 measures of instantaneous weight-specific growth rates of various zooplankton are compared with those predicted using the three models. Comparisons are hindered by the relative lack of growth rate data, particularly those under natural feeding conditions, for which comparisons should ideally be made. The determination of which model produced the closest result for each measurement were made by calculating the difference between the measured and predicted value as a proportion of the measured value. Of the two weight dependent models the Ikeda-Motoda model gave closer results more often than the MLR model, 43 times as opposed to 32. The weight dependent models gave closer results more often than the Huntley-Lopez model, which gave the best prediction on only 15 out of 90 cases. Instantaneous weight-specific growth rates of larvaceans and thaliaceans compiled by Hopcroft and Roff (1995) may also be compared to those predicted from Huntley and Lopez (1992). Such a comparisons demonstrates that the model gives predictions generally towards the lower end of observed ranges or below observed ranges (although in 2 cases predicts results above those found). Huntley-Lopez model predictions have been compared to *Oikopleura dioica* by Uye and Ichino (1995), who estimated actual growth rate to be much greater than those predicted from the model of Huntley-Lopez. Actual rates being 2.1 times the predicted at 10°C and 2.7 times at 25°C.

The MLR equation may be used in the estimation of production of natural zooplankton communities. The basic form of the production equation being:

$$P = (B_1 \times g_1) + (B_2 \times g_2) + \ldots(B_n \times g_n) \qquad (8)$$

Where P is the total production rate (mass area^{-1} d^{-1} or mass volume^{-1} d^{-1})

B_i is the copepod biomass (mass area^{-1} d^{-1} or mass volume^{-1} d^{-1}) of body weight class i

g_i is the weight-specific growth rate (d^{-1}) of body weight class i

and n is the number of individual body weight classes

In application of this equation, body weight of each individual could be applied, alternatively the entire size distribution could be divided into groups (eg. see Ikeda and Motoda, 1978), therefore facilitating simpler estimation. Application of the models must allow for the fact that adult male copepods are generally regarded as having negligible growth and therefore negligible production, their biomass should therefore be excluded when it makes up a significant portion of the total. When other groups are known to be non-growing or undergoing diapause (Huntley and Lopez, 1992) then they may also need to be removed, depending upon their relative importance. This is an important point, although it appears not to have always been acknowledged in previous applications of the Ikeda-Motoda model (eg. Ikeda and Motoda, 1975; 1978; Uye *et al.*, 1987).

For the prediction of growth and production of meso- and macro-zooplankton, when data are not available on a species specific basis, the weight dependent models would commonly appear better than the model of Huntley and Lopez (1992). The MLR empirical model should be extended and tested further as data collection allows. As it is a better description of copepod growth rates than the other models, it should be applied to copepods. Since copepods may dominate zooplankton samples, under such circumstances it may also be best in application. The application of any of the models in the prediction of growth of a single species, is probably not advisable. Rather suites/community application is more appropriate given the methods of construction for all the 3 models examined here. Indeed such a recommendation was made by Huntley and Lopez (1992) regarding the application of their model, they point out 'The strengths of the method lies in its ability to provide estimates of community production at high resolution over large scales of time and space -a result that cannot practically be accomplished through cohort analysis or physiological methods'. There are very few estimates of production of suites of zooplanktonic organisms. Often single (possibly dominant) species have been chosen and examined in more detail. Application of the MLR model will however, allow more extensive examination, and may allow better determination of community processes, with less effort. There is as yet an apparent shortage of size distributed biomass measurements. Traditional net catch method employing limited mesh sizes, used most extensively to determine zooplankton biomass, may need to be replaced by automated techniques allowing rapid size distributed biomass. Furthermore, given the net avoidance behaviour of many active zooplankton, automatic *in situ* techniques which do not require the 'catching' of zooplankton may potentially give better resolution as well as greater synoptic measurements of zooplankton size distributed biomass without some of the problems encountered using net sampling. Given that taxonomic identification may be less relevant using the equation derived in this chapter, then its application would also suit such techniques.

CHAPTER 5

THE PRODUCTION OF GELATINOUS ZOOPLANKTON AND THEIR PREDATORY IMPACT

5.1 INTRODUCTION

Gelatinous zooplankton is a term used to describe a heterogeneous, non-taxonomic group of organisms which have a very high body water content (usually 70-95%), and therefore a low organic content. Their dry weight is typically 3.5-30% of their wet weight (Larson, 1986a), while carbon weight is 1-32% of their dry weight (Schneider, 1989d), although for some forms it may be greater (eg. *Oikopleura dioica* 46.3%, polychaete larvae 52.7%: Uye, 1982b). Members have a low metabolic rate on a wet weight basis, but are comparable to non-gelatinous zooplankton on a carbon basis (Schneider, 1992). Included in the gelatinous group are the true "jellies" such as the ctenophores, medusae, siphonophores and thaliaceans (dry weight around 3.5-5% of wet weight: Larson, 1986a), as well as the semi-gelatinous forms which include chaetognaths, molluscs (heteropods and pteropods) and polychaetes (dry weight around 3.5-30% of wet weight: Larson, 1986a). The group as a whole feeds on a great variety of prey types and spans many trophic levels, more than the three suggested in the review by Alldredge (1984). They may act as herbivores, carnivores or omnivores to varying degrees, and may prey upon other gelatinous zooplankton (Lebour, 1922; 1923; Fraser, 1969; Phillips *et al.*, 1969; Arai and Jacobs, 1980; Greve, 1981; Fancett and Jenkins, 1988; Gröndahl, 1988; Matsakis and Conover, 1991; Båmstedt *et al.*, 1994). In addition to preying upon meso- and macrozooplanktonic organisms some may also consume microzooplankton including non-loricated ciliates, tintinnids, and phytoplankton (Stoecker *et al.*, 1987a, 1987b; Båmstedt, 1990; Larson, 1987c; Larson, 1991). Some species, ie. the larvaceans, may also consume aggregated or free-living bacteria (Sorokin, 1978; King *et al.*, 1980). Single gelatinous species may be extremely diverse with respect to prey types and the size range of prey taken. The carbon weight of prey cleared by *Aurelia aurita*, for example, spans over 8 orders of magnitude, ranging from phytoplankton of 28pgC ind.$^{-1}$ (Stoecker *et al.*, 1987) to fish of 2-3cm body length with a carbon weight of ~6.4mgC ind.$^{-1}$ (Båmstedt *et al.*, 1994; assuming fish carbon to be 37.5% of dry weight: Beers, 1966).

Medusae, ctenophores, and chaetognaths may compete against other gelatinous and non-gelatinous predators including fish (Fraser, 1970; Möller, 1980a; Frank, 1986) for similar food

resources eg. copepod and crustacean prey. Of particular economic interest is that their prey items may also include the larvae and eggs of fishes (Lebour, 1922, 1923; Fraser, 1969; Tungate, 1975; Möller, 1980a; 1980b; 1984; Purcell, 1981; Bailey and Batty, 1983; 1984; Purcell, 1985; van der Veer, 1985; Purcell *et al.*, 1987; Båmstedt *et al.*, 1994). Gelatinous organisms can also form a dominant portion of the diet of some fishes (Scott, 1913, 1924; Hansen, 1949; Kamshilov, 1960; Fraser, 1962; Phillips *et al.*, 1969; Arai, 1988). For example Wilborg (1960) reported that medusae constituted 11.1-73.7% of the stomach contents of pelagic haddock fry taken in offshore waters of northern Norway.

At times gelatinous zooplankton are the dominant pelagic carnivores, with their importance being attributable to various characteristics. Unlike many other predators, the feeding rates of some gelatinous predators appear not to become saturated over an extremely large range of prey concentrations, with ingestion rates being proportional to food concentration (Bishop, 1967; Miller, 1970; Reeve and Walter, 1978; Purcell, 1982; Frid *et al.*, 1994). Although at great extremes of prey density, often unnaturally high or low, this may not be the case (Rowe, 1971; Reeve *et al.*, 1978; Bailey and Batty, 1983). Gelatinous species may rapidly increase their size, fecundity and predation rates in the face of favourable conditions (Kremer, 1976; Reeve *et al.*, 1978; Båmstedt, 1990; Hopcroft and Roff, 1995). Indeed, some gelatinous organisms have the fastest metazoan growth rates recorded (Hopcroft and Roff, 1995). Their high water content allows, through small energetic input, rapid increases in wet biomass, surface area and prey capture abilities, and predation rates (Larson, 1991). All ctenophores (Hirota, 1972; Baker, 1973; see review by Reeve and Walter, 1978) and chaetognaths (Reeve, 1970) are hermaphrodites, ctenophores (Reeve and Walter, 1978) and chaetognaths (Hyman, 1959; Reeve, 1970) are also capable of self-fertilization. Combining such reproductive strategy with their ability to produce relatively great numbers of young in comparison to other plankton (Baker, 1973), often from a very young age (Hirota, 1972), means that given favourable conditions their numbers may increase extremely rapidly. The ability of many gelatinous species to be able to withstand longer periods of food shortage than many other predators, through de-growth, and their subsequent full recovery (Hamner and Jenssen, 1972; Reeve and Walter, 1978) aid their predatory dominance. These characteristics result in them being potentially extremely important as predators, having growth which may be tightly coupled to ephemeral prey production (Larson, 1986c). They may directly and indirectly determine many pelagic energy, carbon and nutrient fluxes (Schneider, 1989c; Lucas *et al.*, *in press*). Medusae, siphonophores and ctenophores are also in a position to take advantage of imbalances brought about by pollution, overfishing, and other major environmental changes (Mills, 1995).

Quantifying the relative importance of gelatinous species within pelagic systems has chiefly been undertaken within the last three decades. They have also been shown to have insignificant predation rates in comparison to prey production at times (Daan, 1986, 1989; Miller and Daan, 1989). However, they have also been reported to function as organisms of 'key' importance in pelagic ecosystems (see review by Alldredge, 1984). Under some circumstances they may determine gross ecosystem structure, species composition, and prey abundance, with the potential of influencing sub-prey trophic levels through 'cascade effects'. Such 'cascade' or secondary effects may include increases in phytoplankton density caused by reduced grazing as a consequence of gelatinous predation upon copepods (Hulsizer, 1976; Greve, 1981; Deason and Smayda, 1982a). Huntley and Hobson (1978) believed that feeding by the leptomedusa *Phialidium gregarium* in Saanich Inlet reduced herbivore populations and allowed a second bloom of phytoplankton. The scyphomedusa *Aurelia aurita* has been shown to rapidly reduce the copepod population in Kiel Bight, with resultant increases in the phytoplankton and protozoan populations in this area (Möller, 1979). Deason and Smayda (1982a) suggested that the ctenophore *Mnemiopsis leidyi* regulated summer zooplankton and phytoplankton dynamics, controlling phytoplankton blooms indirectly through their predation on herbivorous zooplankton and directly through their nutrient excretion. Lindahl and Hernroth (1983) believed that predation by *A.aurita* in Gullmar fjord reduced zooplankton stock, in turn resulting in oxygen depletion at depth as unutilized phytoplankton sank and decayed. Gelatinous predation may therefore lead to fundamental structural changes in the benthic community. Many authors have speculated that ctenophores, scyphomedusae and chaetognaths are important in the population dynamics and productivity of marine planktonic communities (Fraser, 1962; Cronin *et al.*, 1962; Hopkins, 1966; Frank, 1986; Greve and Reiners, 1980; Greve, 1981; Feigenbaum and Kelly, 1984; Omori *et al.*, 1995; Lucas *et al., in press*). Reductions in the numbers of mesozooplankton (particularly copepods) and negative predator-prey relationships have often been observed during periods when these three groups are abundant (Burrell and van Engel, 1976; Hulsizer, 1976; Möller, 1979; Greve and Reiners, 1980; Greve, 1981; Deason and Smayda, 1982a; Lucas and Williams, 1995; Lucas *et al., in press*). However, some systems have proven not so easy to understand through simple negative predator-prey correlations (see Feigenbaum and Kelly, 1984). Evidence of the structuring influence of gelatinous zooplankton simply through examinations of abundance changes, which is a common method, may be deemed as anecdotal at times (Miller and Daan, 1989), and may certainly lead to erroneous conclusions regarding the true predator impact (Begon *et al.*, 1986; Daan, 1989; Miller and Daan, 1989).

Gelatinous species may not only cause mortality of other groups through ingestion, but significant mortality may occur simply through their encounter activities, even though subsequent

ingestion may not occur (Fraser, 1969; Walter, 1976; Reeve and Baker, 1978; Bailey and Batty, 1983; Båmstedt *et al.*, 1994). Such 'over-hunting' by pelagic predators may prove important for production and recycling processes in marine ecosystems (Ikeda, 1977b). The importance of gelatinous organisms in nutrient recycling has not gone without examination in schyphomedusae (Biggs, 1977; Muscatine and Marian, 1982; Schneider and Weisse, 1985; Morand *et al.*, 1987; Schneider, 1989c; Lucas *et al.*, *in press*) and ctenophores (Ikeda, 1977; Kremer, 1977, 1982; Deason and Smayda, 1982a; Ikeda and Mitchell, 1982; Båmstedt, 1985; Kremer *et al.*, 1986), and occasionally may be an important regenerative source for phytoplankton (Schneider, 1989c).

Several methods have been utilised in the estimate of production and predation rates of gelatinous zooplankton. With regard to production one of the easiest and probably most accurate is the application of cohort equations to natural populations which behave appropriately (McLaren, 1969; Zo, 1969; Sameoto, 1971; 1973; van der Veer and Oorthuysen, 1985; García 1990; Lucas *et al.*, *in press*). Such methods are usually preferable as growth and mortality may be followed over time, and production estimates made using these methods are also likely to be fairly accurate, depending upon the accuracy and completeness of the available data. The identification of cohorts through time has however, proven to be extremely difficult (Reeve and Walter, 1978). Reasons for this include rapid growth rates when food is abundant (Hirota, 1974; Larson, 1986), de-growth, and intermittent spawning. Often gelatinous predators do not breed synchronously, indeed they often reproduce continuously. Furthermore, water mass movements and the mixing of different populations may make the following of cohorts impossible. *Aurelia aurita* is one of only a few species studied which shows near synchronous breeding (Möller, 1980b; Papathanassiou *et al.*, 1987; Schneider, 1989c) and cohortic behaviour, allowing direct *in situ* growth and production estimation (van der Veer and Oorthuysen 1985; Lucas *et al.*, *in press*). Such characteristics are not universal in this species however (Olesen *et al.*, 1994; Lucas *et al.*, *in press*). Other medusae, including *Aglantha digitale* (McLaren, 1969) and *Phyllorhiza punctata* (García 1990), and also the chaetognath *Sagitta elegans* (Zo, 1969; McLaren, 1969; Sameoto, 1971) have also been examined using cohortic methods. Other techniques utilised in the estimation of production include laboratory examination of growth and mortality rates (Greve, 1972; Hirota, 1974; Reeve and Walter, 1976) or under manipulated field conditions (ie. mesocosm work: Reeve and Walter, 1976), with the application of these rates to natural biomass and abundance data (Hirota, 1974; Reeve and Baker, 1975, 1976; van der Veer and Sadée 1984; Roff *et al.*, 1990). These methods assume that laboratory populations behave in a similar way to those in the field. In fact there are many problems left unresolved with regards to relating laboratory food concentrations and prey patchiness to those in the field (Reeve and Baker, 1975; Reeve and Walter, 1978; Miller and Daan, 1989). Estimates of production have also been made

by examination of changes in total standing stock (McLaren, 1969; Larson, 1985; Schneider, 1989b; Lucas *et al.*, *in press*), called here the 'Total biomass change' method. This method generally underestimates production considerably compared to more accurate cohort derived estimates (personal observations from examination of various *Aurelia aurita* production studies), although overestimation is possible when de-growth occurs. The assumption that the population is closed and samples representative of an area should be met and patchiness accounted for or errors may arise.

The construction of simple (van der Veer and Sadée, 1984; Larson, 1985; Båmstedt, 1990; Larson, 1991) or complex energy-budgets (Kremer, 1976; Schneider, 1989b; Hansson and Norrman, 1995) have been applied in attempts to model or assess growth, assimilation or ingestion demands. Such budget construction is limited by the information available for a species. Respiration rate estimates have been applied in an attempt to estimate minimum ingestion demands (Bishop, 1967; Sameoto, 1972; Larson, 1987d). Efforts have also been made to construct more complete *in situ* energy budgets of gelatinous predators, incorporating; growth, reproduction, respiration and DOC release (Hansson and Norrman, 1995). The production or consumption by a population may be determined using an energy budget approach. Thus production (P, somatic and reproductive) is given by:

$$P = C-(F+U+R) \qquad (1)$$

Where C is consumption (food ingested)
F is faeces (food lost through defecation)
U is excretion (food lost through DOM release)
R is respiration (food lost through metabolic demand)

Studies combining data of abundance of prey and predators with gut content analysis and digestion rates have been undertaken to assess the ingestive impact of gelatinous species (Larson, 1987d; Daan, 1989). Clearance rate experiments conducted in the laboratory (Morand *et al.*, 1987; Stoecker *et al.*, 1987a; Båmstedt *et al.*, 1994; Frid *et al.*, 1994; Olesen, 1994), or under *quasi*-natural conditions (Miller and Daan, 1989), have also been used in quantifying gelatinous predation rates.

There are still some important problems to be overcome regarding the quantification of the production of gelatinous organisms before their true role may always be correctly assessed.

Schneider (1992) highlighted the importance of measuring metabolic rates of gelatinous zooplankton in carbon-specific terms. Elemental specific rates are particularly important when comparisons are made between gelatinous organisms, which have a carbon content between 1-32% of dry weight, and crustaceans, which have a carbon content of 24-67% of dry weight (Schneider, 1989d).

Our understanding of the quantitative significance of gelatinous zooplankton has been constrained by the small amount of information available which integrates consumption rates with information on the growth rates and population dynamics of these predators and their prey (Alldredge, 1984). Gelatinous predators have only rarely been incorporated into ecosystem models. Not only have they been commonly ignored, but some species are notoriously difficult to sample or preserve without their destruction. Some effort has even been made to actively exclude them from plankton samples (Heinle, 1965; Williams and Deubler, 1968; Burrell and van Engel, 1970). Indeed, an examination of much of the current literature on the impact of gelatinous species often reveals shortfalls regarding the study of their prey abundance and consumption, and the impact of their feeding.

The gelatinous species within Southampton Water have been examined by several workers including; Zinger (1989) and Williams and Reubold (1990). Although a more recent and exhaustive study of this group was made by Lucas (1993), with further population analysis presented in Lucas and Williams (1994), Lucas and Williams (1996), Lucas *et al.* (1995) and Lucas *et al.* (*in press*). Lucas (1993) has not only made extensive measurements upon gelatinous zooplankton, and attempted to quantify their production rates, but has also attempted to assess their impact upon the mesozooplankton. In the present investigation the aim of assessing the impact and role of gelatinous zooplankton within Southampton Water is continued. The gelatinous group in Southampton Water is dominated by just 4 species; the scyphomedusa *Aurelia aurita*, the hydromedusa *Clytia hemisphaerica*, the ctenophore *Pleurobrachia pileus*, and the chaetognath *Sagitta setosa*. Estimates of their production rates and/or ingestion demands, and an assessment of their predatory impact are made at several sites and over several years within Southampton Water in the present investigation.

5.2 METHOD

The collection, separation and preservation techniques for the gelatinous predators collected during the 14 month abundance investigation are described in section 2.2. Once separated the gelatinous species were identified and counted. Measurements of the bell diameter

of *Aurelia aurita* ephyrae and medusae were made to the nearest millimetre using a ruler for large individuals and to the nearest 0.5 millimetres using an eye-piece graticule for small individuals (made by C.H.Lucas). Möller (1980a) found the diameter of *A.aurita* medusae decreased to 85.6-71.5 % of their live size when stored in 4% sea-water formaldehyde solution for periods of 181 to 197 days. Corrections were also made by van der Veer and Sadée (1984) for *Pleurobrachia pileus*, who used a shrinkage factor of 20% for all size classes after preservation in 4% formaldehyde solution (Oorthuyzen and Sadée, 1982). However, measurements in the present study were made after preservation in low concentrations of formaldehyde (typically less than 0.4%), concentrations of around 0.5% formaldehyde having previously been shown to be the most appropriate for gelatinous species such as *Pleurobrachia.* At such concentrations there being little change in size over periods of up to 27 months (Hirota, 1974). No corrections for preservation shrinkage were therefore made in the present investigation for *A.aurita* or *P.pileus*. Head-tail length measurements were made to the nearest 0.1 millimetres for *Sagitta setosa* in the Calshot and Bury Buoy 5 metre samples (as given in Hunter, 1996) using a microscope with an eye-piece graticule. Since *S.setosa* were separated after several months of preservation in 4% formaldehyde-seawater corrections to allow for shrinkage were made. Reeve and Baker (1975) estimated that *Sagitta* preserved in 5% formaldehyde-seawater decreased in length by 20% after a preservation period greater than 1 month, all *S.setosa* preserved lengths were therefore corrected by multiplying by 1.25. Data for *A.aurita, Clytia hemisphaerica, P.pileus* and *S.setosa* taken from Lucas (1993) and used in the present investigation were not corrected for shrinkage as individuals were measured fresh, measuring techniques are all given in Lucas (1993). All individual sizes were converted to carbon weight to allow biomass and production estimation. Where appropriate the regression equations of size (bell diameter, oral-aboral length or head-tail length) versus dry weight were used prior to carbon conversion. The dry weight equations determined by Lucas (1993) are given below and presented in graphical form in Figure 5.2.1, the measurements being made upon specimens collected from Southampton Water. L and DW being the bell diameter in millimetres, and dry weight in grams for *A.aurita*, and head-tail length in millimetres and dry weight in milligrams for *S.setosa.*

***Aurelia aurita* (g):**

$$\log DW = -5.3733 + (2.8232 \log L) \qquad (2)$$

(n=125, r=0.9760)

***Sagitta setosa* (mg):**

(n=36, r=0.8370)

$$\log DW = -3.5049 + (2.5180 \log L) \quad (3)$$

Individual *Aurelia aurita* and *Sagitta setosa* weights were calculated by converting dry weight (from the equations above) to carbon weight using the conversion factors given in Table 5.2.1. For *Aurelia aurita* the carbon content of medusae was calculated using the relationship given by Schneider (1988), where 1mgDW=0.0514mgC for medusae 20-50mm and 0.0701mgC for <20mm. Since no carbon weights were given for medusae between 50 and 120mm by Schneider (1988) then the conversion factor for the 20-50mm sized individuals were also applied to medusae greater than 50mm. Schneider (1988) found that individuals from 120 to 310mm had a carbon weight which was around 5% of dry weight, as such the percentage which carbon is of dry weight would appear to stabilize in the larger sized individuals. For *Sagitta setosa*, dry weight was converted to carbon by assuming carbon to be 39.4% of dry weight, as determined for *Sagitta elegans* by Sameoto (1971). For *Clytia hemisphaerica* and *Pleurobrachia pileus* direct equations relating carbon to length (bell diameter and pole length respectively) taken from the literature were used. Direct conversions of this type being preferable to dry weight to carbon conversion in the truly gelatinous forms (Hirst and Lucas, *in prep.*). For *Clytia hemisphaerica* individual carbon weights were estimated from: $W(\mu gC)=0.773(\text{Bell Diameter})^{2.012}$ (Daan, 1989), and for *Pleurobrachia pileus*: $W(\mu gC)=1.033(\text{Pole Length})^{2.93}$ (Miller and Daan, 1989). Production and ingestion rates are expressed in units of carbon, once again this being preferable to dry weight and ash-free dry weight when comparisons between trophic levels are being made (Hirst and Lucas, *in prep.*). The sampling sites; Greenland, N.W.Netley and Cracknore were chosen by Lucas (1993). In the present investigation samples were also taken from these sites (in addition to other locations) however, Hamble was used as an alternative site to Greenland. Given the relative closeness of these sites (see Figure 2.2.1) the results from these have been freely interchanged in all further comparisons.

A variety of methods for estimating production and ingestion demands have been applied in the present investigation, depending upon the population dynamics of the species and the information available. It is accepted that a variety of different methods could potentially have been applied, each would have given differing results. However, the methods which have been chosen were believed to be the most appropriate. Each species is dealt with separately below.

SPECIES Size	C%DW [NO.INDIVIDUALS / DETERMINATIONS]	CARBON BODY DIMENSION RELATION (W in µgC)	SOURCE
Aurelia aurita			
†<20mm	7.01 [6]		Schneider (1988b)
†20-50mm	5.14 [6]		
120-140mm	5.42 [6]		
200-220mm	4.88 [4]		
270-310mm	4.76 [5]		
120-280mm	-	$W=(20.85+(0.076296(BD/10)^{2.75}))*1*10^3$ [-]	
20mm	3.29 [-]		Matsakis & Conover (1991)
150mm	2.37 [-]		
20-150mm	-	$W=9.516(BD/10)+58.696$ [8]	
ns	4.3 [6]	$^1W=0.1634BD^{2.9}$ [-]	Larson (1985, 1986a)
†*Phialidium hemisphaericum*	-	$W=0.773*BD^{2.012}$ [48]	Daan (1989)
Phialidium gregarium	9.4 [13]		Larson (1986a)
Phialidium lomae	6.8 [13]		Larson (1986a)
†*Pleurobrachia pileus*[6]	-	$W=1.033PD^{2.93}$ [ns]	Miller and Daan (1989)
Pleurobrachia pileus	-	$W=(0.6493PD^{2.6411})*1.34$ [-]	Hoeger (1983) and Lucas (*pers. comm.*)
Pleurobrachia pileus	3.4 [-]		Hoeger (1983)
Pleurobrachia pileus	2.56-4.74 [26] (mean 3.68[2])		Schneider (1989a)
Pleurobrachia bachei	3.6-5.3 [-]		Reeve & Walter (1976)
Pleurobrachia bachei	2.5 [-]		Reeve (1980)
Pleurobrachia bachei	3.28 [10]		Reeve *et al.* (1978)
Pleurobrachia bachei			Mullin and Evans (1974)
<4mm	-	$W=1.2218ED^{0.92}$ [~15]	
>4mm	-	$W=1.0ED^{2.35}$ [~41]	
Pleurobrachia bachei	3-8 [-]		Kremer *unpublished* (given in Larson, 1985)
Pleurobrachia bachei	5.1 [5]		Larson (1985)

SPECIES Size	C%DW [NO.INDIVIDUALS / DETERMINATIONS]	CARBON BODY DIMENSION RELATION (W in µgC)	SOURCE
Sagitta elegans	†39.4 [10]	$W=0.0382L^{2.365}$ [-]	Sameoto (1971)
Sagitta elegans	-	$W=0.0356L^{2.95}$ [12]	McLaren (1969)
Sagitta elegans	[4]39 [-]		Curl (1962)
Sagitta elegans	39 [-]		Reeve (1980)
Sagitta enflata	18 [-]		Reeve (1980)
Sagitta hispida	45 [-]		Reeve (1980)
Sagitta hispida	[5]40.7 [-]		Reeve and Baker (1975)
Sagitta crassa & *S. crassa* f. *naikaiensis*	-	$W=0.05129L^{3.16}$ [~21]	Uye (1982b)
Sagitta crassa f. *naikaiensis*	49.66 [-]		Hirota (1981)

TABLE 5.2.1 Comparison of measurements of carbon weight (CW) as a percentage of dry weight (DW), and carbon to body dimension relationships, for the gelatinous species examined in this study and their congenerics. † denotes those conversion factors utilized in the present investigation either directly, or in combination with the dry weight equations already given. BD is Bell Diameter (mm), ED is Equatorial Diameter (mm), PD is Pole Diameter (mm) and L is head-tail length (mm).

1 Calculated by applying C%WW=0.1634 to equation relating BD to WW. 2 Mean of 3 monthly averages. 3 Relationship determined by applying the data of Hoeger (1983), who found carbon weight equal to 0.134% of live weight (WW) in *Pleurobrachia pileus*, to a length to wet weight equation derived from data supplied by Lucas (*pers. comm.*), where logWW(mg)=-0.18755+(2.6941logPD) (n=99, r=0.884). 4 Curl (1962) found that the total carbon value for a sample of *Centropages* sp. and *Sagitta elegans* in equal numbers to be 38.7%, and for a sample of *Centropages* sp. alone was 38.5%, as such the value for the chaetognath alone must be around 39%. 5 Text unclear on conversion (2 values given), first conversion used. 6 Length measurements although not defined in paper are pole diameters (R.J.Miller, *pers. comm.*).

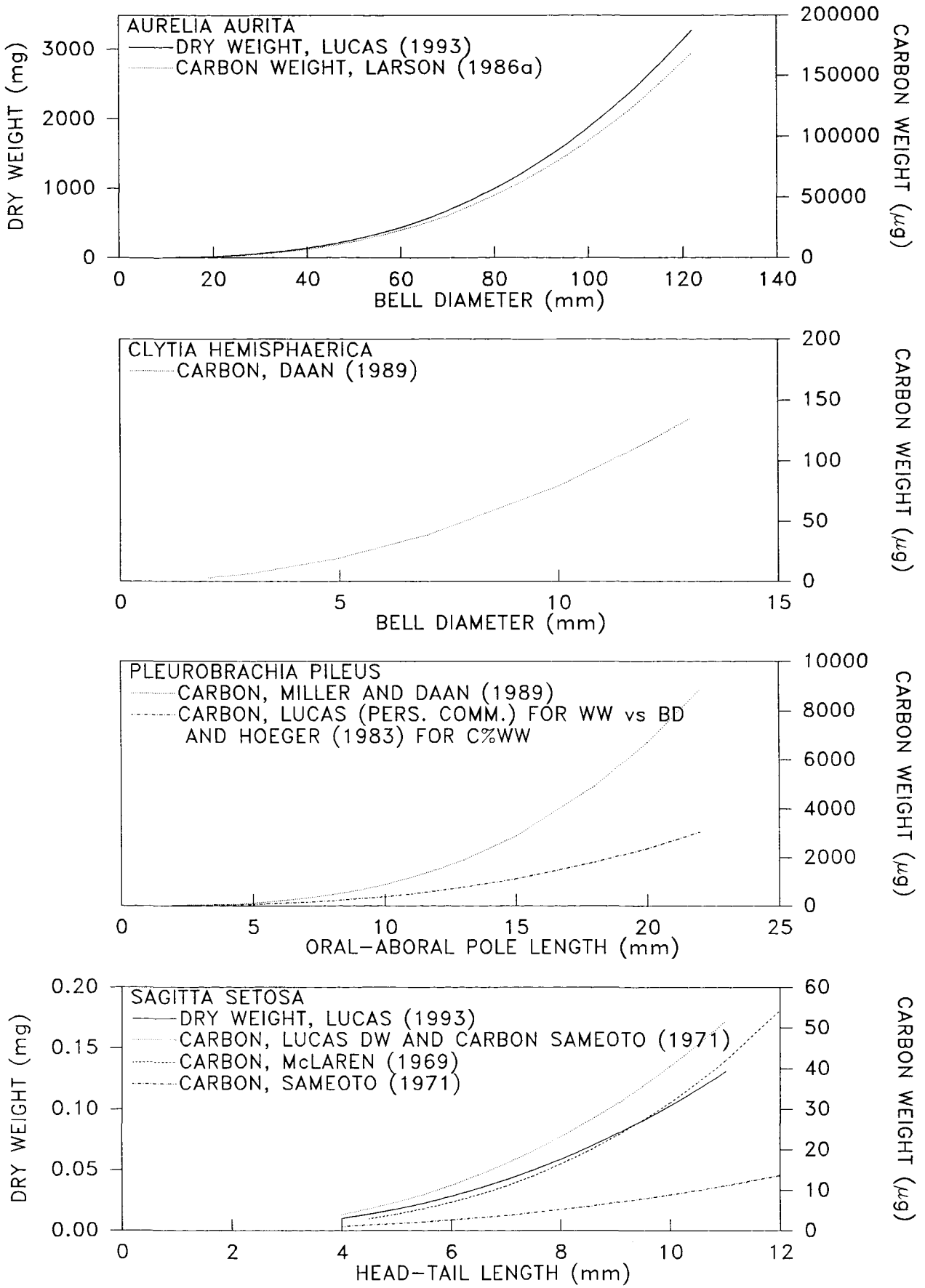


FIGURE 5.2.1 Length–weight regressions for the major gelatinous predators within Southampton Water. See text and Table 5.2.1 for details.

***Aurelia aurita*:**

The extensive data set available for *Aurelia aurita* allowed an examination of production of this species not only during 1993 but also for some sites during the years 1990, 1991 and 1994 from data supplied by C.H.Lucas. Recalculation of production of *A.aurita* from those values given by Lucas (1993) was necessary for various reasons. Mean weights should not be estimated directly from mean bell diameters as the equations describing individual dry weight as a function of size are non-linear. To avoid biased estimates of mean weight it is essential that each bell diameter should be converted to weight, the mean weight may only then be made from this data set (Bird and Prairie, 1985). Using the mean weights calculated from a mean bell diameter can make great differences to the production estimates for this particular data set (for example, at Cracknore during 1993 production would be underestimated by 19%). This procedural mistake appears to have been made previously by several authors in the assessment of gelatinous production (eg. Sameoto, 1971). No corrections for other biases because of transformation were made in the present investigation (see Bird and Prairie, 1985). It should also be noted that rather than estimating recruitment production at the time when individuals first appeared, it should be made from the point where density reaches is maximum. Such an error leads to an underestimation of true production for *Aurelia aurita* as produced biomass may be missed. In the present investigation however, since most production occurs at the end of the pelagic presence of *A.aurita*, then this makes only a small difference to the annual estimates. In the estimates of Lucas (1993) the Removal-Summation method was used and the results from this technique were heavily drawn upon in analysis. However, this equation was incorrectly applied by Lucas. When correctly applied it should give results identical to those from the Increment-Summation method (over the entire life span of a cohort). Dry and ash-free dry weight were also used in balancing the production of *A.aurita* with the supply of mesozooplankton (Lucas,1993; Lucas and Williams, 1995). Such comparisons may lead to erroneous conclusion through quantification problems (Hirst and Lucas, *in prep.*). To give an example, if *A.aurita* had a dry weight production of $1 mgDWm^{-3}d^{-1}$, whilst copepod prey had a daily production of $1 mgDWm^{-3}d^{-1}$, it would appear there rates of production were equal. However, assessing production in these units gives a totally false impression of the energy-matter transfer, given that such rates represent $0.4 mgCm^{-3}d^{-1}$ for the copepods and as little as $0.051 mgCm^{-3}d^{-1}$ for the *Aurelia aurita*.

The production of *Aurelia aurita* was calculated assuming a single cohort per year. This assumption is not strictly true, as recruitment was of a non-instantaneous nature, thus the population was quasi-cohortic. Two cohort production methods; Increment-Summation (IS) and Instantaneous-Growth Rate (IG) were used. The formulas of each of these methods being taken

from Morin *et al.* (1987):

$$IS = B_1 + \sum_{i=1}^{ndate-1} 0.5(D_i + D_{i+1}) \cdot (M_{i+1} - M_i) \quad (4)$$

$$IG = B_1 + \sum_{i=1}^{ndate-1} 0.5(B_i + B_{i+1}) \cdot \ln(\frac{M_{i+1}}{M_i}) \quad (5)$$

Where D_i is the mean density on sampling date i,

M_i is the mean individual mass on sampling date i,

B_i is the total biomass on sampling date i,

ndate is the number of sampling dates after and including date of peak densities.

It is important to note that B_1 is the biomass of individuals at the point where densities of individuals peak and not at the point where recruitment begins. Rates of daily production were estimated by dividing the production estimates attributable between two consecutive sampling points by the number of days between these two points. The rates of production per day for the period up to the point where densities reached their peak (the initial or 'recruitment' production) was calculated by dividing the biomass increase since the previous production estimate by the number of days between points. The 'recruitment' production estimate for the IS and IG methods are therefore identical. As individuals are recruited from benthic polyps the benthic release weight of pelagic individuals should be removed from their subsequent weights before estimating (pelagic) production. However, since these initial weights will be very small with ephyrae of less than 1mm being released into the water column (Lucas, 1993), and no release weights having been measured, then this term has been ignored in all calculations. In several instances after the point where maximum densities were observed, the density of individuals increased between consecutive sampling points. When this occurred the production between the two periods was estimated in the Increment-Summation calculations as the total biomass at the point of greater density minus the biomass found on the previous occasion. In estimating production using the Increment-Summation method production should be handled as detailed here. The continued application of the equation (as applied by Zo, 1969) leads to potentially large underestimates of true production. At Cracknore during 1994 for example, production of *Aurelia aurita* would be 13% less if such effect were not accounted for. It is important to note at this point that since temporally distributed production and ingestion rates of this species were compared to temporally distributed prey production, then Increment-Summation was appropriate rather than Removal-

Summation. Although this point has apparently gone ignored in the literature, Increment-Summation gives production for the periods when growth occurs, while Removal-Summation distributes production into the periods when the biomass of the examined population is lost. Thus the methods give identical results for total production of a cohort, but distribute the production differently over that period. The Removal-Summation method does not allow temporally distributed estimates of production, in fact strictly only allows production to be measured over the entire life-span of a cohort, over parts of the life-history it does not even measure what has been defined as 'production'.

During the 14 month investigation discrete samples of *Aurelia* were collected from two depths (5 and 10 metres), the data sets being combined prior to the calculation of production and growth, to allow for vertical movements. Mean density for each size class were calculated on each date eg. for the individuals of 3mm length, if there were 0.5 per m^3 at 5 metres depth and 1.0 per m^3 at 10 metres then there are 0.75 per m^3 on an integrated basis. Mean individual weight for each point in time could then be calculated by converting each size class per m^3 to the appropriate weight per m^3. All the weight classes per m^3 were then added to give total weight per m^3. The mean weight was calculated by dividing the total weight per m^3 by the total number of individuals per m^3. In other years of study (ie. 1990, 1991, and 1994) samples were collected only from 5 metres, in such cases there could be no depth integration.

Instantaneous specific growth rates (μ, d^{-1}) were also calculated between sampling points, after the point of recruitment production (thus assuming no more individuals were recruited into the population), by using the following equation:

$$\mu = \frac{\ln (M_{i+1} / M_i)}{t} \qquad (6)$$

Where t is the number of days between sampling date i and i+1,

Mean individual mass (M) in units of dry weight rather than carbon were used to allow comparisons with Olesen *et al.* (1994).

Although the problems of using dry weight as a measure of biomass will be highlighted and associated problems discussed in detail by Hirst and Lucas (*in prep.*), in the present investigation Instantaneous specific growth rates (ISGRs) for *Aurelia aurita* are compared between studies using dry weight. In this instance this would appear appropriate since

comparisons of dry weight estimates from the equation of Lucas (1993) with those from Olesen *et al.* (1994) showed that the two are very stable proportions of one another for equally sized individuals, ie. dry weight from Lucas is ~2.45-2.48 times greater than dry weight estimated from Olesen *et al.* (1994) over the range 1mm to 100mm bell diameter. ISGR values may therefore be compared directly without the need for body weight correction as a result of salinity effects. A cautionary note must be made however: application of other dry weight equations would not produce comparable results if there were not this constancy in their relationships.

The coefficient of daily exponential population biomass increase (K) was also calculated for each of the gelatinous predator species as follows:

$$K = \frac{\ln (B_{i+1} / B_i)}{t} \qquad (7)$$

Where Biomass (B) was applied in units of dry weight rather than carbon to allow comparison with Larson (1985; 1986b)

Two new equations have been derived in the present study for calculating the 'upper' and 'lower' possible limits to the production of a cohortic species (UPL and LPL respectively). These are presented below and have been applied to the *Aurelia aurita* data. They may be used on cohortic populations and allow, assuming that the densities and mean weights at each point in time to be correct, the maximum and minimum limits of production during a period to be determined. The assumptions for the equations are that the mean weight of individuals at no point strays outside the limits set by the mean weights at the start and end of the period. The other assumptions are the same as those which apply to all cohort methods, ie. no weight dependent mortality, instantaneous recruitment etc.

During periods in which the mean weight increases the equations applied are:

$$UPPER\ PRODUCTION\ LIMITS = B_1 + \sum_{i=1}^{ndate-1} (D_i) \cdot (M_{i+1} - M_i) \qquad (8)$$

$$LOWER\ PRODUCTION\ LIMITS = B_1 + \sum_{i=1}^{ndate-1} (D_{i+1}) \cdot (M_{i+1} - M_i) \qquad (9)$$

During periods when mean weight decreases the equations are:

$$UPL = B_1 + \sum_{i=1}^{ndate-1} (D_{i+1}) \cdot (M_{i+1} - M_i) \qquad (10)$$

$$LPL = B_1 + \sum_{i=1}^{ndate-1} (D_i) \cdot (M_{i+1} - M_i) \qquad (11)$$

Production calculations may be complicated by the fact that during the life of a cohort the number of individuals may appear to increase. When this occurs it is not possible, given the information available in the present investigation, to calculate the upper and lower limits. Such periods have therefore been treated differently. Rather than estimating limits between consecutive points, when there is a subsequent increase in numbers, the lower values are ignored and the equations utilised between the point before the temporary low and the point after it. An index has also been derived which allows an assessment of the potential accuracy of a cohort measure. The equation for this index is:

$$INDEX\ OF\ VARIABILITY = \frac{LPL}{UPL} \qquad (12)$$

Index values tend towards one as the limits converge, thus indicating restricting limits and that the measure itself must lie close to true value. Values tend towards zero as the limits diverge and the possible range of values increase.

A carbon budget approach has also been undertaken regarding the *Aurelia aurita* population of 1993, thus allowing an estimate of carbon divisioning and ingestion demands both temporally and spatially within the estuary. An energy-budget was completed for *Aurelia aurita* by Schneider (1989b) in Kiel Bight, with subsequent extension by Hansson and Norrman (1995). Lucas (1993) also constructed an energy budget for *A.aurita* within Southampton Water. In the present study respiration was estimated by applying the equations given by Larson (1987a) where respiration at 10°C may be estimated from:

$$\mu lO_2\ hr^{-1}\ ind.^{-1} = 0.20X^{0.92} \quad (13)$$

and at 15°C it becomes:

$$\mu lO_2\ hr^{-1}\ ind.^{-1} = 0.39X^{0.91} \quad (14)$$

Where X is individual dry weight in mg

When the temperature at time of sample collection was less than 12.5°C the first equation was applied, and when greater than 12.5°C the second equation was applied. Rather than applying the equation to each individual it was applied more simply to the mean individual dry weight at each point in time. As the dry weight relationship given by Larson (1985) is similar to that for Southampton Water no correction for salinity effects need be made. Calculated oxygen consumption rates were then converted to carbon consumption applying a respiratory quotient (RQ) of 0.8 (as applied by Larson, 1987a). Kremer (1977) found that in a ctenophore the RQ was 0.74. Since *Aurelia* is predominantly carnivorous its respiratory quotient (RQ) should be between 0.7 (lipid catabolism) and 0.8 (protein catabolism). Thus:

$$\mu gC.m^{-3}.d^{-1} = (\mu lO_2.ind^{-1}.hr^{-1}) \times 24 \times N \times 0.8 \times \frac{12}{22.4} \quad (15)$$

Where N is the density of individuals (ind. m^{-3})

0.8 is the RQ

12 is the atomic weight of carbon

22.4 is the volume of 1 mole of O_2 at STP

Release of DOC by *Aurelia aurita* medusae ranging in bell diameter from 9.5 to 18cm was measured by Hansson and Norrman (1995). They found no relationship between DOC release rate and medusae size (diameter, wet weight or ash-free dry weight). Utilising their release rates (mg DOC released d^{-1}) with their estimated medusae weights (mgC $individual^{-1}$), it is possible to determine rate of release per mgC medusae weight. As such release rates vary from 0.025 to 0.0065mgC (mgC medusae)$^{-1}$ d^{-1}. An average value of DOC release equal to 1.55% of mean body weight per day (mgC $ind.^{-1}$ d^{-1}) was chosen for application in this study. A size

dependent rate was chosen contrary to the results of Hansson and Norrman (1995) as their examination included only large individuals (9.5-18cm bell diameter). If DOC release were linked to the metabolism of the animal then it would be expected that there would be a size/weight dependent relationship (Hansson and Norrman, 1995). Since smaller individuals are likely to have a lower rate of DOC release given typical body weight dependence of metabolism this was why a body weight dependent measure was chosen.

Total assimilation demand was derived from the addition of field measured production (reproductive and somatic), respiration and DOC excretion, this total being converted to ingestion demand assuming an assimilation efficiency of 80% (as utilised by Schneider, 1989b). Assimilation efficiency appears to not have previously been reported in this species, however an efficiency of 80% is typical for a carnivorous predator (Valiela, 1984), and it is also mid-range of the values generally found for other gelatinous organisms (ie. 70-90%: Larson, 1985; also see review by Alldredge, 1984). It has however been found to reach as high as 91.1% in siphonophores feeding upon copepods (Purcell and Kremer, 1983) and 100% in *Mnemiopsis mccradyi* (Kremer *et al.*, 1980). *Pleurobrachia bachei* feeding upon copepods were found by Reeve *et al.* (1978) to have values between 19 and >100%.

Comparisons between laboratory feeding experiments and estimates of the natural ingestion demand of *Aurelia aurita* were undertaken utilizing the equation for daily ration (DR), which was estimated as follows:

$$DR\ (\%) = \frac{PREY\ INGESTED\ [CARBON]}{PREDATOR\ MASS\ [CARBON]} \times 100 \qquad (16)$$

***Clytia hemisphaerica, Pleurobrachia pileus and Sagitta setosa* :**

Estimates of the secondary production of the gelatinous species *Clytia hemisphaerica*, *Pleurobrachia pileus* and *Sagitta setosa* have been made for Southampton Water by Lucas (1993) and Lucas *et al.* (1995). In these studies cohort dependent production equations were applied after dividing the populations into cohorts by eye. As already outlined the equations used were in part or entirely misapplied, the units chosen for analysis were also problematic for interpretation. Furthermore, for these 3 species cohort identification and separation was not appropriate. New estimates of production have therefore been calculated using more suitable methods.

***Clytia hemisphaerica*:**

Estimates of the annual production by *Clytia hemisphaerica* were made by Lucas (1993) and Lucas *et al.* (1995). In both works cohorts were separated by eye and then utilised in the estimation of production. Lucas *et al.* (1995) believed that there was continuous reproduction in 1990, with no discernible cohorts. In 1991 five cohorts were distinguished, being produced at 21-80 day intervals. Unfortunately the cohort identification was inappropriate due to the variation in densities and sizes. In this study the 'Total biomass change' method was chosen to estimate production. The 'Total biomass change' method for estimating production has been utilised previously for gelatinous predators when cohorts have not been discernible (Larson, 1986b; Lucas *et al., in press*). This method involves summing the total biomass increases over time. To estimate total assimilation an estimate of daily respiratory carbon demand was added to this estimate of production. Larson (1987a) found that for *Phialidium lomae* (*Clytia hemisphaerica* formely named *Phialidium hemisphaericum*) daily respiratory carbon turnover was equal to 5% of body carbon per day (at 15°C), and for *Phialidium gregarium* it was between 3 and 5% (at 10 to 15°C). Schneider's (1992) compilation study showed a mean body carbon turnover per day of 4.7% for cnidarians and ctenophores (assuming an RQ of 0.8) at 15°C. In the present study a value of 3% was therefore applied to the biomass data when the environmental temperature at the time of sampling was nearer to 10°C, and a value of 5% when it was closer to 15°C. As ~70 to 90% of the carbon ingested is generally assimilated in gelatinous predators the value of assimilation was multiplied by 1.25 (assuming an assimilation efficiency of 80%) to give an estimate of ingestion demand. No estimates for carbon excretion were included.

***Pleurobrachia pileus*:**

Southampton Water is a tidally dominated estuary in which great changes in gelatinous biomass over short time periods have been observed. Such changes may be the result of growth and mortality, although the movements of water may also be important. Some gelatinous predators, including *Pleurobrachia pileus*, have also been shown to be partially allochthonous to estuarine areas. *P.pileus* has been shown to be transported into coastal and estuarine areas from more offshore regions through the influx of offshore water (Möller, 1977; Schneider, 1987), this process being facilitated at times by tidal migration patterns (van der Veer and Sadée, 1984). In the intensive study of Hirota (1974), the size frequency of *Pleurobrachia pileus* was found to change drastically on a short terms basis. These changes were attributed to 'immigration of individuals into advected water'. For these reasons it was therefore unadvisable to use the 'Total biomass change' method which relies upon autochthonous production of biomass. In addition,

since there were rapid changes in *Pleurobrachia pileus* biomass and abundance within Southampton Water, and since there were no discernible cohorts, then a non-cohort method had once again to be used. The method chosen was therefore one based upon the ratio of growth and ingestion to carbon demand of respiration. Firstly respiration was estimated by applying the equations given by Larson (1987a) for the congeneric *Pleurobrachia bachei*, where respiration at 10°C is:

$$\mu lO_2\ hr^{-1}\ ind.^{-1} = 0.14X^{1.05} \qquad (17)$$

and at 15°C it becomes:

$$\mu lO_2\ hr^{-1}\ ind.^{-1} = 0.85X^{0.71} \qquad (18)$$

Where the terms are as previously defined. When temperature was closer to 10°C the first equation was applied, and when nearer to 15°C the second was used. Calculated oxygen consumption rates were then converted to carbon consumption by applying an RQ of 0.8 (Larson, 1987a). Thus:

$$\mu gC.m^{-3}.d^{-1} = (\mu lO_2.ind^{-1}.hr^{-1}) \times 24 \times N \times 0.8 \times \frac{12}{22.4} \qquad (19)$$

Pleurobrachia pileus daily production and ingestion could then be estimated through application of ratios of growth and ingestion to carbon respiration given in the literature (see Table 5.2.2), the three methods used (a-c) were as follows:

Temperature (°C)	Size (mm)	Food Concentration Copepods l^{-1} (μgCl^{-1})	Carbon respiration as % of Total Carbon Ingested	Total Growth as % of Total Carbon Ingested	Total Growth as % of Respiration	Source
Pleurobrachia bachei						
[a]13	6	10 (*24*)	84.0	11.0	13.1	Reeve *et al.* 1978
[b]13	6	100 (*240*)	17.2	2.9	16.9	
[c]15	Adult	10-25 (*35*)	21	6.8[1]	31.8	Hirota 1972
Mnemiopsis mccradyi						
26	5	3	-	~5.0-6.5	-	Walter 1976
26	5	12	-	~4.7-5.4	-	
26	5	33	-	~2.3-4.2	-	
26	5	115	-	~1.6-3.4	-	
26	5	329	-	~2.3-2.7	-	

Table 5.2.2 Compilation of growth, respiration and ingestion studies on *Pleurobrachia bachei*. Results of growth efficiency for the ctenophore *Mnemiopsis mccradyi* also included for comparative purposes.

1 Calculated assuming that body carbon is 5% AFDW and that Hirota estimated it incorrectly at 50% of AFDW.

a Ratios used in Method a, b Ratios used in Method b, c Ratios used in Method c.

Method a

Calculated carbon respiration rates were converted to daily ingestion and growth using ratios calculated from Reeve *et al.* (1978) for *Pleurobrachia bachei*, measured in laboratory experiments with 10^3 copepods per m^3. Carbon respired was converted to ingestion demand assuming that respired carbon was 84.0% of total ingestion. Total growth was estimated from it being equal to 13.1% respiration.

Method b

Calculated respiration rates were converted to daily ingestion and growth also using ratios calculated from Reeve *et al.* (1978) for *Pleurobrachia bachei*. In this case measured in the laboratory with 10^4 copepods per m^3. Carbon respired was converted to ingestion demand assuming that respired carbon was 17.2% of total ingestion. Total growth was estimated as being equal to 16.9% of respiration.

Method c

Calculated respiration rates were converted to daily ingestion and growth also using ratios calculated from Hirota (1972) for *Pleurobrachia bachei*, measured in laboratory experiments with $1*10^4$ to $2.5*10^4$ copepods per m^3. Carbon respired was converted to ingestion demand assuming that respired carbon was 21% of total ingestion. Total growth was estimated from it being equal to 31.8% of respiration (values recalculated from Hirota (1972) assuming carbon to be 5% of AFDW rather than 50% as assumed in the original study).

***Sagitta setosa*:**

Sagitta setosa may be allochthonous to Southampton Water (Lucas, 1993), given the population changes apparent, with either the individuals being moved into the area and/or substantial parts of the population being missed on occasion (probably because of mesh sizes or vertical/horizontal patchiness). Other workers have also found *Sagitta setosa* populations to be advected in water masses (Jakobsen, 1971; Øresland, 1986). The 'Total biomass change' method could not be used to estimate production, neither could cohort estimates of growth be made. No method could be found for determining the production rate of *Sagitta setosa*. An apparently suitable method for estimating ingestion demand however was found. From temperature and prey size dependent estimates of digestion time, Frid *et al.* (1994) estimated that the average rate of food consumption by *Sagitta elegans* in Northumberland coastal waters was 0.4 prey chaetognath^{-1} d^{-1}. Reeve (1980) also made estimates of the ingestion rate of copepods by *S.elegans* at 13°C in the laboratory. At food concentrations of 60,000 copepods m^{-3}, ingestion rate of adults (16mm in length) saturated at around 4 prey d^{-1}, the prey consisting of adult and stage V *Acartia tonsa*. These experiments were run for 24 hours in the dark and therefore feeding rates may have been

overestimated because of changes in diel feeding behaviour. Reeve (1980) also quotes unpublished data of Sullivan in which mature *S.elegans* in large enclosures could consume 8 prey d^{-1}. Kuhlmann (1977) found that in the laboratory, *Sagitta* of 10-22mm (at 15°C) would feed at a rate of 1.8 copepods d^{-1}, the copepod prey consisting of *Pseudocalanus elongatus*, *Centropages* sp., and *Temora* sp. Øresland (1987) estimated that *S.elegans* in Gullmarsfjorden had a maximum feeding rate of 1.0 prey d^{-1}, while *S.setosa* had a mean rate of feeding of around 2.3 prey d^{-1}. These estimates were derived from gut content analysis conducted over a 24 hour period, and from estimates of digestion time. The maximum temperature at which *S.setosa* were found in Southampton Water was 18.8°C, but usually it was much lower than this. A maximum ingestion demand for *S.setosa* was made by assuming that maximum prey ingestion rate was 2.3 prey chaetognath^{-1} d^{-1} as found for *S.setosa* by Øresland (1987). This estimate being determined from a sample of *S.setosa* with a median length of 7mm, at a time when temperatures were around 14°C. This value was chosen as it was determined for *S.setosa* of similar median size to those in Southampton Water, and at temperatures near the maximum found in Southampton Water. Furthermore, these estimates took account of the changes which occur in feeding on a diel basis. Unfortunately Øresland (1987) gives no estimate of prey weights, however, prey ingestion was dominated by 'small' copepods. Assuming a mean weight at 4µgC (around an adult *Acartia* size) it is possible to estimate a feeding rate of 9.2µgC ind.$^{-1}$ d^{-1}. This value was therefore applied directly in the present investigation to density estimates to give ingestion demands. Although this method takes no account of changes in ingestion with size, application of this ingestion rate to the largest and smallest sizes found in Southampton Water (lower limit: 2mm or body weight 0.706µgC and upper limit: 15mm or body weight 112.7µgC) gives daily rations (in carbon terms) which appear to validate the method. Thus a daily ration (expressed in terms of predator weight) of 1304% for 2mm sized individuals, and 8.2% for 15mm size individuals, may be compared to estimates of daily rations derived from Reeve (1980) for *Sagitta hispida* at ~1000% and ~8% respectively. It should be noted that these values may be overestimates for some natural situations however (see results of Pearre, 1981).

Mesozooplankton Production:

To allow comparisons with the ingestion demands of the gelatinous predators the daily production of copepods was also estimated at the Calshot, Hamble, N.W.Netley and Cracknore sites. The density of calanoid copepodites and adults found by Zinger (1989) using a 100µm mesh net between April 1985 to April 1987 were converted to estimates of biomass by assuming a mean carbon weight of these individuals of 1.2µgC. This value being the average of the mean weights of *Acartia* spp. (copepodites and adults) found at Calshot over the 14 month investigation

(Chapter 2). These samples being collected with a 118μm mesh net (the range of mean weights being 0.54-1.83μgC ind.$^{-1}$). This value should be viewed as being an underestimate of the mean weight of copepods because, although it is the dominant calanoid species, *Acartia* is one of the smaller calanoids within the estuary. Biomass estimates were also made from the values of calanoid copepod abundance values found by Lucas (1993) using a 212μm mesh net. In this case a mean weight of 2μgC per individual was assumed, as a mesh of this size tends to catch predominantly stage 4 copepodites to adults. This weight was chosen as representative of late stage *Acartia* individuals, small stages of *Acartia* being grossly under represented in the mesh size used. Estimate of daily production (P in mgCm^{-3}) could then be made from the biomass estimate (B in mgCm^{-3}) by multiplying it by the instantaneous growth rate (g, d^{-1}).

$$P = B\,g \qquad (20)$$

The instantaneous growth rate being derived from the equation for marine copepods devised in Chapter 4:

$$\log_{10}[g] = -1.1352 + 0.0248\,[T] - 0.2976\,\log_{10}[BW] \qquad (21)$$

Where T is the temperature (°C)

and BW in this instance being simply the mean weight, ie. 1.2μgC and 2μgC

As Zinger (1989) and Lucas (1993) both took measurements of temperature in conjunction with zooplankton, samples site and date specific temperature measurements were applied to the equation for growth estimation.

Estimates of annual production transfer efficiencies were also made by comparing gelatinous production with that of the average annual copepod production estimates derived from the results of Zinger. The production estimates derived from the data of Lucas (1993) were not utilised as these were believed to underestimate copepod production. Annual ecological transfer efficiencies (E.T.E) were estimated as:

$$E.T.E = \frac{P_t}{P_{t-1}} \qquad (22)$$

Where P_t is the annual production on trophic level t

P_{t-1} is the annual production on the lower trophic level.

Annual estimates of the efficiency at which production is ingested at the next trophic level, the Utilization Efficiency (U.E), were also derived:

$$U.E = \frac{I_t}{P_{t-1}} \qquad (23)$$

Where I_t is the annual ingestion demand at trophic level t

and P_{t-1} as previously defined

5.3 RESULTS

***Aurelia aurita*:**

Densities of *Aurelia aurita* at each of the sampling sites and depths over the 14 month investigation are presented in Figure 5.3.1. The greatest depth averaged densities were found towards the head of the estuary, reaching a maximum 3.60 ind.m^{-3} at Cracknore, while maximum densities at N.W.Netley and Bury Buoy were 2.42 and 1.60 ind.m^{-3} respectively. At Hamble, densities reached 0.31 ind.m^{-3}, while no individuals were found at Calshot. The population distribution centred around the Cracknore site, whilst not reaching to the mouth of the estuary at Calshot. As well as these clear horizontal trends in the density of individuals there were also marked vertical differences. Densities were generally greater in the 5 metres depth samples, and only rarely did densities at 10 metres exceed those at 5 metres. Individuals first appeared on the 25th of February in 1993, being found at all sites except Calshot. Densities increased rapidly from this point until March when they peaked; subsequent declines in numbers were rapid. The residence time of the population within the pelagic system varied between sites, being greatest at Cracknore and Bury Buoy. At these two sites individuals were found until the end of June (plankton residence times 117 days). At N.W.Netley individuals were found until the start of May (plankton residence time 70 days), and at Hamble until the end of March residence time 29 days).

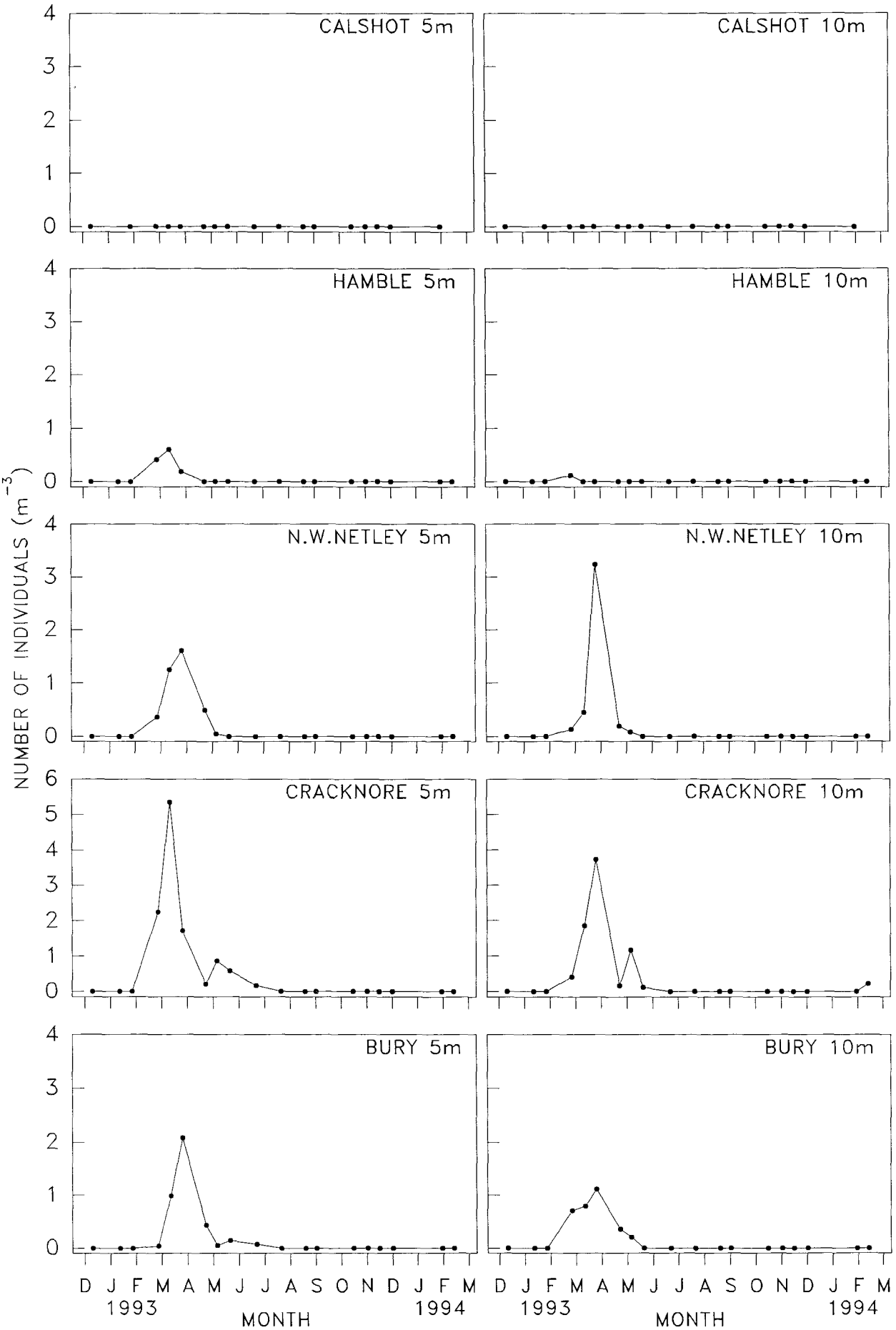


FIGURE 5.3.1 The density of Aurelia aurita at the sites and depths as indicated. (Note scale change).

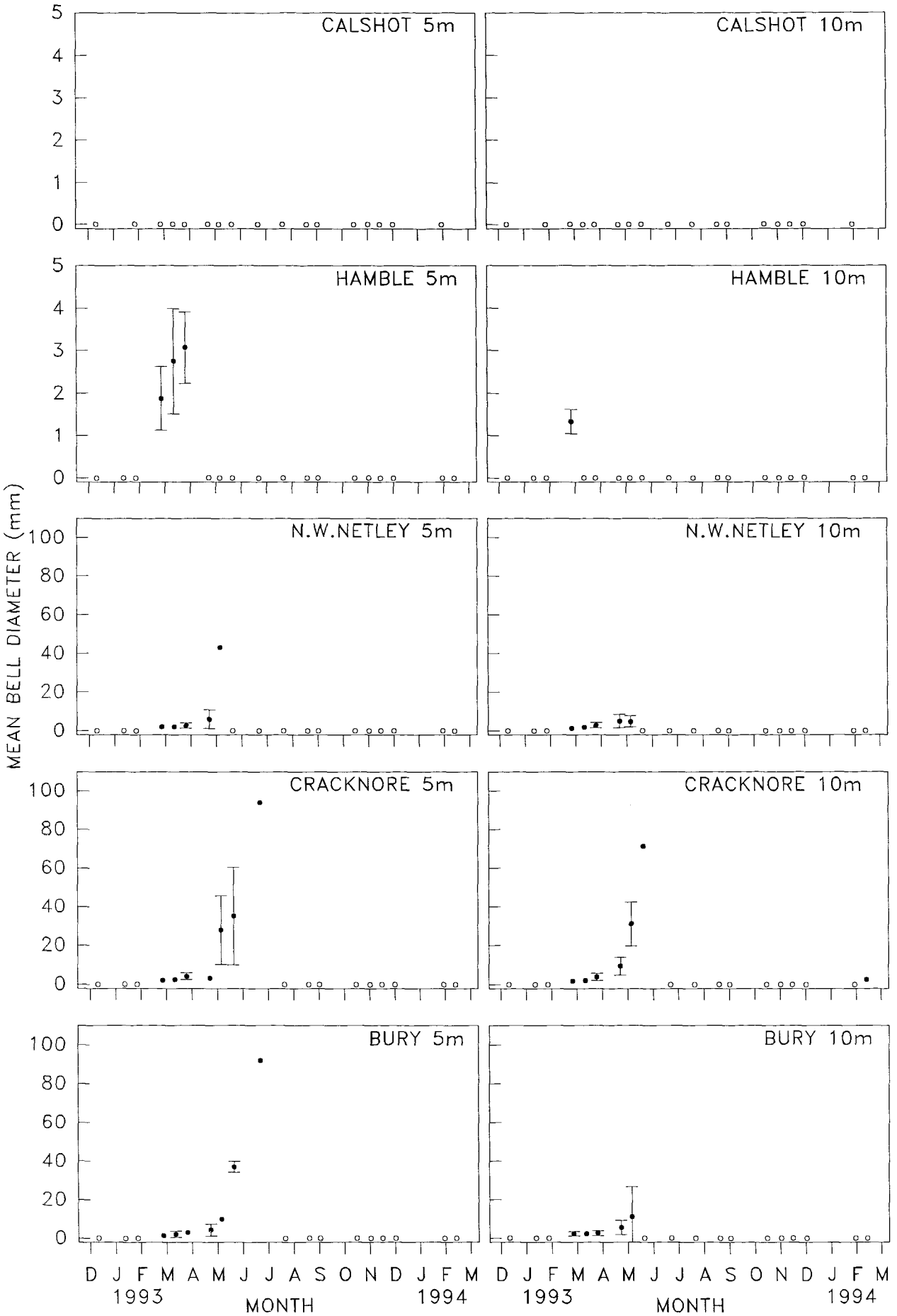


FIGURE 5.3.2 The mean sizes of Aurelia aurita individuals at each site and depth, on each sampling date. Standard deviations given by error bars. Hollow circles indicate no individuals present, filled circles indicate individuals present. (Note scale change).

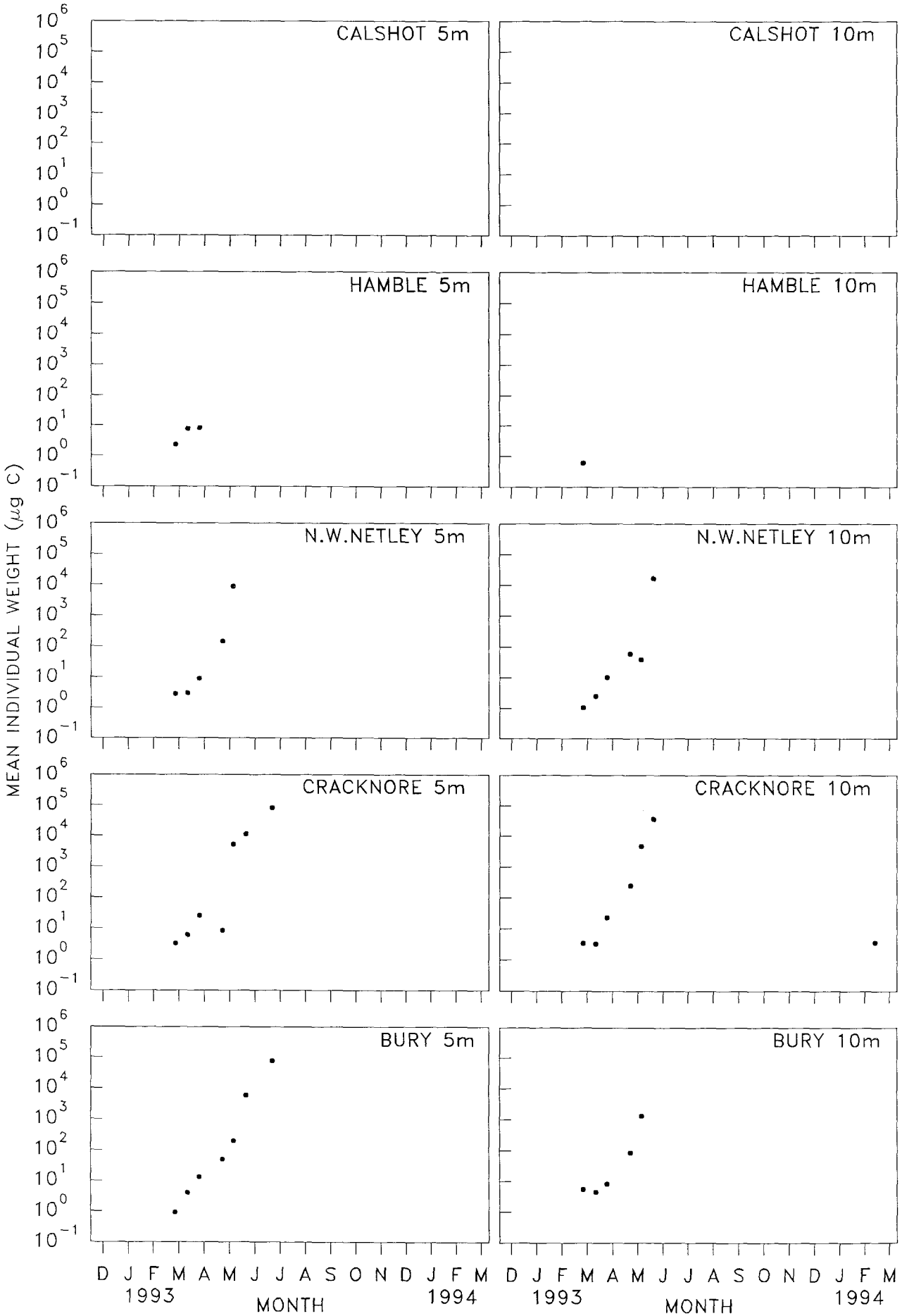


FIGURE 5.3.3 Calculated mean weight of Aurelia aurita individuals at the sites and depths as indicated.

Given the restrictions of sampling protocol, ephyrae appeared to be first released from benthic scyphomistae between the 26th January and 25th February.

The mean and standard deviation of the bell diameter of collected individuals are given in Figure 5.3.2. The mean individual carbon weights of *Aurelia aurita* individuals are given in Figure 5.3.3. The increase in mean size and weight is the result of growth, this however is countered to some degree by the prolonged input of small ephyrae (ephyrae defined as individuals with a diameter of less than 10mm). The 'recruitment' of ephyrae into the pelagic system may be assumed to proceed at least until March when densities at each site reached their maximum. Recruitment was non-instantaneous with numbers increasing and reaching a maximum within 1 month of the initial recording of their presence. After the peak in numbers small individuals continued to be collected, and many of these were probably recruited after the density maxima. The maximum mean bell diameters achieved were greater at sites where planktonic residence times were longer. The maximum mean size achieved at Cracknore and Bury Buoy were 94mm and 92mm respectively, while at N.W.Netley and Hamble they were 43mm and 5.5mm. It would appear that a smaller number of individuals were supplied to the lower estuarine sites and these also disappeared sooner.

Once the data collected from 5 and 10 metres are combined, a more comprehensive picture of true population growth is determinable. Figures 5.3.4 to 5.3.7 demonstrate depth integrated densities, mean bell-diameters, calculated mean carbon weights, total carbon biomass, and instantaneous specific growth rates (ISGR) of *Aurelia aurita*. Temporally distributed estimates of carbon production by *A.aurita* are also given. A full presentation of the calculations of production and growth rates by *A.aurita* are given in Appendix 6. Mean bell diameters and mean individual carbon weights appeared to increase exponentially over much of their pelagic history, although just after their first appearance and towards the end of their pelagic life there were periods when mean weights were almost constant or even declined. The initial slow increase, and at times decreases, in mean weight may in part be due to continual recruitment: while the final period of relatively constant weight and decreases were because of slow net positive or net negative growth.

In the present investigation, production values obtained from the Increment-Summation method are used in all subsequent analyses, although values from the Instantaneous Growth rate method are presented. The results from the two methods are very similar however. In the most extreme case the lower annual production value is ~50% of the higher, although the average difference was 17%.

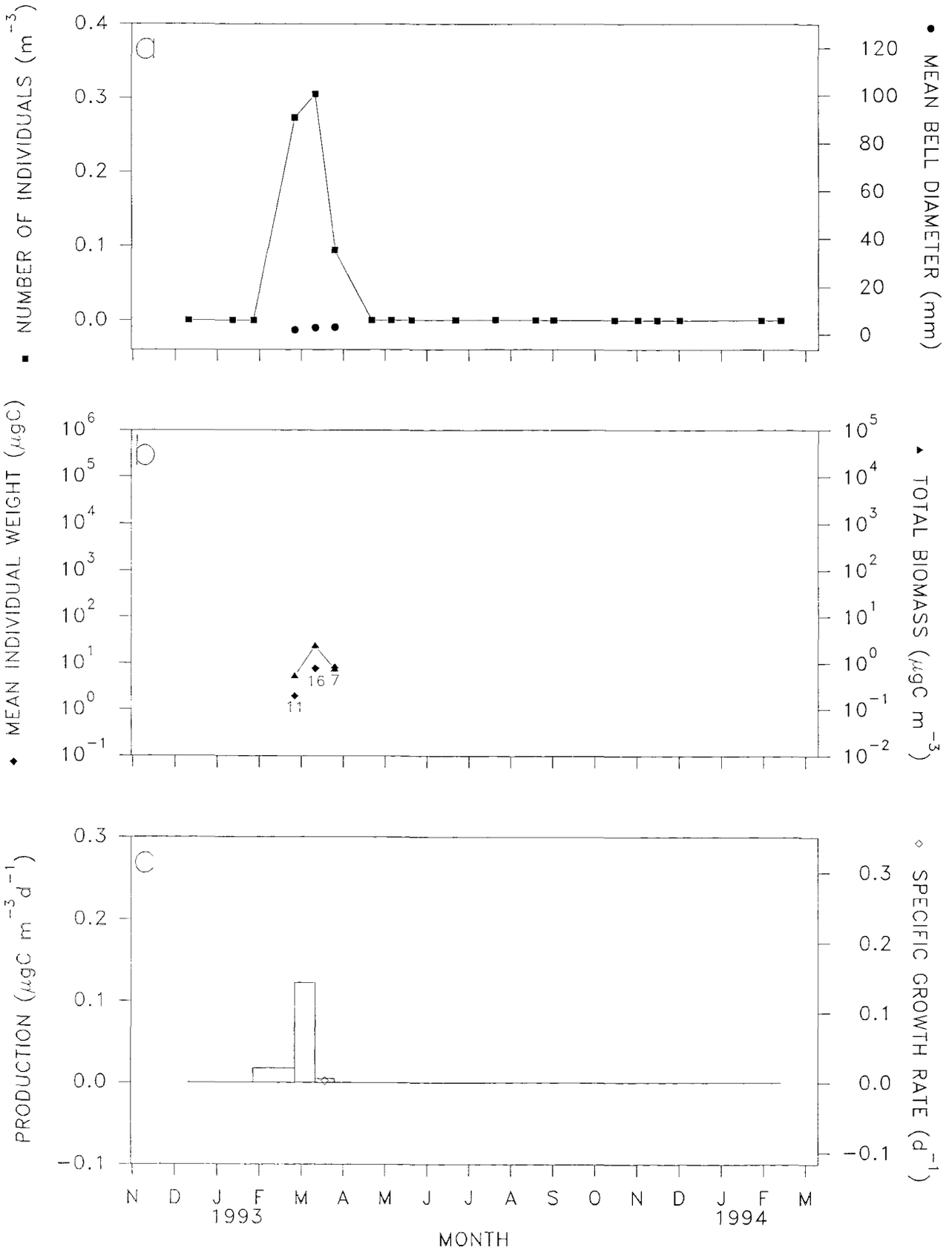


FIGURE 5.3.4 Population parameters of Aurelia aurita collected at Hamble during 1993. a. Density and mean bell diameter of collected individuals, b. Calculated mean and total carbon weight, c. Temporally distributed production estimates (Increment–Summation) and instantaneous specific growth rates. Number of individuals measured given on graph b.

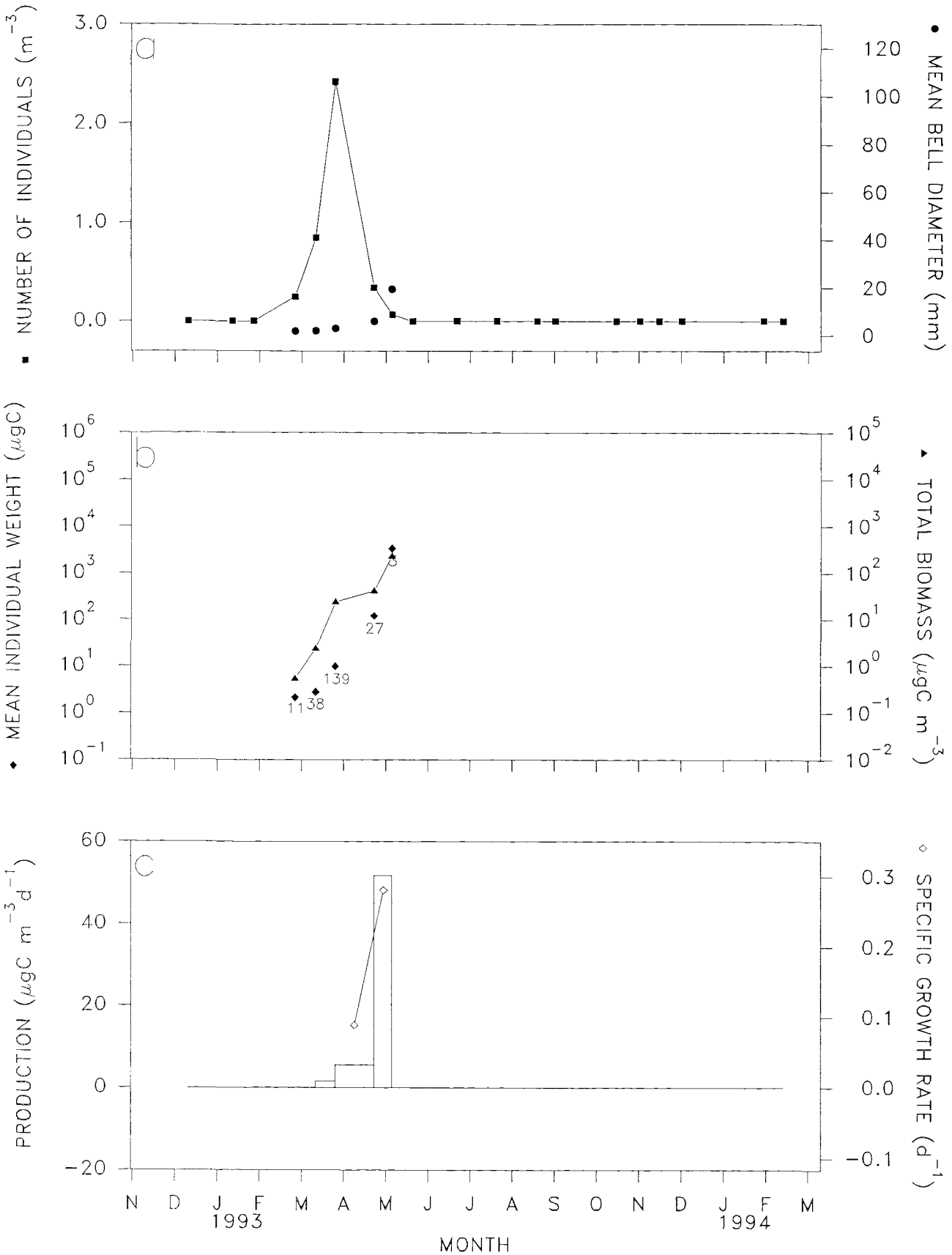


FIGURE 5.3.5 Population parameters of Aurelia aurita collected at N.W.Netley during 1993. a. Density and mean bell diameter of collected individuals, b. Calculated mean and total carbon weight, c. Temporally distributed production estimates (Increment–Summation) and instantaneous specific growth rates. Number of individuals measured given on graph b.

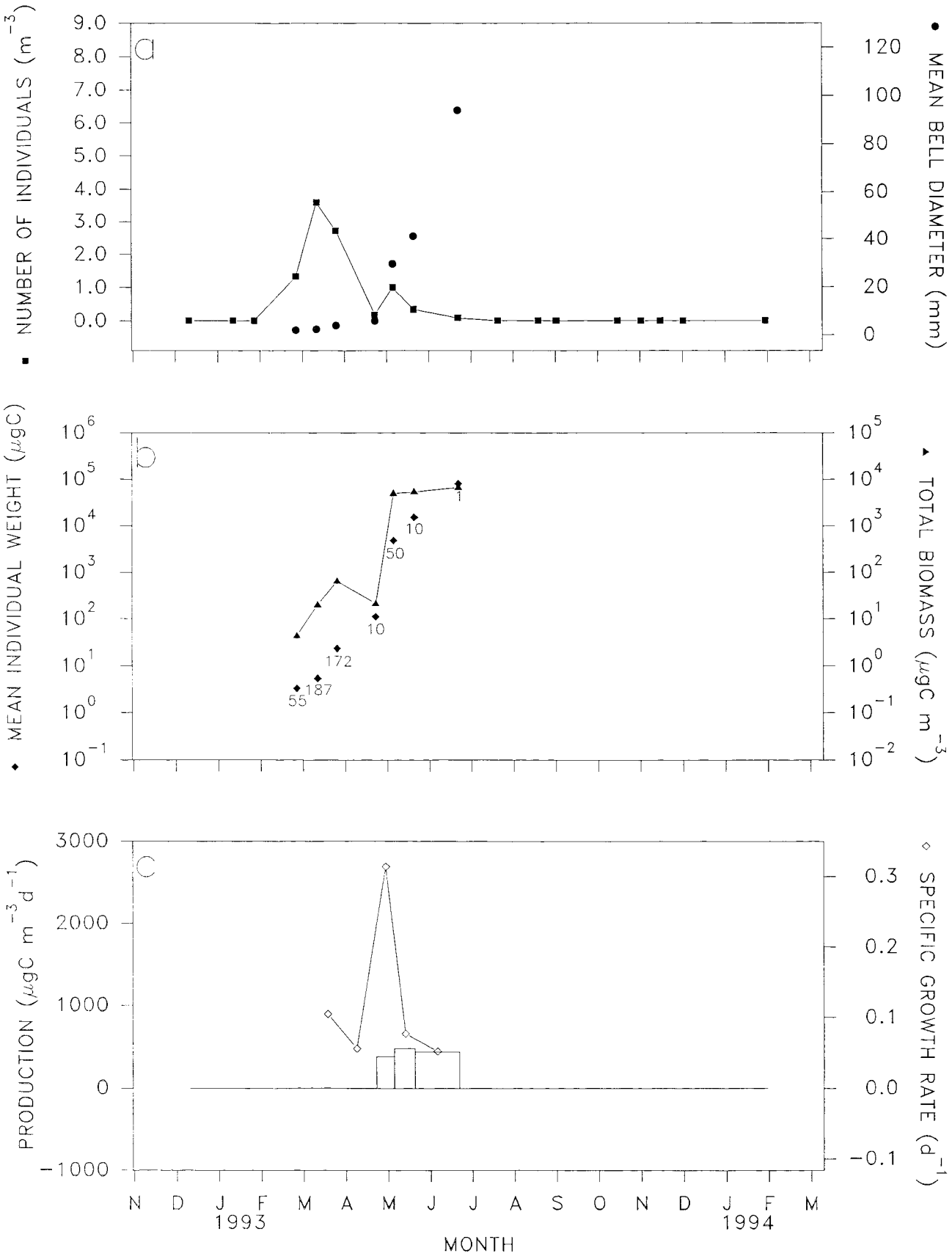


FIGURE 5.3.6 Population parameters of Aurelia aurita collected at Cracknore during 1993. a. Density and mean bell diameter of collected individuals, b. Calculated mean and total carbon weight, c. Temporally distributed production estimates (Increment–Summation) and instantaneous specific growth rates. Number of individuals measured given on graph b.

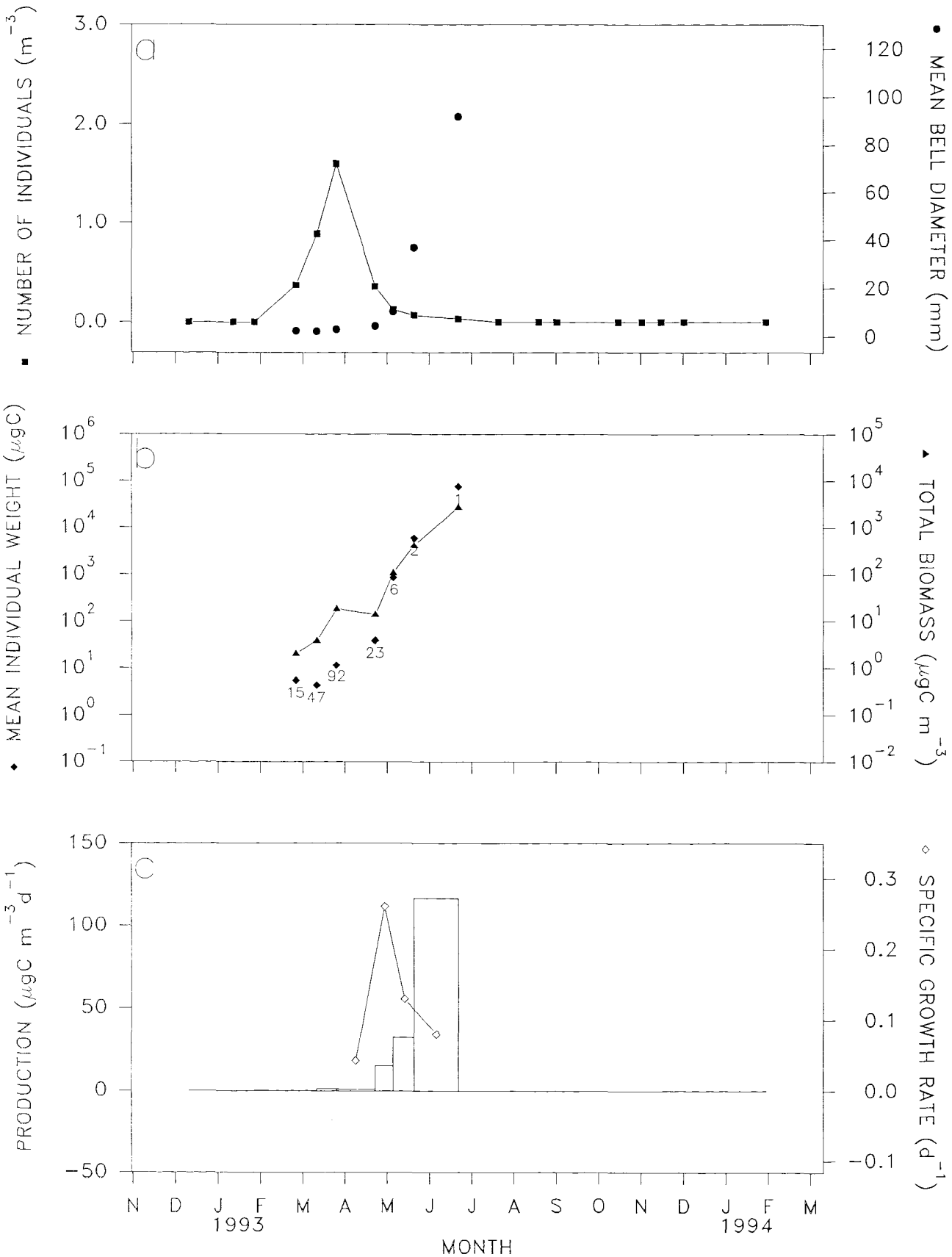


FIGURE 5.3.7 Population parameters of Aurelia aurita collected at Bury Buoy during 1993. a. Density and mean bell diameter of collected individuals, b. Calculated mean and total carbon weight, c. Temporally distributed production estimates (Increment–Summation) and instantaneous specific growth rates. Number of individuals measured given on graph b.

METHOD	SITE	PRODUCTION ($mgC\ m^{-3}\ yr^{-1}$)
INCREMENT-SUMMATION	CALSHOT	0.0
	HAMBLE	0.0024
	N.W.NETLEY	0.849
	CRACKNORE	26.492
	BURY BUOY	4.458
INSTANTANEOUS GROWTH	CALSHOT	0.0
	HAMBLE	0.0024
	N.W.NETLEY	0.564
	CRACKNORE	25.663
	BURY BUOY	4.767
LOWER AND UPPER LIMITS [INDEX OF VARIABILITY]	CALSHOT	-
	HAMBLE	0.0024-0.0025 [0.96]
	N.W.NETLEY	0.287-1.410 [0.20]
	CRACKNORE	14.287-38.698 [0.37]
	BURY BUOY	3.014-5.902 [0.51]

TABLE 5.3.1 Production calculations for *Aurelia aurita* during 1993 for the 5 fixed sites within Southampton Water.

Given that *Aurelia aurita* in the estuary appear to grow in mass exponentially, and mortality is linear with time, then the two methods would be expected to give similar results, with a similar accuracy (see Morin *et al.*, 1987). Highest daily production rates were found at Cracknore where they reached $0.480 mgCm^{-3}d^{-1}$ during May. Daily production rates reached $0.116 mgCm^{-3}d^{-1}$ at Bury Buoy, and $0.052 mgCm^{-3}d^{-1}$ at N.W.Netley. Of the sites where *A.aurita* was found Hamble had the lowest maximum daily production rates at $0.0001 mgCm^{-3}d^{-1}$. Maximum daily production rates peaked earliest at Hamble, during late February to early March.

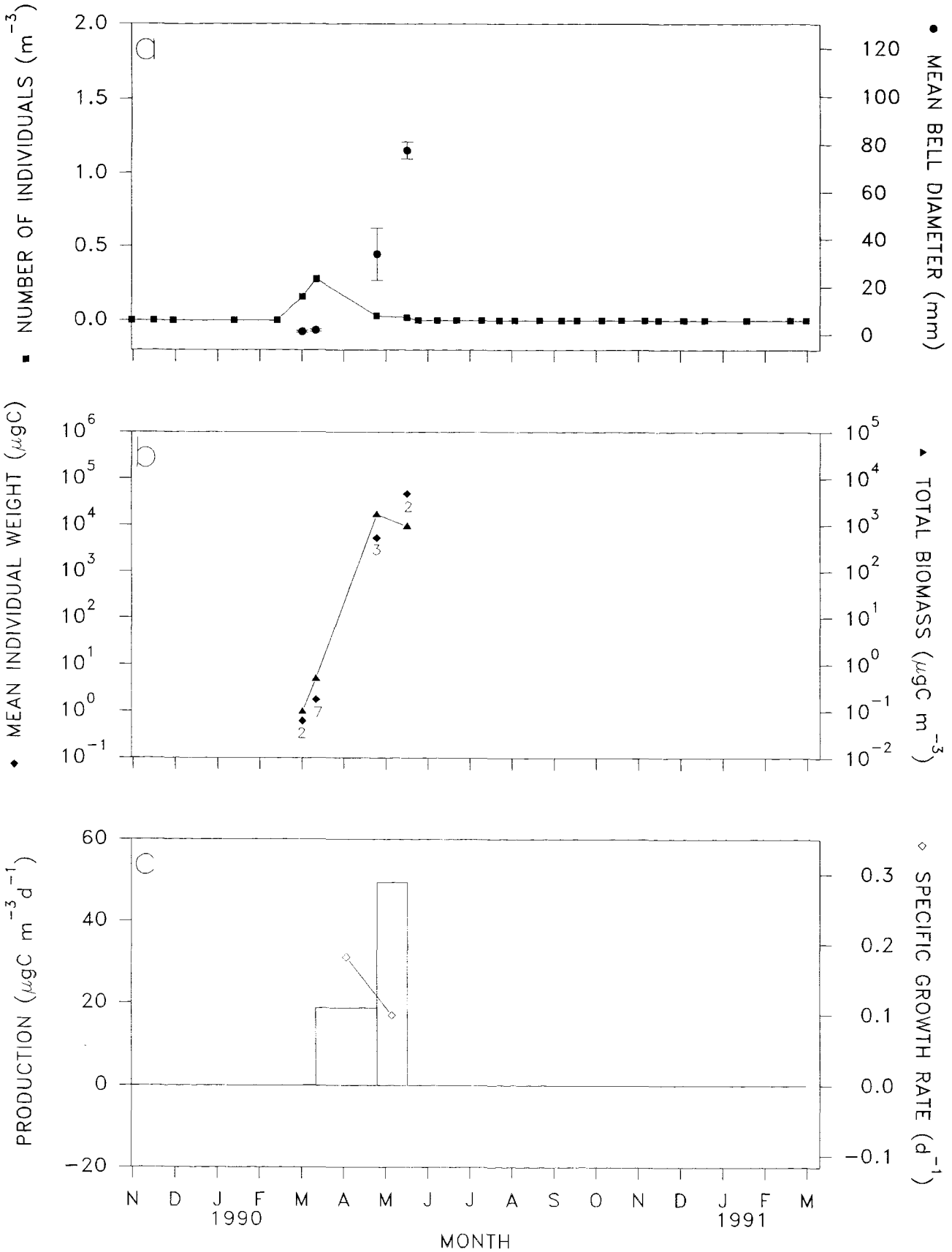


FIGURE 5.3.8 Population parameters of Aurelia aurita collected at Greenland during 1990. a. Density and mean bell diameter (error bars represent S.D.) of collected individuals. b. Calculated mean and total carbon weight, c. Temporally distributed production estimates (Increment–Summation) and instantaneous specific growth rates. Number of individuals measured given on graph b.

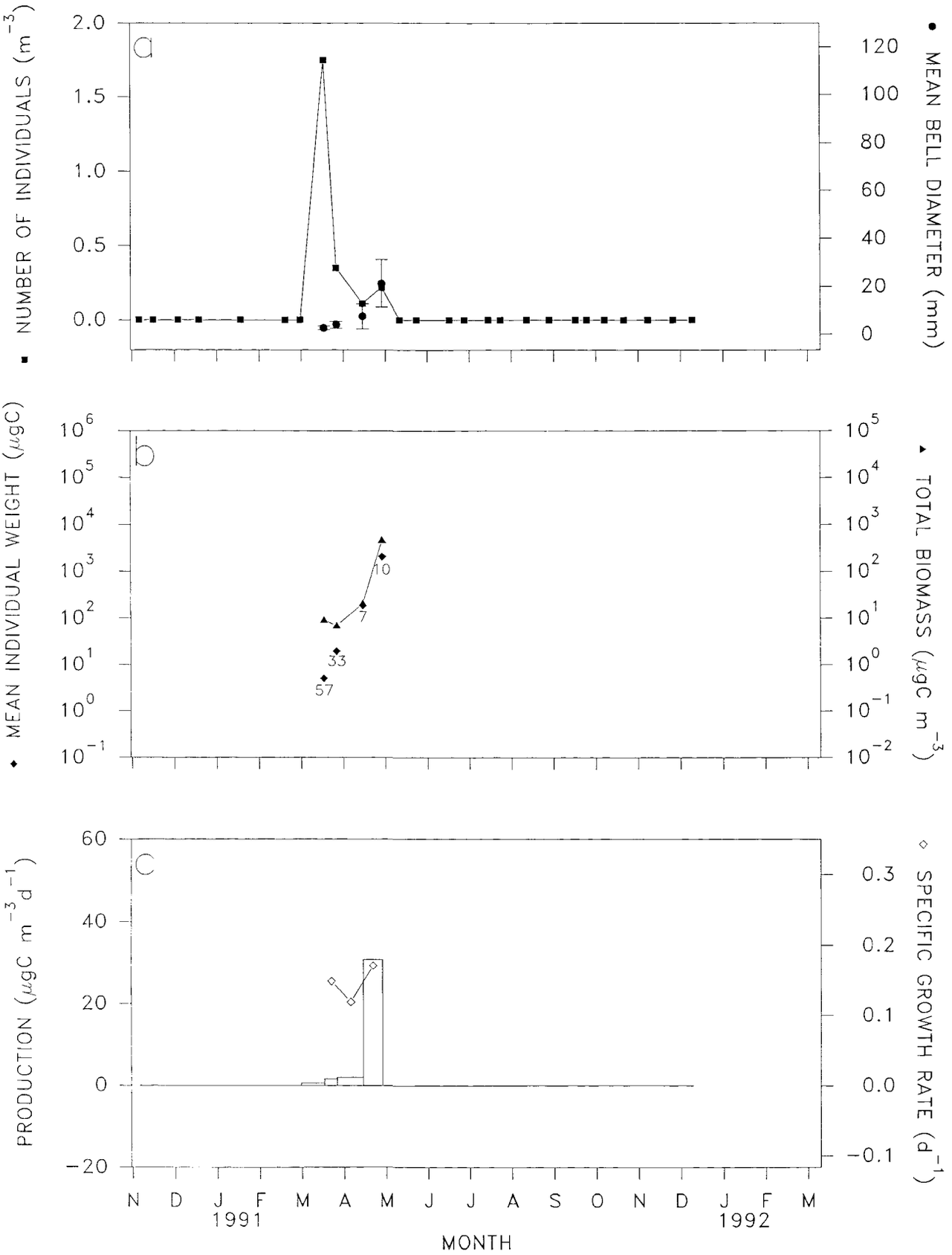


FIGURE 5.3.9 Population parameters of Aurelia aurita collected at Greenland during 1991. a. Density and mean bell diameter (error bars represent S.D.) of collected individuals, b. Calculated mean and total carbon weight, c. Temporally distributed production estimates (Increment–Summation) and instantaneous specific growth rates. Number of individuals measured given on graph b.

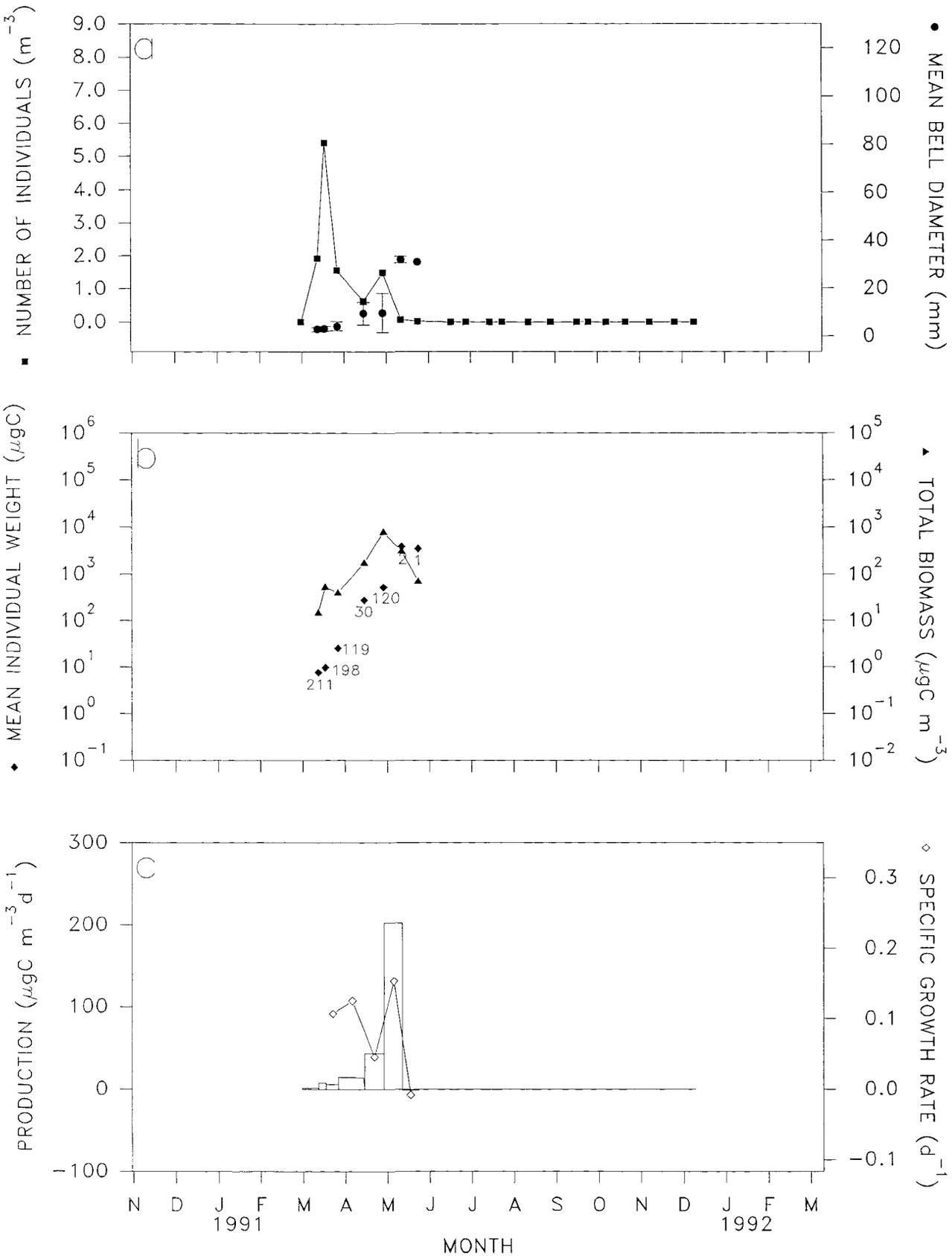


FIGURE 5.3.10 Population parameters of Aurelia aurita collected at N.W.Netley during 1991. a. Density and mean bell diameter (error bars represent S.D.) of collected individuals, b. Calculated mean and total carbon weight, c. Temporally distributed production estimates (Increment–Summation) and instantaneous specific growth rates. Number of individuals measured given on graph b.

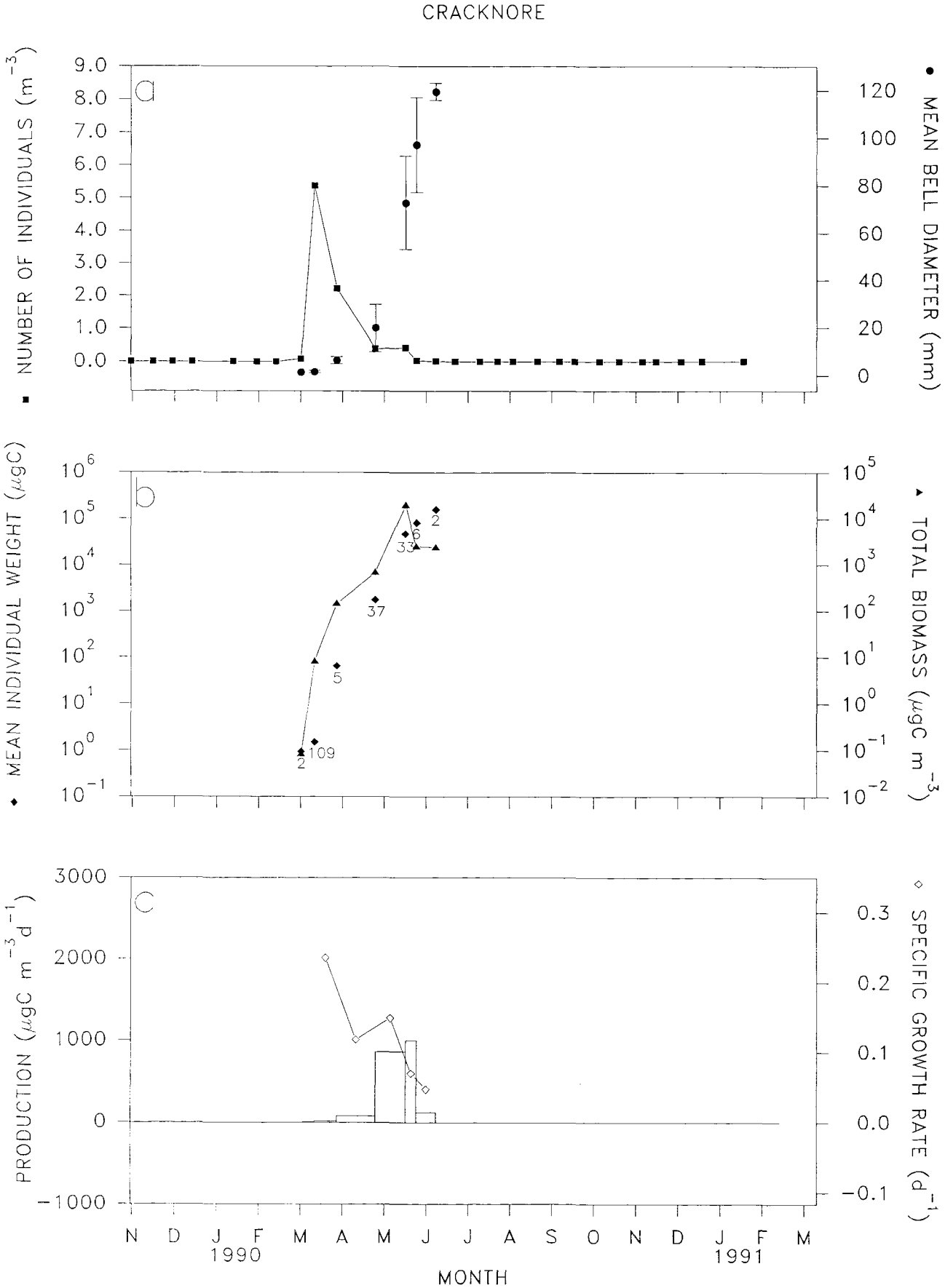


FIGURE 5.3.11 Population parameters of Aurelia aurita collected at Cracknore during 1990. a. Density and mean bell diameter (error bars represent S.D.) of collected individuals, b. Calculated mean and total carbon weight, c. Temporally distributed production estimates (Increment–Summation) and instantaneous specific growth rates. Number of individuals measured given on graph b.

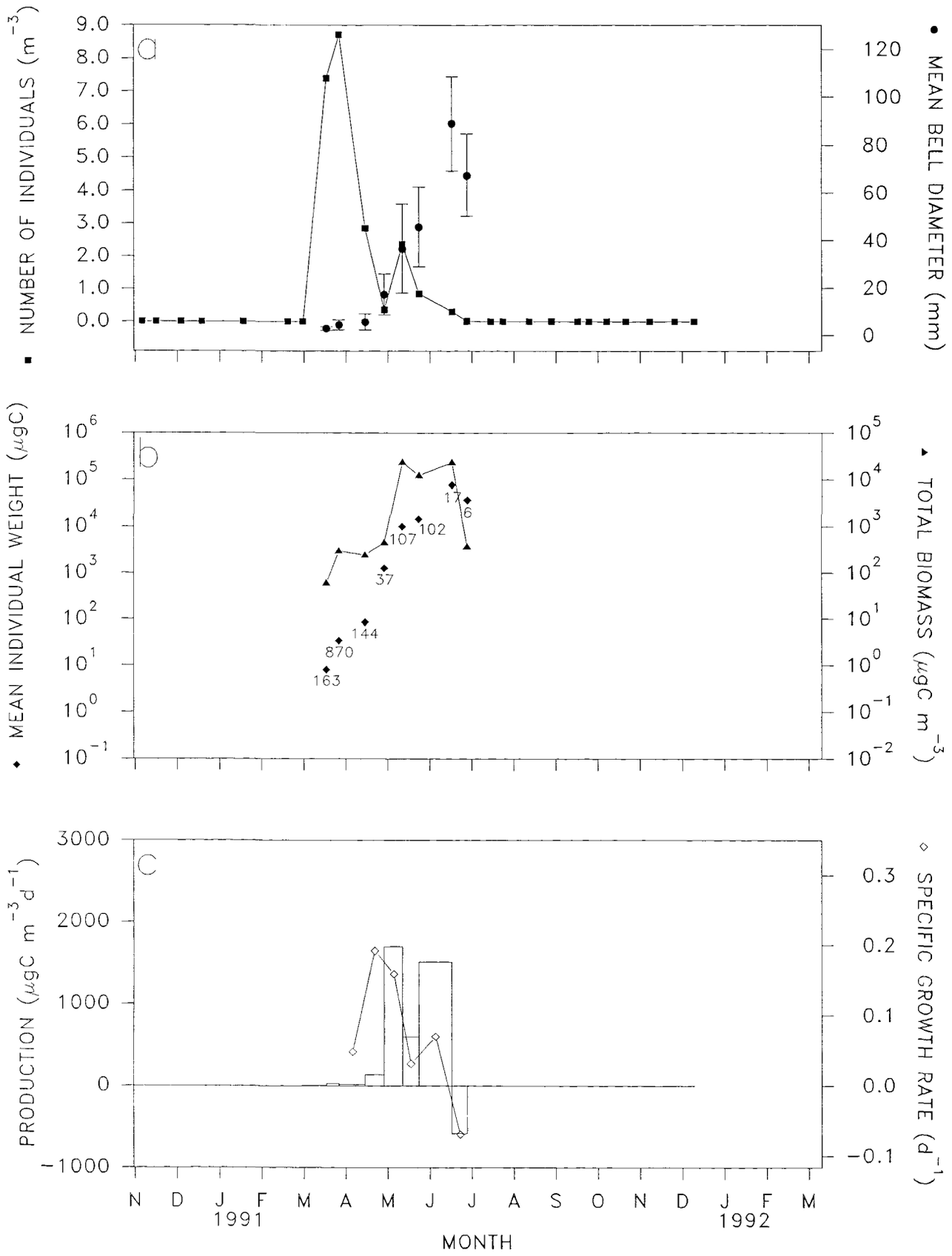


FIGURE 5.3.12 Population parameters of Aurelia aurita collected at Cracknore during 1991. a. Density and mean bell diameter (error bars represent S.D.) of collected individuals, b. Calculated mean and total carbon weight, c. Temporally distributed production estimates (Increment–Summation) and instantaneous specific growth rates. Number of individuals measured given on graph b.

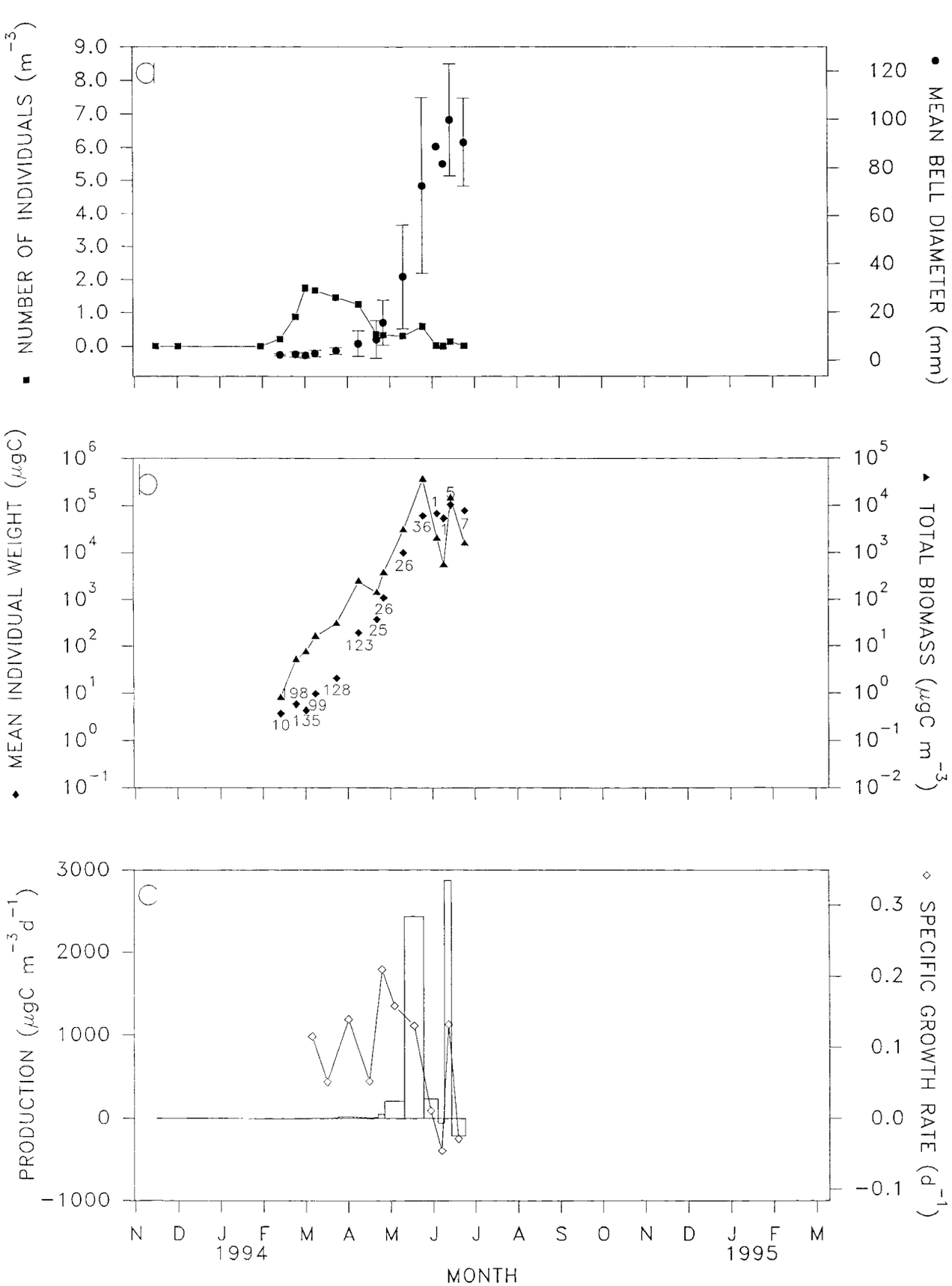


FIGURE 5.3.13 Population parameters of Aurelia aurita collected at Cracknore during 1994. a. Density and mean bell diameter (error bars represent S.D.) of collected individuals, b. Calculated mean and total carbon weight, c. Temporally distributed production estimates (Increment–Summation) and instantaneous specific growth rates. Number of individuals measured given on graph b.

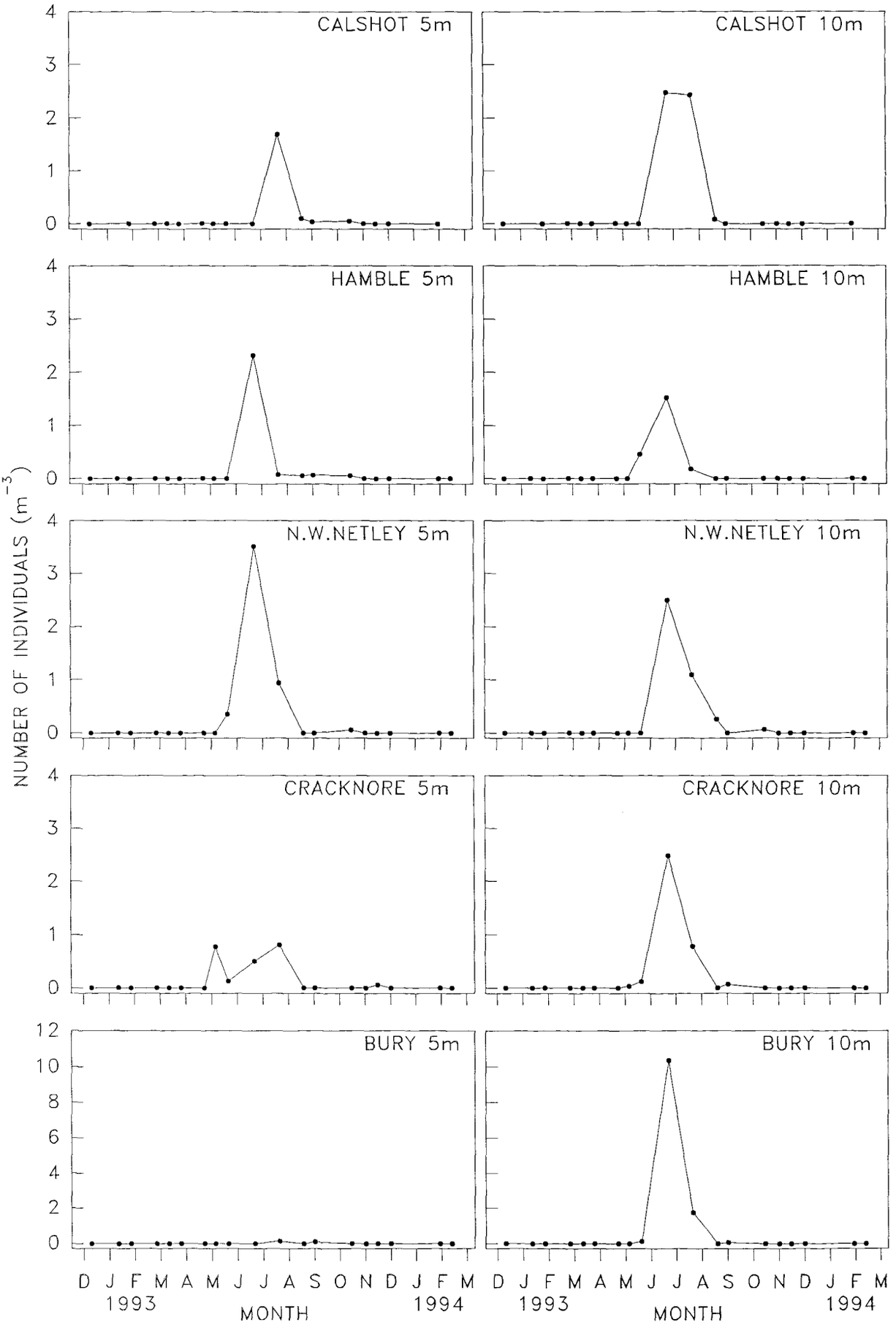


FIGURE 5.3.14 The density of Clytia hemisphaerica at the sites and depths as indicated. (Note scale change).

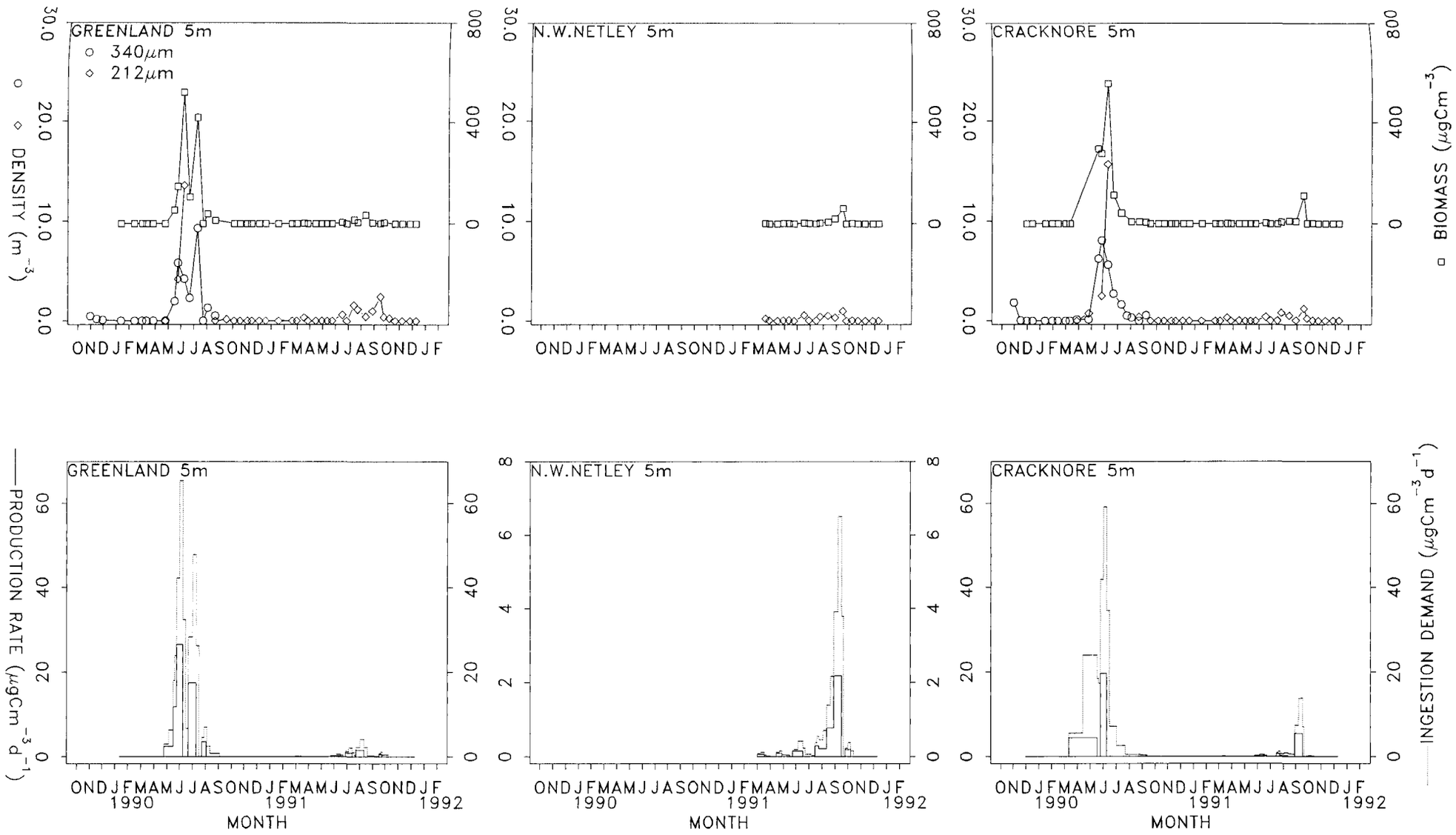


FIGURE 5.3.15 The density and estimated biomass and production of Clytia hemisphaerica at the Greenland, N.W.Netley and Cracknore sites. Density and size distribution data used to calculate biomass taken from Lucas (1993), see text for details. (Note change in scales).

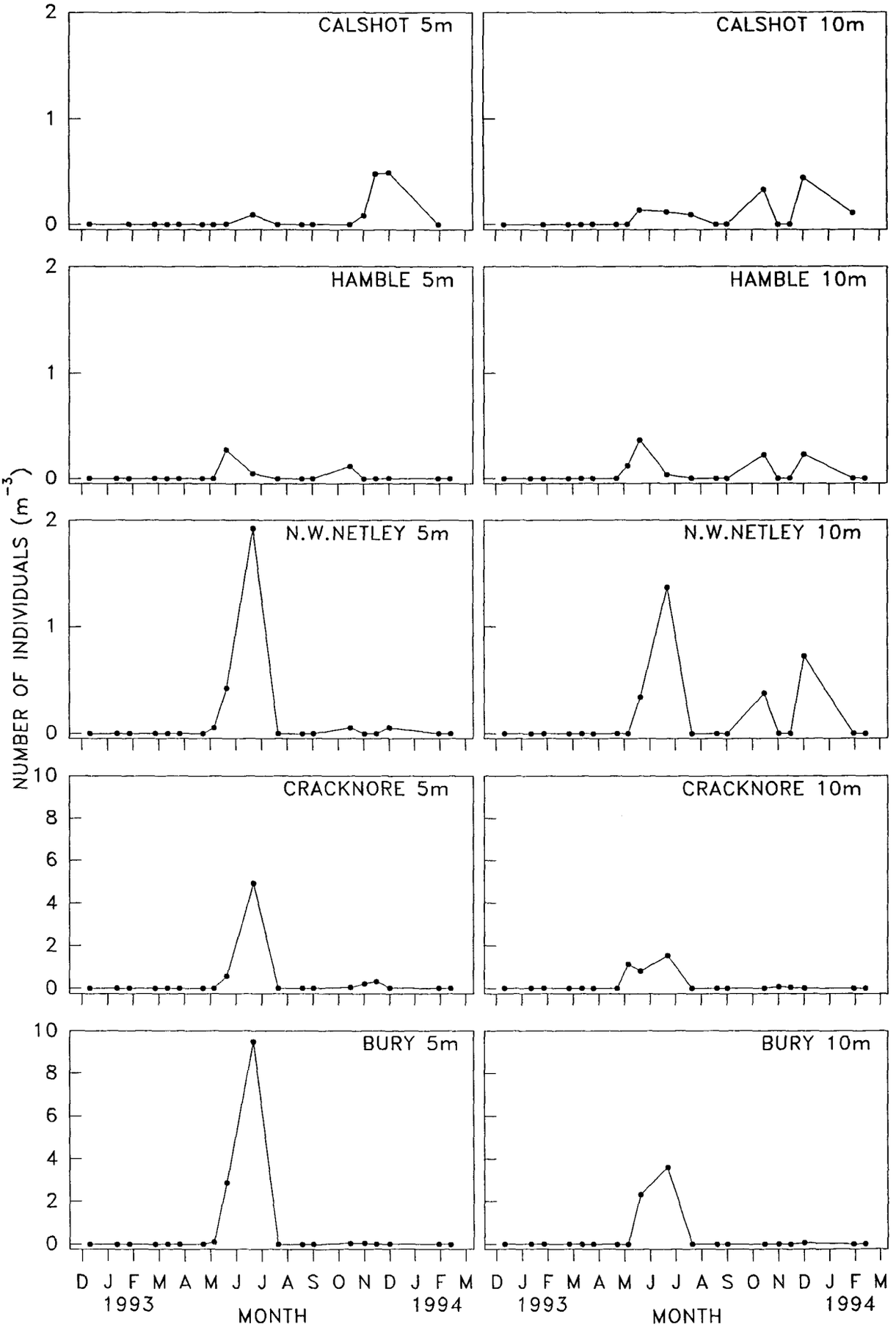


FIGURE 5.3.16 The density of Pleurobrachia pileus at the sites and depths as indicated. (Note scale change).

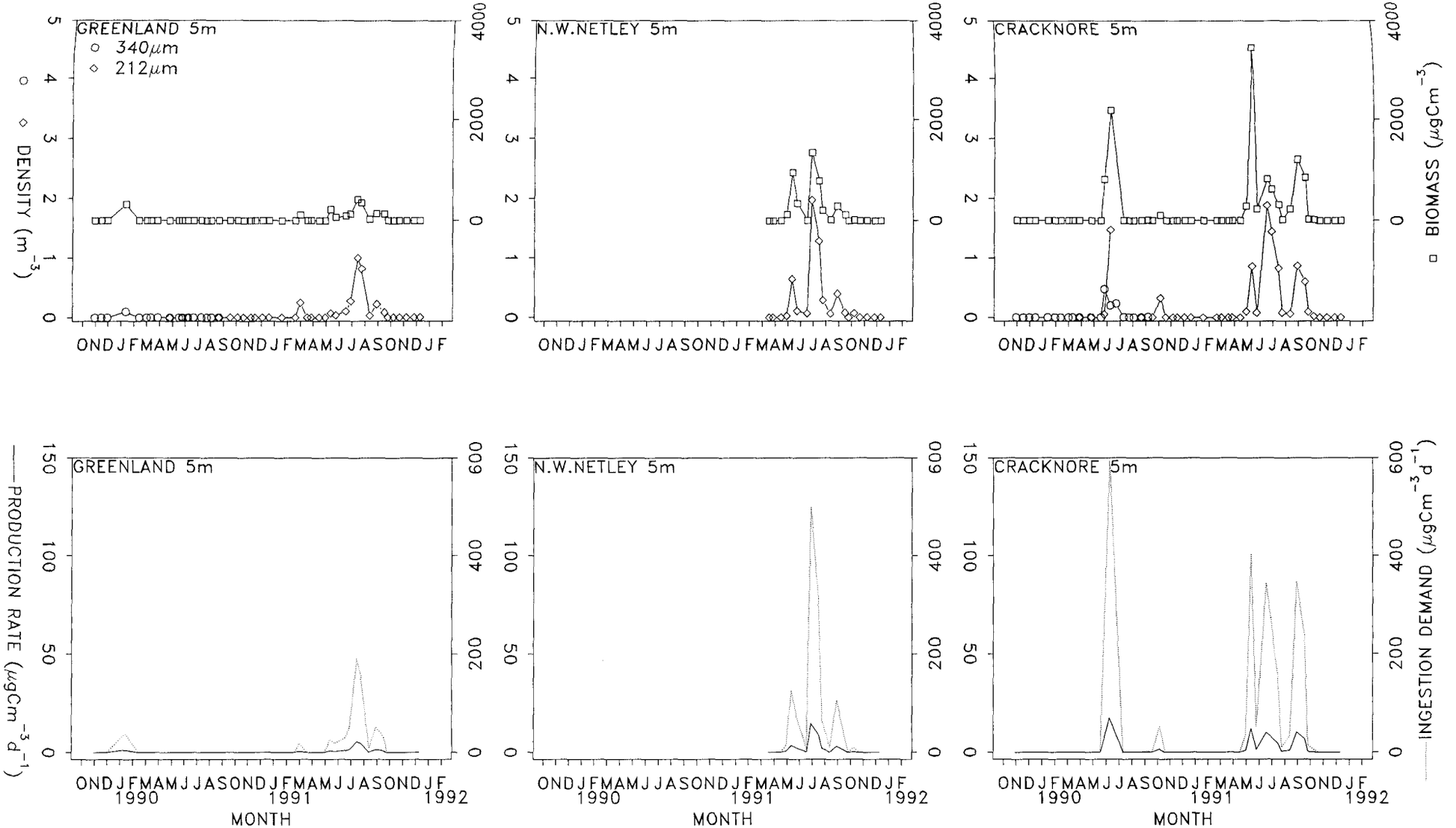


FIGURE 5.3.17 The density and estimated biomass and production of Pleurobrachia pileus at the Greenland, N.W.Netley and Cracknore sites. Density and size distribution data used to calculate production taken from Lucas (1993), see text for details.

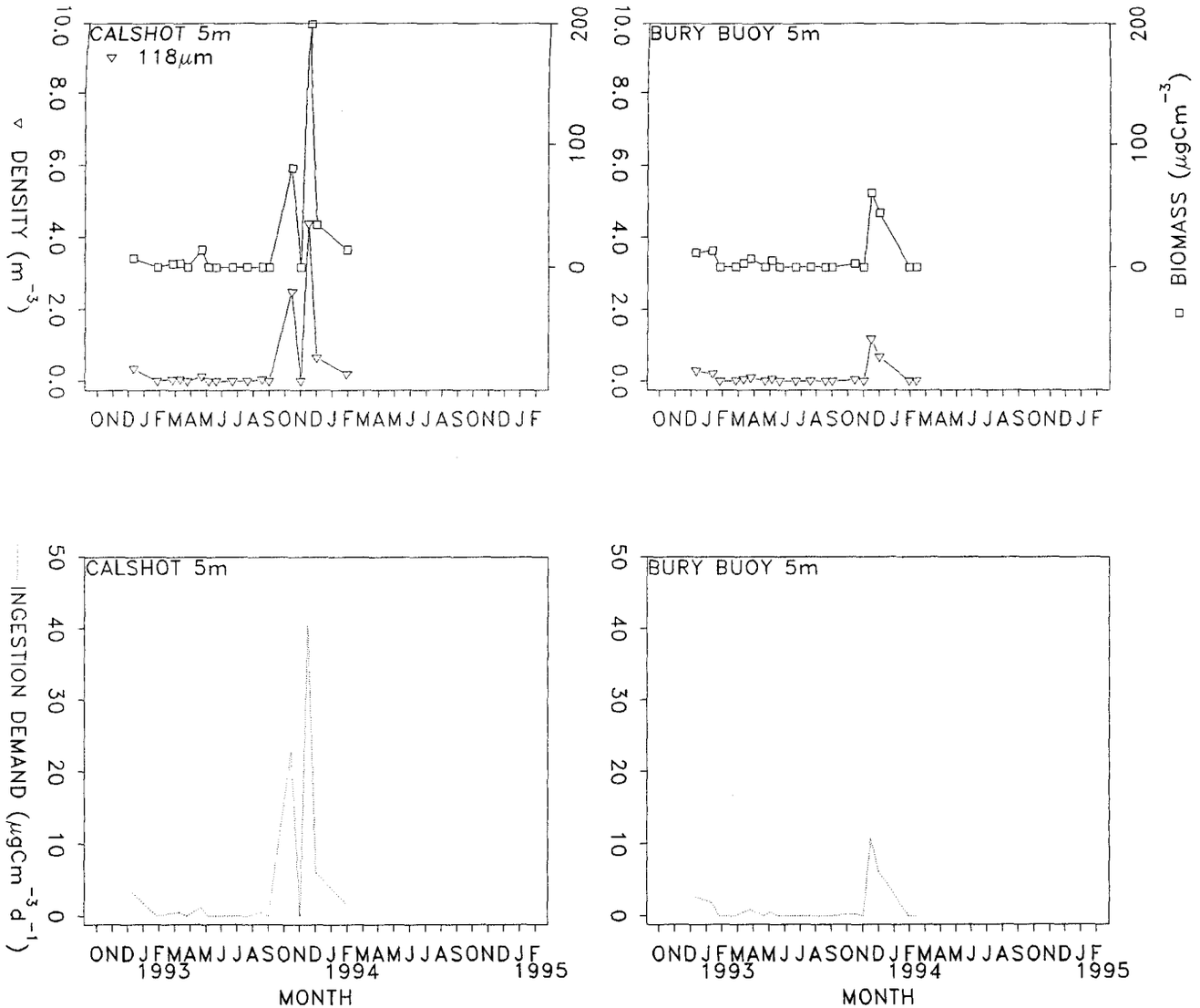


FIGURE 5.3.18 The density and estimated biomass and production of Sagitta setosa at the Calshot and Bury Buoy sites.

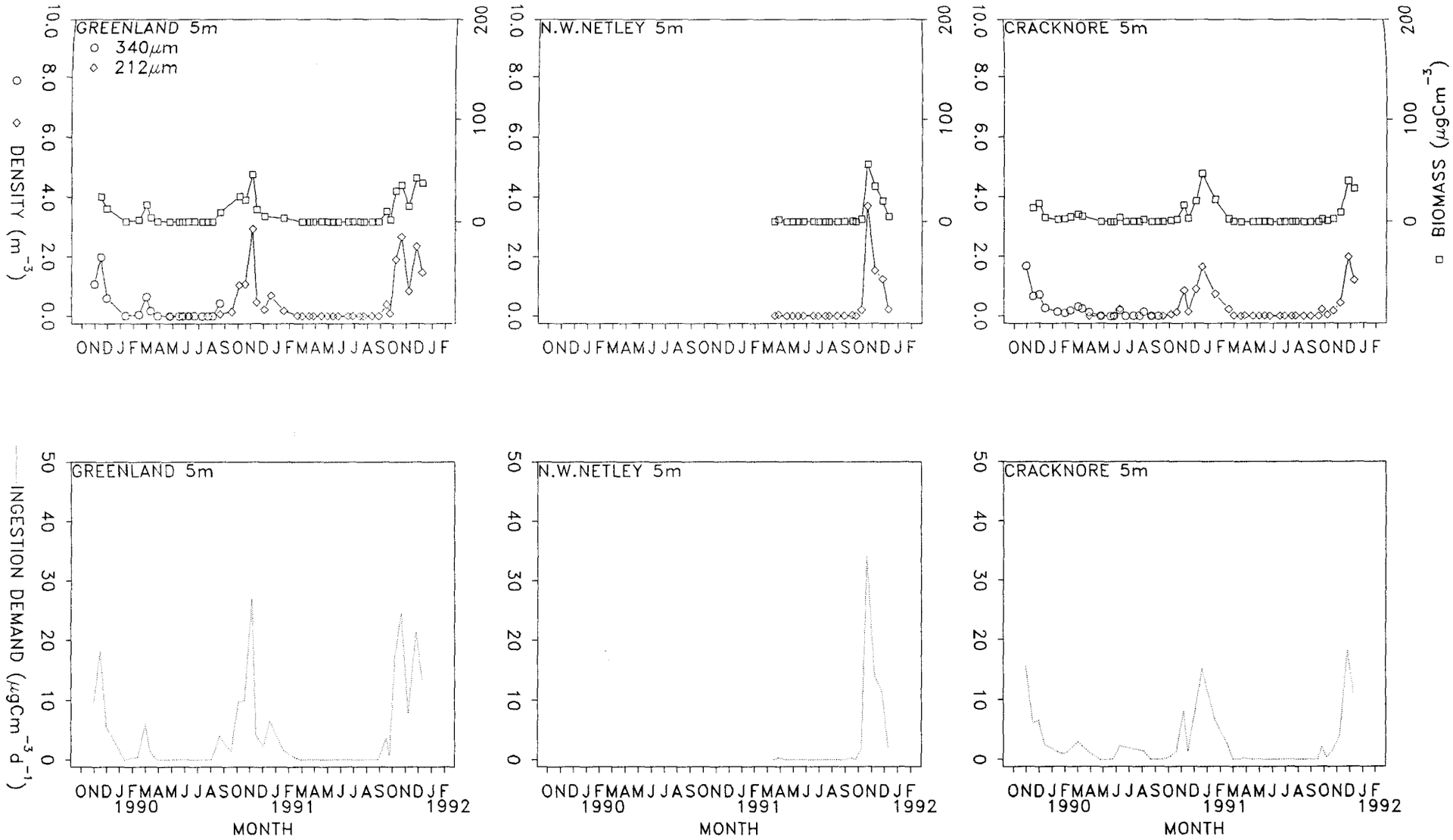


FIGURE 5.3.19 The density and estimated biomass and production of Sagitta setosa at the Greenland, N.W.Netley and Cracknore sites. Density and size distribution data used to calculate production taken from Lucas (1993), see text for details.

This maximum was very small in comparison to those recorded at the higher estuarine sites, and the earlier peak was more a reflection of its short residence time rather than greater production rates during this period at this site (indeed this maximum value was no greater than values found at other sites for this period). At N.W.Netley production peaked in late April to early May, and during May and June at Cracknore and Bury Buoy.

Table 5.3.1 summarizes the annual production estimates of *Aurelia aurita* at all 5 sites during 1993. The two methods employed produced similar annual estimates, with the larger of the two never being more than around 50% greater than the lower, the difference typically being less than 7%. Annual production estimates for 1993 varied greatly between sites. *A.aurita* at Cracknore had the greatest annual production at 26.49mgCm^{-3}yr^{-1}, followed by Bury Buoy where production was 4.46mgCm^{-3}yr^{-1}, less than 20% of that at Cracknore. At N.W.Netley annual production was 0.85mgCm^{-3}yr^{-1}, less than 20% of that at Bury Buoy and around 3% of that at Cracknore. These production estimates generally reflect the nature of the spatio-temporal distribution of *A.aurita*. Thus at Cracknore, where the densities, mean carbon weights, and the plankton residence times were the greatest, the annual production estimate was also the largest. At Hamble where annual production estimates were smallest, the maximum achieved densities, mean carbon weights and plankton residence times were all the least. Maximum daily and annual production rates are found at sites where *A.aurita* had the longest planktonic residence times, this is a result of the periods later in the season being associated with the larger individuals, these having the greatest rates of biomass increase. The predominant part of the production in the estuary by this species is attributable to a small number of the largest size achieving individuals.

Figures 5.3.8 to 5.3.13 demonstrate values of density, mean individual bell diameter, mean individual carbon weight, total carbon biomass, ISGRs and production, all calculated from data supplied by C.H.Lucas for years other than 1993 at the sites Greenland, N.W.Netley and Cracknore. Comparisons of data collected in 1990 and 1991 at Greenland, N.W.Netley and Cracknore, show that densities were once again greatest at the more landward sites. Plankton residence times and the maximum sizes achieved also show broadly similar patterns to those found in 1993. Comparing total annual production rates between the years in which it has been measured shows that rates at the Cracknore and N.W.Netley sites have been generally similar in all the years in which measurements have taken place. At Cracknore the results give greater production rates in 1990, 1991 and 1994 than during 1993, when samples from two depths were combined. The highest annual production values were found at Cracknore where in 1991 they reached 62.54mgCm^{-3}yr^{-1}.

SITE (YEAR)	PRODUCTION		
	INCREMENT-SUMMATION ($mgC\ m^{-3}\ yr^{-1}$)	INSTANTANEOUS GROWTH ($mgC\ m^{-3}\ yr^{-1}$)	LOWER AND UPPER LIMITS [INDEX OF VARIABILITY]
GREENLAND (1990)	1.911	1.893	1.005 - 2.816 [0.46]
GREENLAND (1991)	0.494	0.616	0.462 - 0.747 [0.62]
N.W.NETLEY (1991)	3.604	1.737	1.065 - 5.900 [0.18]
CRACKNORE (1990)	31.293	43.153	22.115 - 121.979 [0.18]
CRACKNORE (1991)	62.539	53.787	34.093 - 92.563 [0.37]
CRACKNORE (1994)	51.927	45.954	38.999 - 83.118 [0.47]

TABLE 5.3.2 Production calculations for *Aurelia aurita* within Southampton Water using the Increment-Summation and Instantaneous Growth Rate methods, lower and upper production limits and index of variability also given. Data used to calculate production estimates supplied by C.H.Lucas.

This large value was predominantly caused by the increase in weight of a relatively great number of large individuals which were present in this year, with 2.36 ind. m^{-3} at 36.6mm and 0.30 ind. m^{-3} at 89.0mm. In other years when individuals reach these mean sizes densities were much less, typically 0.31 ind. m^{-3} at ~35mm and 0.03ind. m^{-3} at ~89mm. The range of annual production values for Cracknore during all 4 years of examination are 26.49 to 62.54mgC$m^{-3}yr^{-1}$, with an average value of 43.12mgC$m^{-3}yr^{-1}$. The values from 1993 are generally less, predominantly as a result of the inclusion of samples from 10 metres. Indeed, comparisons between the data for 1993 with that in other years are complicated by the fact that the data given by C.H.Lucas were collected at only a single depth, 5 metres, however that for 1994 has been derived by integrating samples taken from 5 and 10 metres (this was believed to give more reliable estimates of population parameters). Since densities are generally greater at 5 metres then the estimates made from this single depth will tend to inflate daily and annual production estimates.

Densities varied considerably between years. However, the relatively poor temporal resolution of samples and the rapid fluctuations which may have occurred, particularly during the period of initial recruitment, does not facilitate detailed inter-annual comparison. Daily and annual production rates are variable between sites and years as a result of differences in mean weights, density and temporal sampling resolution. As already indicated, mean carbon weight is initially relatively constant, this is followed by exponential growth and then by a period of decrease in mean weight. This decrease or de-growth is shown in 1991 and 1994 (and 1990 although no density measures are available during this period, see Lucas (1993)) at Cracknore and 1991 at N.W.Netley. It is highly probable that de-growth was missed in other years at the top two sites as a result of the low temporal sampling resolution.

Instantaneous Specific Growth Rate (ISGR) data are sparse at some sites because of the low number of sampling points after the achievement of the density maximum. Initial ISGR estimates are likely to be underestimates because of the continued recruitment of small individuals after the achievement of the density maxima. Some forms of size dependent loss could however result in overestimation of the ISGR values. Such effects would also bias the production estimates. During 1993 the lowest estimate of the ISGR was $0.002d^{-1}$ at Hamble (this value may be particularly biased by continual recruitment). At all the other sites the maximum ISGR exceeds $0.26d^{-1}$. The highest value achieved during 1993 was found at the Cracknore site being $0.314d^{-1}$. No negative production rates were found during 1993 as de-growth was not encountered. At Cracknore and Bury Buoy values did however decline towards the end of the pelagic presence of *Aurelia*. The upper and lower limits give an indication of the potential variability in production which could occur given the values of density and mean weights. At

N.W.Netley there is a five fold difference between the lower and upper limits of production. At Bury Buoy there is less than a two fold difference, and at Cracknore the difference between the limits is just over 3 fold. More intensive sampling would probably result in both an increase in the accuracy of the production estimates (ie. the closeness of the production estimate to the true production) and also a decrease in the ratio of upper production limit to lower production limit.

ISGRs in all years of study varied between -0.069 to $0.314d^{-1}$. At Cracknore and Bury, where the complete reproductive pelagic life cycle was encountered, the values tended to be initially low, increase to a maximum in April and then decline. There is some fluctuation in the ISGRs at a single site over a year. The general pattern is the result of initial slow growth rates (these potentially being influenced by continual recruitment) proceeded by faster growth. Eventually medusae begin to grow more slowly and some members of the population may have begun de-growth, even though there may be no overall net decrease in the population mean weight. Negative ISGR values are encountered when eventually the total decline in mean weight is greater than the total increase and the population shows an overall decrease in mean weight. Although there is some considerable variability in the IGSRs at the 3 upper estuary sites values tend to centre around 0.1.

	$\mu gC\ m^{-3}\ yr^{-1}$ (% OF TOTAL INGESTION)			
	HAMBLE	N.W.NETLEY	CRACKNORE	BURY
TOTAL GROWTH	2.44 (38.1)	849 (66.7)	26,492 (46.8)	4,458 (45.3)
RESPIRATION	1.89 (29.5)	124 (9.7)	13,991 (24.7)	2,381 (24.7)
DOC RELEASE	0.80 (12.5)	45 (3.5)	4,787 (8.5)	865 (9.0)
ASSIMILATION	5.12 (80.0)	1,018 (80.0)	45,271 (80.0)	7,704 (80.0)
INGESTION DEMAND	6.40 (100)	1,273 (100)	56,589 (100)	9,630 (100)

TABLE 5.3.3 Estimated carbon budget and demands of *Aurelia aurita* within Southampton Water during 1993. Total growth estimated using Increment-Summation method. Respiration estimated using regressions of Larson (1987a), DOC release estimated from application of the work of Hansson and Norrman (1995), ingestion demand determined from assimilation assuming an assimilation efficiency of 80%.

The energy budget constructed for *Aurelia aurita* from the data collected in 1993 is given

in Table 5.3.3. Temporally distributed estimates of ingestion demands as well as annual ingestion demands have been completed and are presented in the discussion in an attempt to determine the role and importance of *A.aurita* within the pelagic system of Southampton Water. As would be expected carbon demands show similar temporal and spatial patterning as do the production estimates. The greatest annual carbon demand by *A.aurita* is found at Cracknore, then Bury and N.W.Netley, with the lowest demand at Hamble. Growth makes up a large fraction of the ingestion demand at the higher sites, being around 45-47% at Cracknore and Bury Buoy. At N.W.Netley growth is 67% of ingestion demand, and at Hamble it is 38.1%. At Hamble production must be viewed with some caution as only a few small individuals were found and the apparent increases in size were so small. Ingestion demands at N.W.Netley, Cracknore and Hamble are examined in more detail with regard to their importance and potential effect upon prey in the discussion.

***Clytia hemisphaerica*:**

The densities of *Clytia hemisphaerica* at each of the fixed sites over the course of the 14 month abundance investigation are given in Figure 5.3.14. Individuals first appeared in samples at all sites excluding Calshot on the same date in May, appearing later at Calshot in June. Densities increased sharply in the following one to two months, with maximum depth integrated densities being found at the end of June in the 4 inner estuary sites and at the end of July at Calshot. The highest densities recorded were at Bury Buoy where numbers reached 5.8 ind. m^{-3}, at Cracknore they reached 1.5 ind. m^{-3} and at N.W.Netley they reached 3.0 ind. m^{-3}. At Hamble and Calshot numbers peaked at 1.9 ind. m^{-3} and 2.1 ind.m^{-3} respectively. As with the other gelatinous species *C.hemisphaerica* demonstrated large density changes with depth. Measurements of individual bell diameters were not made upon individuals collected in 1993 and therefore biomass could not be estimated. Individual diameter and density measurements were however made by Lucas (1993) at Greenland, N.W.Netley and Cracknore. These density data are presented in Figure 5.3.15, along with estimates of carbon standing stock, daily production and carbon ingestion. Comparing results between all years of collection suggests substantial inter-annual variability in the density at single sites within the estuary. Although inter-annual differences are difficult to fully appreciate given the limited data set and the variation in mesh sizes used for capture, nonetheless changes in maximum densities would appear to be as much as an order of magnitude between consecutive years. Total population biomass, production and ingestion demand were closely correlated with the density of individuals, and as such these also varied substantially between years. Biomass was greatest at Cracknore in 1990 when it reached 0.552mgCm^{-3}, while at Greenland it reached a maximum of 0.517mgCm^{-3} on the same date. In 1990 maximum daily production rates were

0.026 and 0.020mgCm^{-3}d^{-1} at Cracknore and Greenland respectively, in 1991 values did not exceed 0.006mgCm^{-3}d^{-1} at any of the 3 sites. In 1993 numbers peaked in June to July but only reached maxima similar to those of 1991, with densities never exceeding 3.5 ind. m^{-3} in the 5 metre samples at the 5 sites (those of Lucas (1993) being taken only from 5 metres), although at 10 metres and on a depth integrated basis this was exceeded. Annual production estimates spanning separately the productive periods, also clearly demonstrate the dramatic inter-annual differences. At Greenland production during December 89 to December 90 was over 16 times that from December 1990 to December 1991. Comparing these same periods at Cracknore, production was almost 5 times greater in the first period than in the second. Table 5.3.4 gives the estimates of annual production that have been derived for the 3 sites. Since N.W.Netley was only examined over a single year then production could only be estimated in the apparently less productive year at this site.

SITE	PERIOD	PRODUCTION (mgC m^{-3} yr^{-1})	INGESTION DEMAND (mgC m^{-3} yr^{-1})
GREENLAND	Dec. 89 - Dec. 90	0.870	1.952
GREENLAND	Dec. 90 - Dec. 91	0.054	0.122
N.W.NETLEY	Mar. 91 - Mar. 92	0.069	0.223
CRACKNORE	Dec. 89 - Dec. 90	0.569	2.043
CRACKNORE	Dec. 90 - Dec. 91	0.117	0.236

TABLE 5.3.4 Production and ingestion demand estimates for *Clytia hemisphaerica* within Southampton Water. Biomass data estimated from the size and abundance data of Lucas (1993). 'Total Biomass Change' method used to estimate production, with ingestion demand estimated from summation of respired carbon and production estimates, and assuming an assimilation efficiency of 80%.

Annual averages are also estimated from the annual estimates, and are presented in Table 5.3.5. Maximum ingestion rates were found in 1990, with the results from Greenland and Cracknore being very similar. Estimated ingestion demand reached a maximum of 0.065mgCm^{-3}d^{-1} in 1990, but only for a short period. In 1991 the maximum ingestion demand reached 0.013mgCm^{-3}d^{-1}. Annual ingestion demand were between 2.0 to 3.6 times the production estimates. Production

estimates in particular, but also probably ingestion also, are likely to be underestimates. It is difficult to make any conclusions regarding trends in the distribution of individuals and production along the length of the estuary given the great inter-annual variability, it is apparent that between year differences are much larger than between site differences, and that broad inter-annual differences in density and biomass are reflected at all sites. During 1990 this species achieved a much higher population density, biomass and estimated production than in 1991 and 1993.

SITE	PRODUCTION ($mgC\ m^{-3}\ yr^{-1}$)	INGESTION DEMAND ($mgC\ m^{-3}\ yr^{-1}$)
GREENLAND	0.462	1.037
N.W.NETLEY	0.069	0.223
CRACKNORE	0.343	1.140

TABLE 5.3.5 Annual average estimated carbon demands of *Clytia hemisphaerica* within Southampton Water.

Pleurobrachia pileus achieved much lower densities and biomass during 1990, quite the reverse of the pattern for *Clytia hemisphaerica*, however the differences in mesh size selection cannot be discounted as a possible cause of apparent low densities of *P.pileus* sampled in 1989 to early 1990, as a result of the different nets used. There were no such dramatic inter-annual changes in *Sagitta setosa*, biomass and density showing broadly similar patterns in both years of investigation.

Pleurobrachia pileus:

The density of *Pleurobrachia pileus* at each of the 5 permanent sites over the 14 month abundance investigation are given in Figure 5.3.16. The density of individuals rises initially in May and peaks at most sites in July. Greatest numbers were generally found at the inner estuarine sites, with the highest densities being recorded at Bury where depth integrated densities exceeded 6.5 ind. m^{-3}. The smallest maximum integrated density achieved was 0.33 ind. m^{-3}, found at Hamble. There was a strong summer peak and a smaller more prolonged peak over winter at all sites, although at Calshot the winter densities were greater than those in the summer. Moving towards the head of the estuary the size of the winter peak increases relative to the

summer, with the winter peak being in fact greater than that in the summer at Calshot. Annual estimates of production for 3 sites have been calculated and are given in Table 5.3.6. This species is present for a much longer period than the other species. In 1993 it was present in samples at N.W.Netley and Hamble in May, June, October and December. At Cracknore and Bury it was found during these months and in addition during November, while at Calshot it was found in samples from 8 separate months. As with the other gelatinous species there are clear vertical differences in the densities of individuals. *P.pileus* achieved greater densities, biomass and daily and annual production during 1991 than in 1990. Densities in 1993 were more similar to those achieved in 1991 than in 1990, however this may be the result of bias because of the mesh size used in the early period of sampling. Maximum daily production rates in 1991 reached $11.72\mu gCm^{-3}d^{-1}$ at Cracknore, $14.53\mu gCm^{-3}d^{-1}$ at N.W.Netley and $5.53\mu gCm^{-3}d^{-1}$ at Greenland (estimated utilising the results of method b). Peaks of production in 1990 were $17.23\mu gCm^{-3}d^{-1}$ at Cracknore and $1.11\mu gCm^{-3}d^{-1}$ at Greenland, production occurred over a very much more restricted period of time in the earlier year than the later. The inter-annual differences are reflected in the annual production values given in Table 5.3.6, and in Figure 5.3.17. The annual production estimate for Greenland in November 1990 to November 1991 was $0.243mgCm^{-3}yr^{-1}$, while between November 1989 to November 1990 it was less than one fifth this value at $0.042mgCm^{-3}yr^{-1}$. Comparing values for these two periods at Cracknore, once again the annual production estimate for the later year was almost twice that in the former.

The results of annual production are very similar for all three methods, the lowest estimate being 41% of the highest. The differences between the upper and lower ingestion demands however are much greater, the lower estimates being one fifth of the upper estimate. In subsequent analysis the results from method b have been chosen for use, this method giving mid-range values of the 3 method used.

The results show an apparent trend of increasing production values further into the estuary, with the lowest values towards the mouth. An increase in the density of individuals is also apparent in the abundance data collected in the 14 month abundance investigation (see Figure 5.3.16). Table 5.3.7 demonstrates annual average production and ingestion demands for *Pleurobrachia pileus* within Southampton Water, these averages being derived from method b.

SITE	PERIOD	RESPIRATION CARBON (mgC m^{-3} yr^{-1})	TOTAL PRODUCTION (mgC m^{-3} yr^{-1})	INGESTION DEMAND (mgC m^{-3} yr^{-1})
GREENLAND	Nov. 89 - Nov. 90	0.246	0.032^{a}-0.042^{b}-0.078^{c}	0.293^{a}-1.171^{c}-1.430^{b}
GREENLAND	Nov. 90 - Nov. 91	1.436	0.188^{a}-0.243^{b}-0.457^{c}	1.710^{a}-6.838^{c}-8.349^{b}
N.W.NETLEY	Mar. 91 - Mar. 92	3.046	0.399^{a}-0.515^{b}-0.969^{c}	3.626^{a}-14.505^{c}-17.709^{b}
CRACKNORE	Nov. 89 - Nov. 90	2.891	0.379^{a}-0.489^{b}-0.919^{c}	3.442^{a}-13.767^{c}-16.808^{b}
CRACKNORE	Nov. 90 - Nov. 91	4.891	0.641^{a}-0.827^{b}-1.555^{c}	5.823^{a}-23.290^{c}-28.436^{b}

TABLE 5.3.6 Production calculations for *Pleurobrachia pileus* within Southampton Water, size distributed abundance data used to calculate production estimates taken from Lucas (1993). Respiration estimated using equations of Larson (1987a). 3 methods used to estimate production and ingestion from respiration:

a Reeve *et al.* (1978):Respired carbon = 84.0% of Ingestion, Total growth = 13.1% of Respired Carbon.

b Reeve *et al.* (1978):Respired carbon = 17.2% of Ingestion, Total growth = 16.9% of Respired Carbon.

c Hirota (1972):Respired carbon = 21% of Ingestion, Total growth = 31.8% of Respired Carbon.

SITE	PRODUCTION ($mgC\ m^{-3}\ yr^{-1}$)	INGESTION DEMAND ($mgC\ m^{-3}yr^{-1}$)
GREENLAND	0.143[b]	4.005[b]
N.W.NETLEY	0.515[b]	14.505[b]
CRACKNORE	0.658[b]	18.529[b]

TABLE 5.3.7 Estimated carbon demands of *Pleurobrachia pileus* within Southampton Water. Ingestion demand calculated using values given by: b Reeve *et al.* (1978).

The results from 1993 of *P.pileus* densities would tend to suggest that the highest production values for *P.pileus* would occur at Bury, unfortunately no estimates of production or ingestion are available for this site.

***Sagitta setosa*:**

The densities and estimated biomass of *Sagitta setosa* at Calshot and Bury Buoy during the 14 month abundance investigation are given in Figure 5.3.18. The density, size, and biomass of individuals appeared to fluctuate rapidly. Greater densities were generally found at the more seaward site of Calshot, with the highest densities being recorded at Calshot during November at 4.4 $ind.m^{-3}$. Density also peaked at Bury Buoy during the same period, but maximum recorded densities only reached 1.2 ind. m^{-3} at this site. Densities were low at both sites during much of the year with numbers increasing rapidly and being high during the winter months of October to January. These trends are also apparent at the more central estuarine sites (Greenland, N.W.Netley and Cracknore) examined by Lucas (1993) during 1989 to 1992 (see Figure 5.3.19). Patterns of biomass at these 3 sites; Greenland, N.W.Netley and Cracknore, appear to be strongly correlated with the density values in all years, maximum values being once again during the winter months. Biomass reached a maximum of 60.14μgCm^{-3} at Bury during the 14 month investigation, while over the same period values reached 199.15μgCm^{-3} at Calshot. During the investigation of Lucas (1993) biomass reached 46.38μgCm^{-3} at Greenland, 56.10μgCm^{-3} at N.W.Netley and 46.99μgCm^{-3} at Cracknore. All density and biomass maxima occurred between October and December. Only small peaks in density occurred outside this winter period. As ingestion demand was directly proportional to density it showed a similar seasonal pattern. The greatest daily ingestion demand was recorded at Calshot were it reached 40.29$\mu gCm^{-3}d^{-1}$. At the more inner estuarine sites daily ingestion never exceeded 35$\mu gCm^{-3}d^{-1}$. Total annual ingestion

demand at Calshot was estimated to be 1.625mgCm^{-3}yr^{-1}, whereas at Bury Buoy the annual ingestion demand estimate was only 0.431mgCm^{-3}yr^{-1}.

SITE	PERIOD	INGESTION DEMAND (mgC m^{-3} yr^{-1})
*CALSHOT	Jan. 93 - Jan. 94	1.625
GREENLAND	Dec. 89 - Dec. 90	1.107
GREENLAND	Dec. 90 - Dec. 91	1.458
N.W.NETLEY	Mar. 90 - Mar. 91	1.099
CRACKNORE	Dec. 89 - Dec. 90	0.734
CRACKNORE	Dec. 90 - Dec. 91	1.149
*BURY BUOY	Jan. 93 - Jan. 94	0.431

TABLE 5.3.8 Ingestion demand calculations for *Sagitta setosa* within Southampton Water, data used to calculate production estimates taken from Lucas (1993), except * from samples taken by the author and examined by J.Hunter (*pers. comm.*).

SITE	INGESTION DEMAND (mgC m^{-3} yr^{-1})
CALSHOT	1.625
GREENLAND	1.283
N.W.NETLEY	1.099
CRACKNORE	0.942
BURY BUOY	0.431

TABLE 5.3.9 Estimated carbon demands of *Sagitta setosa* within Southampton Water.

Table 5.3.8 gives the estimates of annual production for all the sites, and averages derived from all years of study are given in Table 5.3.9. Although values for Bury Buoy and Calshot have been derived in different years from the other sites, there would appear to be a gradient of

density, biomass and annual ingestion demands along the length of the estuary, increasing in a seaward direction.

Total Production:

The total production by gelatinous predators was calculated from the addition of the 3 species in which production estimates have been made. All annual production estimates given in Table 5.3.10 are annual averages except for *Aurelia aurita* in which the values from 1993 are used. *A.aurita* production was maximum at Cracknore, being much reduced both seaward and landward of this site. Ignoring the contribution towards total gelatinous production which *A.aurita* makes at Bury (where total measures are incomplete), *A.aurita* had both its maximum production in real terms ($26.49 mgCm^{-3}yr^{-1}$) and as a percentage of total gelatinous production (96.4%) at Cracknore. *A.aurita* dominates gelatinous biomass and production at the three higher estuary sites. Annual production contributions for the species *Pleurobrachia pileus* also reached their maximum at Cracknore being $0.658 mgCm^{-3}yr^{-1}$. This value represents only 2.4% of the total gelatinous production however. There were no clear trends in *Clytia hemisphaerica* production, with similar values at Hamble and Cracknore and a lower value at N.W.Netley. This is the result of there being only one estimate at N.W.Netley (during a less productive year), but two at the other sites including the more productive year. *C.hemisphaerica* was the dominant gelatinous producer at Hamble where it made up 76.1% ($0.462 mgCm^{-3}yr^{-1}$) of the total annual gelatinous production. The production dominance by this species at Hamble is, however, more the result of there being a general lack of production by the other gelatinous species rather than it having a clearly increased production at this site. Indeed at Cracknore its annual production was very similar at $0.343 mgCm^{-3}yr^{-1}$, but this represented only a minor contribution (1.2%) of the total gelatinous production. There was a strong trend in total gelatinous production along the length of the estuary, with values increasing progressively between sites from the mouth to the head. This was the result of the production contributions made by *A.aurita*. The lowest total gelatinous production value was $0.607 mgCm^{-3}yr^{-1}$ at Hamble. Gelatinous production at Calshot was estimated as zero. This was because although the species *C.hemisphaerica*, *P.pileus* and *Sagitta setosa* all occurred here, only *A.aurita* was included in the estimate. Highest total annual production was at Cracknore being $27.493 mgCm^{-3}yr^{-1}$. Although there are no annual production estimates for *P.pileus* or *C.hemisphaerica* at Bury Buoy it is likely, given the similar densities and temporal abundance patterns at these two sites (see Figures 5.3.14 and 5.3.16), that production of these two species at Bury would have been as great or greater than that at Cracknore.

SITE	PRODUCTION $\mu gCm^{-3}yr^{-1}$ (% OF TOTAL QUANTIFIED)			
	A.AURITA	*C.HEMISPHAERICA*	*P.PILEUS*	TOTAL
CALSHOT	0.0	*	*	0.0
HAMBLE	2.4 (0.4)	462 (76.1)	143 (23.5)	607.4 (100.0)
N.W.NETLEY	849 (59.2)	69 (4.8)	515 (35.9)	1,433 (100.0)
CRACKNORE	26,492 (96.4)	343 (1.2)	658 (2.4)	27,493 (100.0)
BURY BUOY	4,458 (100)	*	*	4,458 (100.0)

TABLE 5.3.10 Summary of the production estimates of the major gelatinous species within Southampton Water, and the percentage which they make of the total quantified gelatinous production.

* denotes no value available

***Comparisons with calanoid copepod production*:**

Separate comparisons of the ingestion demands of each of the gelatinous predators with estimates of calanoid copepods production are presented in Figures 5.3.20 to 5.3.22. Samples were taken by Lucas (1993) using a 212μm mesh net. This will generally sample late stage copepodites, and much of the meroplankton will also be missed. Although the methods used to estimate copepod production are far from ideal, it does allow a first comparison. Combined gelatinous demands, calanoid production, and the abundance of dominant mesozooplankton are presented in the discussion (see Figures 5.4.2 to 5.4.4.) The abundance of dominant plankton are generally much lower in the work of Lucas (1993), than in that of Zinger (1989), although over short periods those of Lucas may be greater. This indicates inter-annual variability in abundance, or patchiness effects. The copepods will almost certainly always be underestimated using the coarser mesh size. The individual investigations show clear inter-annual differences. The copepod production rates follow similar temporal patterns to the abundance data, although temperature effects cause some variation.

It would appear at Hamble (see Figure 5.3.20) that daily ingestion demands of any single gelatinous species only exceeds the estimated daily calanoid production rates over very limited periods of time, and not in every year. *Aurelia aurita* demand is extremely small in comparison to the estimates of copepod potential production, and never exceeds it. *Clytia hemisphaerica* daily ingestion demands appeared to exceed copepod production estimated from Lucas (1993) during part of the months of June and July 1990. During all the other years it would appear to be very much less. Demands by this species never exceeded the production rates estimated from the data of Zinger (1989). *Pleurobrachia pileus* ingestion demands were also very much less than the copepod production rates derived from Zinger's (1989) abundance data, although during June 1991 they did exceed the production rates estimated from the abundance data of Lucas (1993). The daily demands of *Sagitta setosa* are always a very small portion of the estimated copepod production rates at this site.

Figures 5.3.21 compares the ingestion demands of the gelatinous zooplankton with the production of the calanoid copepods at the N.W.Netley site. *Aurelia aurita*, *Clytia hemisphaerica* and *Sagitta setosa* individual ingestion demands at no point exceed the estimated daily production rates. *Pleurobrachia pileus* ingestion demand do however appear to exceed production rates of the calanoid copepods estimated from Lucas (1993) abundance data in June-July, and in one year also the estimates made from Zinger's (1989) data.

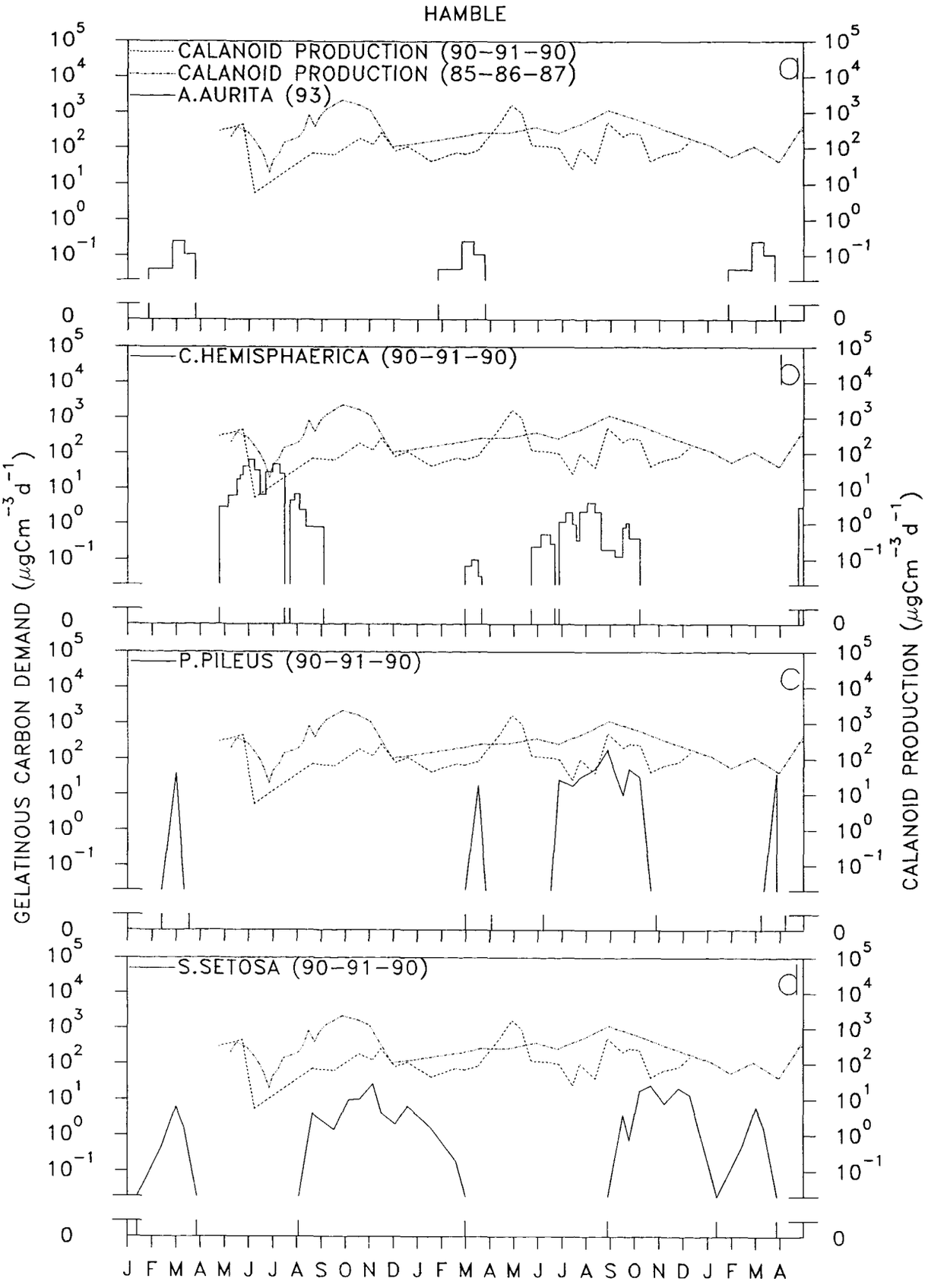


FIGURE 5.3.20 Comparisons of estimated copepod production with the estimated ingestion demands of the dominant gelatinous predators for the Hamble site. a. Aurelia aurita, b. Clytia hemisphaerica, c. Pleurobrachia pileus, and d. Sagitta setosa. Years from which estimates are made given.

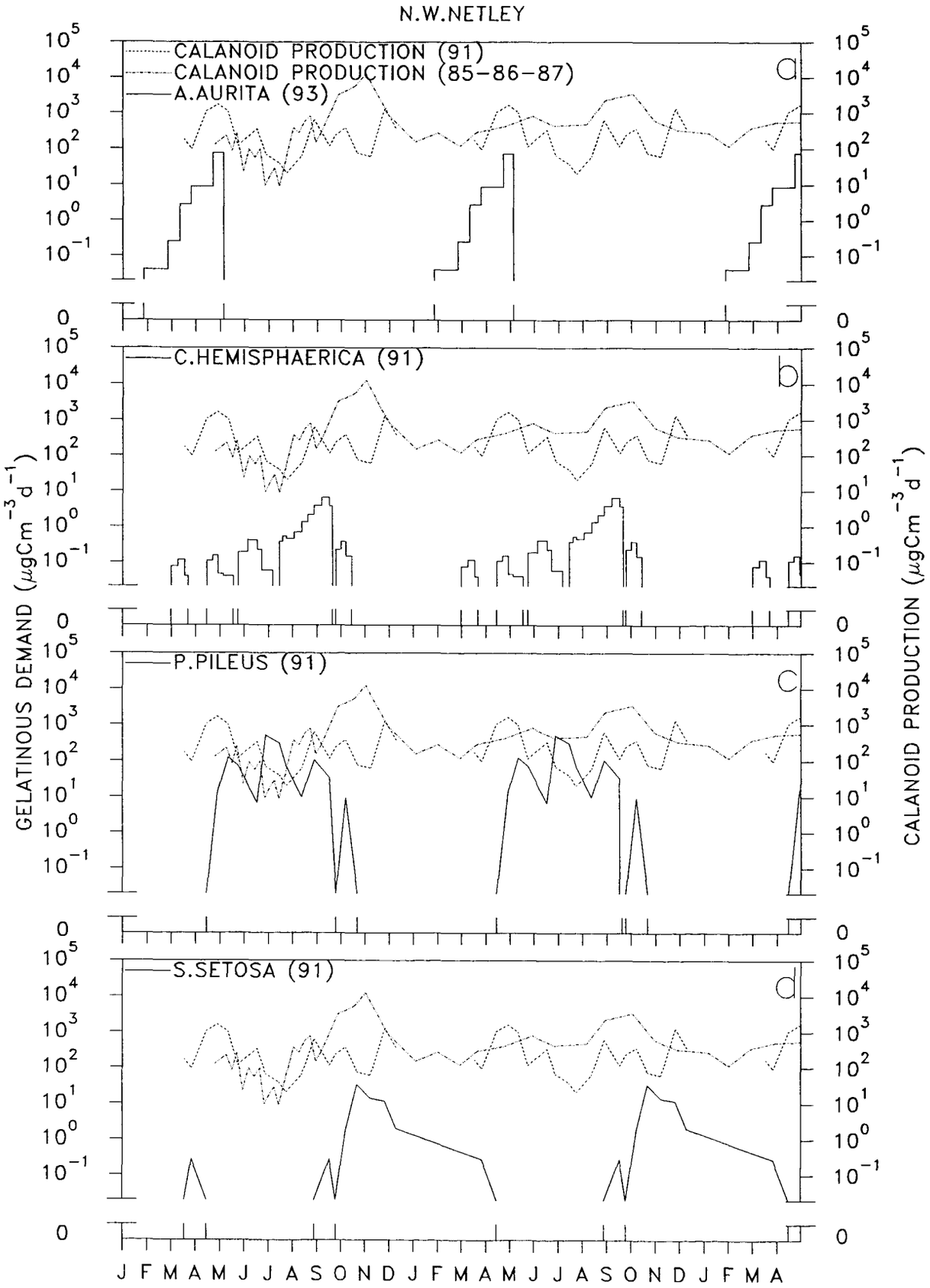


FIGURE 5.3.21 Comparisons of estimated copepod production with the estimated ingestion demands of the dominant gelatinous predators for the N.W.Netley site. a. Aurelia aurita, b. Clytia hemisphaerica, c. Pleurobrachia pileus, and d. Sagitta setosa. Years from which estimates are made given.

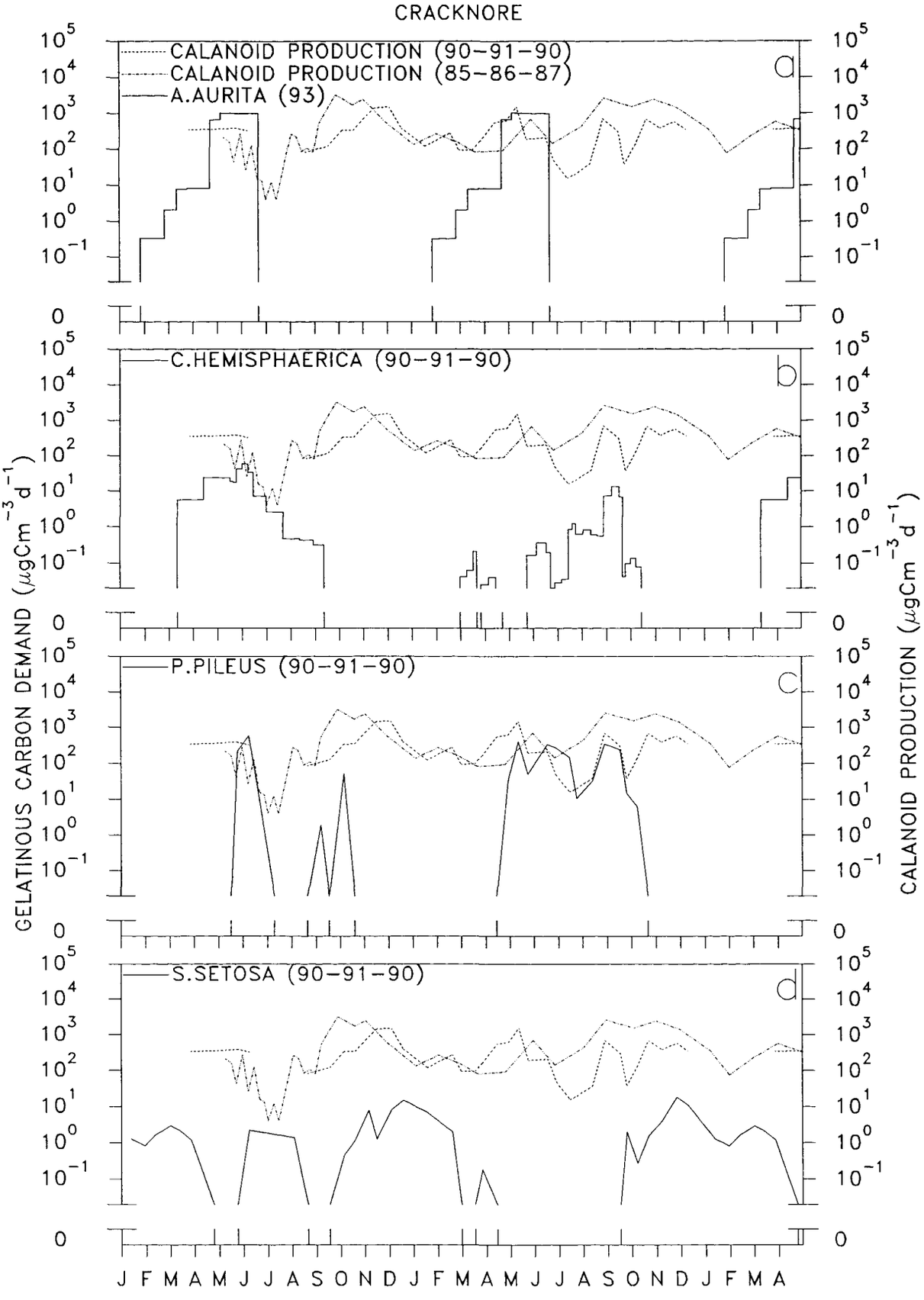


FIGURE 5.3.22 Comparisons of estimated copepod production with the estimated ingestion demands of the dominant gelatinous predators for the Cracknore site. a. Aurelia aurita, b. Clytia hemisphaerica, c. Pleurobrachia pileus, and d. Sagitta setosa. Years from which estimates are made given.

Figure 5.3.22 gives a comparison of gelatinous ingestion demands and estimated copepod production rates at Cracknore. *Aurelia aurita* demand exceed the calanoid production rates estimated from Lucas and Zinger during the last 3 months of its presence ie. late April, May and June. *Clytia hemisphaerica* demands were almost always lower than calanoid production. *Pleurobrachia pileus* had an ingestion demand which exceeded that of calanoid copepod production during part of the June and July 1991, but during none of 1990 for the estimates from Lucas (1993). The estimates of production for 1989 from Zinger would be exceeded by the ingestion demands found in 1990 and 1991. *Sagitta setosa* ingestion demands never exceeded the production rates of copepods.

5.4 DISCUSSION

***Aurelia aurita*:**

Population dynamics:

The population dynamics of *Aurelia aurita* within Southampton Water has been examined in detail by Lucas and Williams (1994). Maximum abundance of pelagic *A.aurita* are found at the higher estuarine sites in Southampton Water, where the population is believed to be endemic (Lucas and Williams, 1994). Olesen *et al.* (1994) found medusae density to be higher in the inner part of Kertinge Nor, Denmark. Hamner and Jenssen (1974) commented that *A.aurita* in Tomales Bay, California, were restricted to the inner reaches, while Möller (1977) believed enclosed bays were places of relatively high production [input] of ephyrae. Other estuaries including the Tamar, U.K., show a similar up estuary increase in medusae abundance (*personal observations*). The benthic scyphistomae of *A.aurita* have found to be abundant in sheltered bays and fjords (Möller, 1979; Olesen *et al.*, 1994), and Gröndahl (1988) found evidence that scyphistomae are rare outside protected lagoons and fjords. Distribution patterns of the benthic scyphomistae may in part explain the apparent spatial abundance patterns found within Southampton Water. Greater inputs of ephyrae in the areas Cracknore and Bury may occur as a result of the abundance of the necessary hard substratum sites at Dock Head and above. Lucas and Williams (1994) reported that SCUBA assisted searches for scyphistomae on the dock walls and pier pilings towards the head of the estuary were unsuccessful. An understanding of the distribution of this species throughout its life-cycle can only be postulated at present, given the lack of full information. It is certainly likely that the abundance of pelagic *A.aurita* may in part be limited by the availability of suitable substratum or conditions for the survival of the benthic polyps.

Van der Veer and Oorthuysen (1985) believed the existence of a continuous ebb surplus

of medusae in the Western Wadden Sea suggested an origin from polyps living in the inner parts of the estuary and a transport of the medusae out into the North Sea. Möller (1980b) attributed the reduction in the density of medusae in Kiel Fjord during June to out-drifting into the open Bight. Although no measurements comparing ebb and flood tide abundances were made in the present investigation, it is certainly possible that a continued flushing of medusae out of the estuary could occur. In fact Southampton Water is unusual in having ebb currents which are faster than corresponding flood tides (Webber, 1980), and the flushing of *Aurelia aurita* in a seaward direction may therefore be particularly exaggerated. The presence of *A.aurita* at the more seaward sites may furthermore be attributable to the flushing of individuals from higher within the estuary. Densities reached a maximum and subsequently fell rapidly not only in 1993 (see Figure 5.3.1), but in all years in which examination has occurred (see Figures 5.3.8 to 5.3.13). This decline may be strongly indicative of rapid loss of individuals through tidal flushing rather than mortality, particularly as these rapid losses are before sexual maturation, the period associated with lower survival rates. Möller (1980b) found that medusae had low mortality rates over the summer in Kiel Bight prior to their maturation. If the same is true of the population in Southampton Water, then this would reinforce the suggestion that the reduction in numbers may be predominantly the result of flushing. In areas where there are low flushing rates there may be low loss rates and consequently individuals may be present for longer periods, achieve higher densities, total biomass, and greater rates of daily and annual production. This success may result in high scyphistomae abundances and high numbers of pelagic individuals year after year. The enclosed populations studied by Olesen *et al.* (1994) and Lucas *et al.* (*in press*) would certainly appear to reinforce this hypothesis. The site studied by Olesen *et al.* (1994) has a mean water residence time of approximately 2 months, the maximum achieved density of 304 ind. m^{-3} and biomass of 450mgCm^{-3} being amongst the highest ever recorded in the literature, while from my own calculations the highest daily and annual production (on a per m^{-3} basis) for truly gelatinous organisms ever recorded also occurs at this site (see Table 5.4.8). The study by Lucas *et al.* (*in press*) in Horsea Lake (on the South coast of England) also shows high density, biomass and daily and annual production, this area being one of little or no flushing throughout most of the year.

Aurelia aurita appears at Cracknore in January to March and disappears in May to June, with a mean population residence time in the plankton of 97 days. Ephyrae were present from February to May in 1993, and medusae from April to June. Release of the free-swimming ephyrae from the sedentary scyphistoma has been studied by many workers and is known to be controlled by several different environmental factors including temperature, light, food and chemical factors (Kakinuma and Sugiura, 1980). The results of Hernroth and Gröndahl (1985a)

suggest that light is one of the more important factors. Strobilation has been found to occur in the spring (Yasuda, 1969; Hamner and Jenssen, 1974; van der Veer and Oorthuysen, 1985; Omori *et al.*, 1995), although it may occur during autumn or winter (Thiel, 1962; Hernroth and Gröndahl, 1985a; Omori *et al.*, 1995), or possibly bimodally in winter and spring (Hamner and Jenssen, 1974). Since there is generally close coupling of ephyrae appearance to strobilation (Hernroth and Gröndahl, 1983), then period of strobilation at Cracknore can be assumed to occur when temperatures range around 7-9°C during the early spring period. This closely coincides with the range given by Van Erp (1958), who demonstrated in the laboratory that strobilation is dependent upon water temperature, occurring from 6 to 10°C. Lowering of temperature to 15°C after previous culture temperatures of 25°C was found to cause maximum strobilation of polyps collected from Mutsu Bay, Japan (Kakinuma, 1962). Omori *et al.* (1995) found in Tokyo Bay that peak release of ephyrae occurred in December/February, and believed that a drop in temperature to below 15°C was the cue for strobilation. They also reported that in the laboratory the period to initiation of strobilation was shortened with starvation. Temperature changes may therefore be as important as the actual temperature. It is probable that many other factors also effect the strobilation date, but light, temperature and feeding conditions may be the most influential. Hernroth and Gröndahl (1985) reported that ephyrae were released in Gullmar fjord, Sweden, from October to November. They subsequently sank to deeper water, where they overwintered, and ascended to the surface in April. In Southampton Water there is no evidence that overwintering ephyrae occurs as none have been found during autumn/early winter, a time when the water column is well mixed. Möller (1980b) found that rapid increase in size after a period of winter growth 'stagnation' began around May and peaked in June. Start of growth was related to the occurrence of large masses of copepods (Möller, 1979). Furthermore, shifts in the initiation of over-wintering ephyrae growth was described as differing by as much as 4 weeks in different years, and being controlled by temperature. The factor controlling final size was described as being undeterminable, being either temperature or food (or presumably both). Changes in the date of initial occurrence of ephyrae was found to vary by as much as 8 weeks in Southampton Water (Lucas and Williams, 1994).

The months of appearance of ephyrae and medusae of *Aurelia aurita* on a world wide scale have been compiled from the literature by Lucas and Williams (1994). There would appear to be great variability in both their time of appearance in the pelagos as well as the variability in the length of time over which they are present. Pelagic *A.aurita* are present for relatively short periods of generally around 4 months at Cracknore. Such short residence times at sites are uncommon, but similar length of residence have been found. Within Southampton Water medusae are typically present at the higher sites until June/July. In other European waters, *A.aurita*

medusae may be present over similarly short periods of the year. For example van der Veer and Oorthuysen (1985) found them to be present in the Wadden Sea until July/August, with a residence time of around 5 months. Comparison of the mean size data of Lucas and Williams (1994) with those in the west Wadden Sea (van der Veer and Oorthuysen, 1985) show that the growth patterns for the two areas are remarkably similar, although in the latter study the medusae have a longer residence time and therefore continue to increase in size. In Kiel Bight Möller (1980b) found medusae to occur until November. Papathanassiou *et al.* (1987) also found medusae present until November in Elefsis Bay, Greece. In European waters pelagic *A.aurita* have been also reported to occur all year round (Olesen *et al.*, 1994; Lucas *et al.*, *in press*). Individual longevity of medusae in nature may exceed one year but not two (Spangenberg, 1965; Yasuda, 1969, 1971). Indeed under laboratory conditions medusae have been shown to live for up to 2 years (Zahn, 1981), although high adult mortality after planula larvae release is a common phenomenon. In Southampton Water maximum biomass of *A.aurita* was found from April to June in most years. Strong spring/summer blooming of *A.aurita* has often been reported in European waters, including in Kiel Bight (Möller, 1980b; Schneider, 1989c), the west Wadden Sea (van der Veer and Oorthuysen, 1985), the Mediterranean (Papathanassiou *et al.*, 1987) and additionally in Japanese coastal waters (Yasuda, 1969). Some workers however have reported maximum abundance and biomass to occur at other times in the year (Omori *et al.*, 1995). Not only have different life-history patterns been found between areas but changes have been found to occur between years at a single site (Hamner and Jenssen, 1974; Omori *et al.*, 1995).

Lucas and Williams (1994) believed *Aurelia aurita* to be endemic to the estuary. It would appear that it only completes its full life cycle towards the head of the estuary. It is probable that planula larvae could not survive long enough in the pelagic phase to allow recruits to commonly enter from outside Southampton Water, Schneider and Weisse (1985) having estimated from metabolic demands that the larvae may only live a few days to less than one week in the plankton. Several reasons were discussed by Lucas (1993) as to why *A.aurita* individuals do not reach the sizes attained by individuals in other areas, the most plausible explanation for this is that individuals are flushed out so quickly, resulting in their early disappearance and small size. Lucas (1993) pointed out that the population at Greenland is flushed out before it reaches sexual maturity, and this may also be the case at sites further up the estuary in some years. The maximum size achieved may be dependent upon food availability as this most probably affects the size at sexual maturity, which in turn controls to a great degree mortality rates. As ISGRs decline towards the end of the pelagic presence of *A.aurita* (at the higher sites) this could either indicate that the population is becoming food limited, or be the result of the reproduction induced de-growth.

Differences in the maximum achieved bell diameter at fixed sites occur between years, these differences may be attributable to some extent to the sampling resolution. Inter-annual comparisons of size at similar points in the year however also reveal differences, such differences are attributable to different growth rates and differences in the timing of strobilation. Considerable inter-annual differences in maximum achieved bell diameter have also been found in other locations. In Kiel Bight, Schneider (1989c) found that in a year when densities and standing stocks were much greater the final achieved bell-diameter was around 70% of that in years in which densities and standing stocks were lower. These differences were not attributed to temperature (as the temperature regimes were very similar in all 3 years), rather they were believed to have been associated with higher density resulting in food shortage. In Southampton Water the low densities found at N.W.Netley did not coincide with greater sizes, even though food supply would appear to be greater at this site. This may therefore indicate control of the population by flushing. From the data of van der Veer and Oorthuysen (1985) it is apparent that in the western Wadden Sea maximum mean bell diameter varied between 24cm in 1981 and 20cm in 1982. Great inter-annual differences in density have been found to occur in Southampton Water, 30 ind.m^{-3} were found at Cracknore by Zinger (1989) in 1985 and 28 ind.m^{-3} at this same site in 1987 by Williams and Reubold (1990). Comparing this to the maximum in 1994 of 1.75 ind.m^{-3} shows that order of magnitude changes may occur. These highest densities being composed of ephyrae although great differences are also seen in medusae abundances. Order of magnitude changes in maximum medusae densities were recorded by Schneider (1989c) for consecutive years in Kiel Bight. Van der Veer and Oorthuysen (1985) found only two fold changes in abundance and maximum daily production in the Western Wadden Sea, although their study only extended over two years. Hernroth and Gröndahl (1985a) found differences in the number of ephyrae released to be two orders of magnitude between consecutive years in the Gullmar fjord. Omori *et al.* (1995) found great inter-annual variability in abundance and biomass, and believed that the population in Tokyo bay 'did not show any discernible seasonal pattern'. Gröndahl (1988) described the great year to year variability in abundance of this species as 'characteristic'.

Many factors may potentially be responsible for inter-annual abundance changes, Hernroth and Gröndahl (1985a; 1985b) proposed that changes in predation by the nudibranch gastropod *Coryphella verrucosa* upon *Aurelia aurita* polyps, and mortality of ephyrae may both account for inter-annual variability in the population size. *C.verrucosa* has not previously been recorded in Southampton Water (M.Sheader, *pers. comm.*), although it is likely that there are many other potential predators of the polyps which could be present. Phillips *et al.*, (1969) comment that limpet *Diadora cayenensis* is known to feed upon sessile scyphozoan stages. Since

each polyp may potentially produce around 10 ephyrae per year (Thiel, 1962), small changes in success of polyps or predation upon them could certainly effect subsequent pelagic densities dramatically. Gröndahl (1988) working in the Gullmar fjord, found the amphipod *Hyperia galba* to be a parasite on scyphozoans, and contributed a great extent to the disappearance of *A.aurita* in autumn. This parasitic amphipod has never been reported in Southampton Water however (M.Sheader, *pers. comm.*). Arai and Jacobs (1980) found under laboratory conditions that *A.aurita* were eaten by several gelatinous species including; *Stomotoca atra*, *Eutonina indicans*, *Leuckartiara* sp. and *Aequorea victoria*. Lebour (1923) also found under laboratory conditions that *Chrysaora isosceles* took *Aurelia aurita* medusae. The common north-east Atlantic scyphozoan *Cyanea capillata* also preys upon *A.aurita* (Båmstedt *et al.*, 1994). None of these predators except a single *Aequorea* sp. individual have been found within Southampton Water (C.H.Lucas, *pers. comm.*). We have a very limited understanding of the effects of predation pressure upon inter-annual variability. Indeed no major predators have as yet been identified which are likely to bring about such variability. It may be that physical factors or prey abundance during critical periods are the cause of these changes. Schneider (1988) proposed that inter-annual variability in medusae density could be the result of variations in the fecundity of female medusae and in larval release in the previous year. Many of the suggestions as to the control of inter-annual variability are not mutually exclusive, not enough is yet known to allow firm conclusions. Given the apparent importance of flushing, its variability from year to year is certainly likely to have profound effects.

Some authors have also commented upon trends of increased abundance and biomass of *Aurelia aurita* over several years (in the Black sea, Shushkina and Musayeva, 1983). In the case of the Black Sea these increases have accompanied increased eutrophication (Mutlu *et al.*, 1994). Broad temporal shifts in the increased dominance of *A.aurita* at the expense of other species have been reported in the Gullmar Fjord (Hernroth and Gröndahl, 1983), while decreases in *A.aurita* abundance and total biomass as a result of competition by invader gelatinous species may affect *A.aurita* populations dramatically (ie. *Mnemiopsis* sp. invasion in the Black Sea; Mutlu *et al.*, 1994). Omori *et al.* (1995) reported that within Tokyo Bay until the 1950's the zooplankton community was dominated by relatively large copepods, these were replaced by the smaller species *Oithona davisae* with the almost simultaneous occurrence of *A.aurita*. This change has also led to increased deposition of diatoms which are no longer cleared by large copepods. The data available for Southampton Water are at present too sparse to draw any conclusions regarding longer term changes. The study of *A.aurita* and important factors of potential influence over many years would certainly aid understanding of population control.

Although there have been few reports of predation upon the pelagic stage of *Aurelia aurita* (although see Lebour, 1923; Metz, 1967; Arai and Jacobs, 1980; Gröndahl, 1988; Strand and Hamner, 1988; Båmstedt *et al.*, 1994) this does not mean that they may be regarded as a trophic 'dead end' as was suggested by Hansson and Norrman (1995). Indeed such a term should be used with great care. Organisms are only true dead ends if their oxidisable components are not utilised (as a result of becoming completely refractory or buried before biological oxidization). Even top predator production must be passed somewhere (unless it goes entirely into negative production processes or true pool loss). As already discussed, fish, amphipods, parasites and other gelatinous organisms may act as predators upon *A.aurita*. Dead adults are probably utilised by the microbial loop, and as such gelatinous predators may be regarded as only a temporary 'dead end' or store of carbon and nutrients.

Degrowth and sexual maturity:

Periods of decreasing mean weight occurred at several sites in Southampton Water during 1990, 1991 and 1994 (Lucas and Williams, 1994; Lucas, *pers. comm.*). De-growth of *Aurelia aurita* has previously been examined under laboratory conditions (Spangenberg, 1965; Hamner and Jenssen, 1974), and has been observed in the field (Tomales Bay, U.S.A.: Hamner and Jenssen, 1974; Kiel Bight, W.Baltic: Möller, 1979, 1980b, Schneider, 1989c; western Wadden Sea: van der Veer and Oorthuysen, 1985; Southampton Water, U.K.: Lucas, 1993, Lucas and Williams, 1994; Kertinge Nor, Denmark: Olesen *et al.*, 1994; Tokyo Bay: Omori *et al.*, 1995). Decreases in the mean weight of individuals within Southampton Water, which occurred during the very initial stages before densities peaked, may be regarded as simply the result of the influx of smaller individuals into the recruiting population and probably do not represent true de-growth. The more notable decreases in mean weight, which occurred towards the end of the pelagic presence of *A.aurita* at the upper sites, do represent de-growth however. De-growth was not encountered in all years of examination, even at the most landward sites of Cracknore and Bury Buoy. The reason that de-growth is not found in every year is probably a result of the resolution of sampling points, although there is evidence that in some years there is a complete absence with the premature loss of the population (Lucas and Williams, 1994). In Southampton Water de-growth is not found at the more seaward sites because individuals are lost very early in the season prior to sexual maturity. Spangenberg (1965) examined the life cycle of *A.aurita* in some detail using laboratory reared animals. Commenting upon the deterioration or de-growth period, she said 'little is known of the factors regulating the deterioration of medusae after maturation. During this investigation, it was noted in sexually mature organisms that gastric filaments were extruded at the same time that sexual products were eliminated...If gastric

filaments of *A.aurita* are essential for digestion then the loss of these structures at sexual maturation would lead to starvation'. This conflicts with the work of Hamner and Jenssen (1974) who found that well fed individuals in the laboratory could spawn, renew gonadal tissue and then re-spawn over prolonged periods. Spangenberg (1965) also commented that it was likely that *A.aurita* could begin the deterioration phase before sexual maturation or fertilization. These studies therefore suggest that medusae may be driven into de-growth before sexual maturation. Although release of gonadal products is often followed by subsequent de-growth and death in *A.aurita* individuals, it would appear that this is not obligatory. The period of de-growth is one in which metabolic demands exceed assimilation. The individuals shrink as they metabolise body components, and this is accompanied by negative production.

Within Southampton Water when de-growth was found, it occurred during June, prior to their complete loss from this area. De-growth of *Aurelia aurita* occurred from September to October in Kiel Bight (Möller, 1980b), medusae being present for longer periods and achieving greater sizes. In contrast van der Veer and Oorthuysen (1985) found no decline in the mean weight of individuals. However, all *A.aurita* medusae had already disappeared from the Wadden Sea by July or August and were to be found in the coastal zone of the North Sea, where no information was available. Examination of the data of Yasuda (1971) for Urazoko Bay, Japan, shows there to be apparent de-growth of *A.aurita* in June/July prior to their extinction from the plankton. Shrinkage has been demonstrated to occur in *A.aurita* under conditions of severe food limitation (Hamner and Jenssen, 1974), although in Southampton Water, as in most other areas, de-growth may be associated with sexual gamete release (ie. Omori *et al.*, 1995). Indeed Omori *et al.* (1995) believed that considering the highly eutrophic conditions within Tokyo Bay throughout the year, starvation was not a probable cause of de-growth of *A.aurita*, rather this was associated with gamete release which may have been triggered by food shortage.

Möller (1980b) gave three possible reasons to explain de-growth in *Aurelia aurita*; genetical determination, starvation and parasitization. There does appear to be some form of genetic determination in the process, although starvation or other environmental conditions may initiate its onset. Size at which de-growth occurs would not appear to be genetically predetermined, Spangenberg (1969) having found that *A.aurita* grown on from scyphistomae in the laboratory reached sexual maturity at one fifth the size at which sexual maturity was reached by individuals living in the area from which the scyphomistae were collected. As no *Aurelia* parasites have as yet been found in Southampton Water, parasitization seems unlikely, although this may not be completely excluded.

Hamner and Jenssen (1974) suggested for *Aurelia aurita* that 'sexual maturation is a size-dependent phenomenon, not an age-specific developmental event'. They added however, that this may not be strictly the case and that reproductive state may be more nutrient dependent. Indeed this was also believed to be the case for *A.aurita* in Horsea Lake (Lucas, *in press.*). Spangenberg (1969) found, from rearing animals in the laboratory, that it was not possible to relate closely either the age or size of the medusae with the development of any specific morphological structure. Comparing the results of various workers it would certainly appear that there is great variability in the size at which individuals become sexually mature. Spangenberg (1965) reported sexual maturity to occur from 250-300mm in the Gulf of Mexico, although under laboratory conditions found individuals to become sexually mature at 55mm. Lucas and Williams (1994) reported that the smallest individuals in Southampton Water which were ripe (ie. contained dividing eggs and planula larvae in the brood sacs of the oral arms) had a bell diameter of 64-71mm. On this date 41% of the individuals were ripe, although individuals 64 to 123mm were also found on the same date which were immature. Sexual maturity could be reached within 90 days after ephyrae release in Southampton Water. Spangenberg (1969) found sexual maturity could be reached in as little as 39 days in the laboratory, while Yasuda (1971) found sexual maturation in Urazoko Bay, Japan, took 7 months. In this later study individuals being found containing fertilized eggs and planulae at around 7cm, however more commonly sexual maturity was reached at a size of 10-15cm in a population in which individuals could reach 25cm. Yasuda (1973b) commented that *A.aurita* in Urazoko Bay during late spring ranged in size from 3 to 12cm but they were however, all sexually immature. Lucas (*in press.*) found individuals as small as 19-20mm which were ripe in Horsea Lake, while Olesen *et al.* (1994) found that the maximum mean bell diameter of 54mm was achieved in a Danish Fjord, and sexual maturity may be assumed to occur at or below this size. Omori *et al.* (1995) found that in Tokyo Bay the minimal size of females containing planulae was 8.5 to 9.0cm, and that planula larvae were observed on the oral arms throughout the year. It would appear that in areas where densities are exceptionally high individuals may reproduce at a much smaller size (ie. Olesen *et al.*, 1994; Lucas *et al.*, *in press*), even though growth rates are lower in these areas. There would appear to be no simple relationship between rate of growth and size at sexual maturity, and no fixed age at which sexual maturity occurs. Size and maturity appear to be related to density of medusae, with individuals at low densities growing to larger sizes and for longer periods prior to the onset of sexual maturity. Density of course may not be the factor of control, rather this may be related to food supply or its rate of depletion. Decline in the abundance of suitable food could for example trigger reproductive activity. Lucas and Williams (1994) state that the small size achieved by adult medusae within Southampton Water, in comparison to other areas, may be a consequence of them being 'food limited as a result of either their own predatory impact, or competition for

food resources with subsequent gelatinous predators, notably *Pleurobrachia pileus*, which are present from April through to September'.

Growth rates:

Growth (as measured by ISGR and rate of bell diameter) of *Aurelia aurita* in Southampton Water is great at times, with the highest ISGR values being the greatest ever reported. The maximum diameter is a reflection of the growth rate, time at which maturation occurs, and the residence time. It would appear that fast growth gives way to rapidly reduced growth at Cracknore and Bury, this may be indicative of food shortage. Reproduction may be induced in *A.aurita* when food becomes depleted. It is possible that *A.aurita* may at times be food limited within Southampton Water, indeed at Cracknore this may partially be the result of its own predatory impact. At N.W.Netley and further towards the mouth of the estuary however, any food limitation is likely to be a consequence of impact of other gelatinous predators (see Figures 5.3.20 and 5.3.21). More work is needed to clarify which factors control the onset of spawning, particularly as this may have profound effects upon the population dynamics and predatory impact of this species.

Olesen *et al.* (1994) examined the instantaneous specific growth rates (ISGR) of *Aurelia aurita* in the Kertinge Nor, Denmark, as well as under laboratory conditions. In the laboratory medusae of bell diameters 4 and 10mm were incubated with controlled concentrations of rotifer prey at a temperature of 15°C. Under these conditions specific growth rates saturated at $0.22d^{-1}$. In the field the maximum rates of instantaneous growth they observed were $0.09d^{-1}$. This led them to the conclusion that the natural population was food limited in its growth. It is possible to estimate the growth rate of medusae within Horsea Lake, south coast England (Lucas *et al.*, *in press*), utilising the same growth method (ie. following the increase in greatest size). Calculations show that the greatest ISGR achieved in Horsea Lake was $0.075d^{-1}$ between February and March, and July and August at $0.073d^{-1}$. During the remainder of the year the ISGR never exceeded $0.05d^{-1}$. These two sites both demonstrate growth rates which are well below those found in the laboratory by Olesen *et al.* (1994). It would therefore appear that the populations are either food limited, or that some other growth interfering factor is present. Rates within Southampton Water have been calculated (and are presented in Figures 5.3.4 to 5.3.14). The highest value was $0.31d^{-1}$ at Cracknore between 23/4/93 and 6/5/93. This value is apparently the greatest ever recorded, even exceeding 'food-saturated' rates in the laboratory. Olesen *et al.* (1994) justified comparisons of laboratory growth rates with field growth rates, even though different sized individuals were being compared, by assuming the maximum ISGR values found under food saturated conditions

to be constant irrespective of individual body mass. Over the 14 month investigation ISGRs in the field exceeded the laboratory saturation value of Olesen *et al.* (1994) at 3 sites (N.W.Netley, Cracknore and Bury) on 3 occasions. At these points mean bell diameters were increasing over a range of sizes, including from 1.7 to 6.5mm and from 5.9 to 29.7mm. These sizes are generally outside the ranges of Olesen *et al.* (1994). If the rates measured in Southampton Water are correct, then either the assumption of constant growth rates with size increase must be untrue, and/or the conditions used to estimate maximum ISGR by Olesen *et al.* (1994) were not ideal. Although food was deemed saturating in their study, the mono-culture of rotifers used may not have had an ideal quality or size. Temperatures cannot be cited as the cause of these greater rates as they did not exceed 15°C until June, when the population was near pelagic extinction. The assumption of Olesen *et al.* (1994) that specific growth rates are constant irrespective of size cannot be completely accepted as populations often show a reduction in growth rate and even de-growth later in their life-history. The high specific growth rate found within Southampton Water certainly suggest individual *A.aurita* may not be food limited at certain times. It should be pointed out that this does not mean that total population production of *A.aurita* is not limited by food availability however. Over much of their presence growth is well below the maximum levels found, and below the maximum value of $0.22d^{-1}$ found by Olesen *et al.* (1994), food limitation is therefore likely to occur over some periods in the area.

The growth rates achieved in Southampton Water may be compared with those found in other natural populations. Delap (1907) found an increase in diameter from 35 to 60 mm within 10 days under laboratory conditions. Utilizing the dry weight equation of Lucas (1993) this represents a specific growth rate of $0.15d^{-1}$. Sars (1841) found an increase in diameter from 60 to 250 mm over 25 days near Bergen, Norway, which gives a specific growth rate of $0.16d^{-1}$. Davidson and Huntsman (1926) found an increase in diameter from 50 to 185mm within 50 days in Passaquamoddy Bay, USA, giving a rate of $0.07d^{-1}$. Thiel (1959) found an increase from 20 to 105 mm within 3 months in Lübeck Bay, Germany, giving a rate of $0.05d^{-1}$. From the data of van der Veer and Oorthuysen (1985), who found that mean medusae bell diameter in 1981 increased from around 50mm to 150mm in 14 days, a maximum ISGR in the Western Wadden Sea of $0.22d^{-1}$ may be calculated. In the following year at the same location they found mean bell diameter increased from 70mm to 110mm in 7 days, representing an ISGR of $0.18d^{-1}$. Hernroth and Gröndahl (1983) found that *Aurelia aurita* increased its average diameter from 5 to 88mm between April 26th and June 1st, giving an ISGR of $0.23d^{-1}$. This growth rate once again exceeds the value deemed 'food-saturated' by Olesen *et al.* (1994). Möller (1980b) found the average medusa size increased from ~50mm to ~220 through the month of July, giving an ISGR of $0.14d^{-1}$, and a daily size increase of 5.7mm. While Schneider (1985) reported a maximum rate of increase

of 3.7mm d^{-1} in the same area. From Figure 2 of Hamner and Jenssen (1974) it would appear that growth from around 10mm to 130mm bell diameter takes around 3 months in Tomales Bay, California, this represents a specific growth rate of $0.08d^{-1}$. Yasuda (1971) found that medusae increased from around 1cm to 20cm in around 10 months in Urazoko Bay, Japan, this represents a very low ISGR of $0.02d^{-1}$. Within Southampton Water individuals may attain 12cm diameter in just over 3 months, and Lucas and Williams (1995) reported a maximum daily increase for *A.aurita* in Southampton Water of 4.8mm in 1990. Lucas (1993) found the largest medusae present at Cracknore, to be 141mm in 1990 and 123mm in 1991, these sizes were attained in around 4 months. Sizes of around 120mm were attained in the Dutch Wadden Sea over a similar period (van der Veer and Oorthuysen, 1985). Omori *et al.* (1995) found that *A.aurita* within Tokyo Bay increased from an ephyrae size of 0.2-0.4cm in March 1991 to young medusae of around 3.0cm by April. Furthermore, a few individuals reached 25cm by July 1991, this later increase represents an ISGR for the fastest growing individuals of $0.07d^{-1}$. Omori *et al.* (1995) gave an estimate of ISGR for the entire period of March to August of 1991, when individuals increased from 0.3 to 18cm, of $0.07d^{-1}$ also. Omori *et al.* (1995) believed that growth by *A.aurita* in Tokyo Bay was food saturated. However, given the very low ISGRs for this area, which were very similar to those in the low prey high predator abundance areas studied by Olesen *et al.* (1994) and Lucas *et al.* (*in press*), it would seem more probable that these populations are all growing sub-optimally as a result of food limited quality or quantity. To conclude, Southampton Water may be considered an area which has a good food supply for *A.aurita* at least during the first few months of its presence. The high rates of flushing may cause it to be present at low abundance, with a short pelagic residence time. It has lower rate of annual and daily production than in many other areas as a result (see Tables 5.4.1 and 5.4.8). In highly productive areas the population biomass of *A.aurita* has been shown to increase exponentially over a period of at least 2 months (Papathanassiou *et al.*, 1987, Möller, 1980b) and within Southampton Water exponential biomass increase appears to occur at Cracknore and Bury Buoy in some years for 3 months or more (see Figures 5.3.7, 5.3.11 and 5.3.13).

Maximum coefficients of daily population biomass increase (K) were also estimated for the *Aurelia aurita* population within Southampton Water during 1993. The highest values at each of the sites were $0.10d^{-1}$ at Hamble (between 25/2/93 and 12/3/93), $0.16d^{-1}$ at N.W.Netley (between 12/3/93 and 26/3/93) and $0.18d^{-1}$ at Bury (between 23/4/93 and 6/5/93). At Cracknore the greatest value was found to reach $0.44d^{-1}$, this value being estimated for the period over which the greatest ISGR measurement also occurred (ie. between 23/4/93 and 6/5/93). This period was one in which there was an apparent increase in *A.aurita* density even though recruitment was believed to have finished. This may indicate lateral movement or

unrepresentative sampling, as such the estimate will be biased. Larson (1985) estimated a coefficient of $0.3d^{-1}$ from the work carried out at 16°C in the laboratory by Hamner and Jenssen (1976), while in the field he estimated from the results of other workers that values varied between 0.1 and $0.3d^{-1}$ (compiling the work of: Rasmussen, 1973; Hamner and Jenssen, 1974; Möller, 1980b and Shushkina and Musayeva, 1983). Estimates made from the results of Olesen *et al.* (1994) show K to reach a maximum at $0.20d^{-1}$, while in Horsea Lake *A.aurita* may be estimated to have a maximum K value of $0.17d^{-1}$ between February and March, the same point when the ISGR was also estimated to be its greatest. From the *A.aurita* biomass data given in Schneider (1989c) for Kiel Bight, over 3 years of study, maximum K values reached 0.11 to $0.19d^{-1}$ (these values calculated from carbon rather than dry weight). The population biomass growth rates are certainly as great or greater at times within Southampton Water compared to those previously measured in any other area. It must be remembered that rates of population biomass increase are not only the result of the growth of individuals but are countered by the rate of biomass loss through mortality and flushing. Given the apparent rates of rapid loss of the population in the area, K would still appear to be high, this is the result of the rapid weight gain by individuals.

Vertical distribution:

Illumination has been describe as a factor possibly influencing the vertical distribution of many medusae (eg. *Mastigias* sp., Hamner and Hauri, 1981; *Phyllorhiza punctata*, García, 1990). The vertical distribution of *Aurelia aurita* has been reported in many studies including; Agassiz (1862), Mayer (1900), Brown (1901), Verway (1942), Ôshima *et al.* (1967), Kuwabara, (1969), Kuwabara *et al.* (1969), Yasuda (1970; 1973a; 1973b; 1974), Mackie *et al.* (1981) and Papathanassiou *et al.* (1987). Clear changes in their vertical position have been previously found, these changes being related to light conditions (Yasuda, 1973; Mackie *et al.*, 1981). Vertical differences in density of *A.aurita* were found by Kuwabar *et al.* (1969) in Tokyo Bay, Japan, with 48 individuals per $100m^3$ in the surface layers and 24 per $100m^3$ at depths below 7 metres. Much more distinct vertical heterogeneity was also found by Kuwabar *et al.* (1969) with 116 individuals per $100m^3$ at the surface and only 9 per $100m^3$ at 1 metre. In Southampton Water, during 1993, the maximum density recorded *in situ* was 5.35 ind. m^{-3} at 5 metres. The density at 10 meters at the same time was found to be only 1.86 ind. m^{-3}. In *A.aurita* light increases bell pulsation frequency (Mackie *et al.*, 1981). This may result in the migration of individuals to nearer the surface in daylight hours (Mackie *et al.*, 1981; Papathanassiou *et al.*, 1987), and sinking during darker periods.

The diel vertical migration of *Aurelia aurita* was examined in natural populations in more depth by Yasuda (1973a; 1973b), who found close correlation between the vertical distribution of medusae and the underwater illumination. *A.aurita* medusae were found to sink in dark hours, while after sunrise the population rose to the surface. They were collected in the surface layer by Yasuda (1973a) when the light intensity was around 10^3 lux, but sank down when it fell below or increased above this level. Other factors such as air and water temperature, chlorinity and wave strength were described as having no significant influence upon vertical distribution. Yasuda (1974) also found during summer the main patterns of vertical migration to be controlled by illumination. However, temperatures above 30°C seemed to restrict their activity and resulted in medusae being restricted to deeper water than would be expected. Although migration was not examined within Southampton Water it was clear that the density of individuals at 5 metres was almost always greater than the density at 10 metres during this study. These samples being taken during the day, usually in the morning to late afternoon. Lucas (1993) stated that 'it was assumed that because Southampton Water is shallow and partially mixed in the area examined, [that] a single mid-depth sample would be adequate', however this would appear to not to be the case. Strong vertical changes in the distribution of a population hinder the collection of quantitative samples. In the present investigation data from 5 and 10 metres were combined prior to estimation of integrated density and biomass when possible. In years other than 1993 data were collected only at 5 metres. This explains why the production rates were lower in 1993 than in other years. Sampling which allows full depth integration is preferable, although which method produces results which are best descriptions of the entire water column still needs to be examined. Further studies of this species in this area should be designed to allow full depth integration.

Production rates and biomass:

The main sources of error in estimating the production and growth of *Aurelia aurita* in this investigation are likely to arise from the lack of temporal resolution, and the small sample size of individuals, particularly towards the end of the season when densities were low. The fact that the population did not behave truly cohortically will also lead to error, although since most production is attributable to the large individuals (when there is no longer continued recruitment) this may be a minor problem. There may also be additional quantification problems associated with net avoidance by the medusae and under sampling of the very largest individuals (Reubold, 1988). Shushkina and Musayeva (1983) found that net catches underestimated the density of *A.aurita* by two to three times those estimates produced using underwater cameras and submersibles. Gomoiu (1980) also reported an underestimation of density with net catch in

comparison to underwater camera observations. Such results demonstrate that there are still many problems regarding density estimation, consequently estimates of production and energy demand may also need to be increased when net catches are utilised. Although patchiness was not explored in the present investigation, this may also potentially have a considerable effect upon calculations. Möller (1979) found order of magnitude changes in the abundance of *A.aurita* in replicate tows taken 10 minutes apart in Kiel Bight. Yasuda (1969) also examined the variability of estimated density in replicate hauls, although such changes appeared to be much less than an order of magnitude. Sampling larger volumes may give more representative data, and this certainly needs examination. More intensive sampling during the most productive periods (ie. toward the end of their presence) would result in better estimates for any given sampling effort (see Morin *et al.*, 1987).

Initial or recruitment production was the dominant form of production of *Aurelia aurita* at Hamble. Since no corrections were made for the actual initial release weight of ephyrae, whose initial release weights are correctly attributable to the benthic system, then some caution must be given to the production estimates made there. Inclusion of the release weight of individuals would reduce production values, although this reduction would be very small at N.W.Netley, Cracknore and Bury Buoy in comparison to the total population production. Other major improvements which could be made in estimation of production and growth would be to sample more frequently during the period when the pelagic *A.aurita* are present. Since the collection in 1993 was designed for the collection of copepods and mesozooplankton it was not ideal to allow examination of gelatinous species. The mesh sizes used by Lucas (1993) were more ideal for *A.aurita* collection, although even larger mesh sizes and nets combined with greater tow speeds may have been better for the quantification of medusae, although damage to medusae may also create some problems with size measurements.

The maximum densities, bell diameter and daily production rates for *Aurelia aurita* within Southampton Water are compared with those from other areas in Table 5.4.1, allowing an indication of the variability between areas for this species. Great densities have been recorded in many areas, including abundances as high as 304 ind. m^{-3} in a Danish fjord (Olesen *et al.*, 1994), and 596.4 ind. m^{-3} in a Japanese Bay (Yasuda, 1968). Abundances within Southampton Water as high as 30 ind.m^{-3} have been recorded. However, only small ephyrae achieve these high abundance, indeed small medusae and adult densities in Southampton Water are often lower than in many other areas. The maximum size achieved is also much less than in many other studies, although not as low as those found in the areas where densities are exceptionally great (ie. Olesen *et al.*, 1994; Lucas *et al.*, *in press*).

Species	Max. Abundance (ind. m^{-3})	Max. Size (mm)	Max. Biomass (mgC m^{-3})	Max. Daily Production (mgC m^{-3} d^{-1})	Area	Source
Aurelia aurita		Bell Diameter				
	71.0	-	-	-	Urazoko Bay, Japan	Yasuda 1969
	596.4	-	15,411.2[c]	-	Urazoko Bay, Japan	Yasuda 1970
	-	310	-	-	Urazoko Bay, Japan	Yasuda 1971
	-	120	-	-	Urazoko Bay, Japan	Yasuda 1973
	24.92(patch)	260	23,703.1[c]	-	Tokyo Bay, Japan	Kuwabara *et al.* 1969
	1.53	310	411.8[c]	-	Tokyo Bay, Japan	Omori *et al.* 1995
	-	460	-	-	-	Quoted in Kuwabara *et al.* 1969
	103	64	980.7[c]	-	Lake Hamana, Japan	Kuwabara 1969
	-	170	-	-	Tomales Bay, U.S.A.	Hamner & Jenssen 1974
	-	-	433[f]	-	Chesapeake Bay, U.S.A.	Feigenbaum and Kelly 1984
	<1	150(max. mean)	-	-	Bedford Basin, Canada	Matsakis and Conover 1991
	-	-	11.2[c]	-	North Sea and Baltic	Möller 1980c
	0.23	~330	54.8	-	Kiel Bight, W.Baltic	Schneider 1989b, 1989c
	5.17	-	49.4[f]	-	Kiel Bight, W.Baltic	Möller 1977
	0.43(*)	-	36.1[d]	-	Kiel Bight, W.Baltic	Möller 1979
	0.03(** & ***)					
	-	-	50.1[c]	-	Kiel Fjord, W.Baltic	Möller 1980a
	0.07(*)	440	47.3[d]	0.8[de]	Kiel Fjord, W.Baltic	Möller 1980b
	0.12(** & ***)					
	0.16(total)					
	2.44	220	49.4[f]	-	Black Sea	Gomoiu 1980

-	150(observation)	-	-	Baltic Proper	Hernroth & Ackefors 1979
14.96(*)	-	-	-	Gullmar Fjord, Western Sweden	Hernroth & Gröendahl 1983
304	54(max. mean)	450[b]	22.7[e]	Kertinge Nor, Denmark	Olesen *et al.* 1994
0.49(** & ***)	290	17.5	2.0	western Wadden Sea	van der Veer & Oorthuysen 1985
-	331	-	-	Kiel Bight, W.Baltic	Kerstan 1977
44(*)	200	120.4[b](total)	1.0[d,e]	Elefsis Bay, Mediterranean	Papathanassiou *et al.* 1987
~30(**)		150.5[b](patch)			
~1.5(***)					
0.4(*)	-	-	-	Killary Harbour, Western Ireland	Ryan *et al.* 1986
24.1	105	135.8	3.3	Horsea Lake. U.K.	Lucas *et al. in press*
28	-	-	-	Southampton Water, U.K.	Williams & Reubold 1990
30.0	-	-	-	Southampton Water, U.K.	Zinger 1989
5.38 (1990)	130 (1990)	19.8 (1990)	1.0	Southampton Water, U.K.	This study, Lucas *pers. comm.*
8.71 (1991)	123 (1991)	23.5 (1991)	1.8		
3.61 (1993)	94 (1993)	6.8 (1993)	0.5		
1.75 (1994)	135 (1994)	37.1 (1994)	2.9		

TABLE 5.4.1 Comparisons of maximum recorded abundance, individual bell diameter, total carbon biomass and daily production of *Aurelia aurita*, compiled from literature sources and for Southampton Water.

a DW= 2.8%WW (mid-range figure from Hirst and Lucas *in prep.*). b CW= 4.3%DW (from Larson, 1986a). c CW= 0.1204%WW (combination of two previous factors). d Calculated from original paper using conversion factor/s given above. e Calculated from data given in paper using 'Total biomass change' method. f CW= 0.1204%WW, and 1.44g WW= 1ml Displacement Volume (estimated from comparing Stoecker *et al.*, 1987 with WW regression). * Ephyrae size <10mm bell diameter. ** Young medusae size 10-40mm bell diameter. *** Medusae size >40mm bell diameter.

There is an obvious exception to the general rule that the greater the density the smaller the size of individuals in that Kuwabara *et al.* (1969) found patches of 260mm individuals at densities of 24.9 ind.m^{-3}. Biomass of *A.aurita* in Urazoko and Tokyo Bays has been estimated in the present investigation from the authors' data to be as high as 15.4 (Yasuda, 1970) and 23.7gCm^{-3} (Kuwabara *et al.*, 1969). This second figure is the highest biomass of *A.aurita* ever found. Such biomass levels are likely to be unsustainable and may be the result of the concentrating effects of tides, wind or migration. In areas where produced biomass is autochthonous (eg. very enclosed areas), it has been found to reach 450mgCm^{-3} (Olesen *et al.*, 1994) and 42mgCm^{-3} (Lucas *et al.*, *in press*). Maximum biomass in Southampton Water at 6.8-37.1mgCm^{-3} is very similar to other estuarine sites such as Kiel Bight (Möller, 1979; Schneider, 1989b; 1989c) and the western Wadden Sea (van der Veer & Oorthuysen, 1985) where maximum biomasses were 19-54mgCm^{-3} and 17.5mgCm^{-3} respectively. Maximum daily production rates within Southampton Water were 0.5-2.9mg$Cm^{-3}d^{-1}$. These rates are comparable to those found in other coastal/estuarine areas of between 0.8 and 2.0mg$Cm^{-3}d^{-1}$ (although different methods of calculation have been used and this range should certainly be extended upwards when the 'Total biomass change' method has been used). In enclosed areas daily rates may be greater at up to 22.7mg$Cm^{-3}d^{-1}$ (Olesen *et al.*, 1994), once again this values is certainly underestimated as the 'Total biomass change' method was used for its estimation. Production of *A.aurita* was highest during May-June in the western Wadden Sea (van der Veer and Oorthuysen, 1985), and was also highest in Southampton Water during these two months. Examination of the total biomass records of Schneider (1989b) for *A.aurita* in Kiel Bight reveals that maximum increases in biomass occurred between June-August. From the data of Olesen *et al.* (1994) it would appear that greatest biomass increase was between the months of July and August in 1991 but in June 1992. In the study of Lucas *et al.* (*in press*) biomass increase was greatest during the months of April and May. The work of Omori *et al.* (1995) however shows that production of *A.aurita* varies in some areas with no clear seasonal pattern. The growth of *A.aurita* medusae is probably tightly coupled to the abundance of zooplankton prey. The production of these medusae and their predatory impact is also dependent upon their abundance which in turn is determined by other factors including physical ones.

Schneider (1989c) found that *Aurelia aurita* made up over 30% of the total zooplankton carbon biomass greater than 20μm (including micro- to macroplankton) in Kiel Bight during the summer of 1983, while in 1982 he believed that it could well have exceeded that of the micro-to macrozooplankton. Olesen *et al.* (1994) estimated that *A.aurita* biomass could reach as high as 0.45gCm^{-3} in the enclosed environment of Kertinge Nor, Denmark. This value greatly exceeded that of the >20μm plankton maximum throughout most of the year, at times by over an order of magnitude.

	KIEL BIGHT		SOUTHAMPTON WATER	
	$mgCm^{-3}Season^{-1}$ *1982 †1983	% OF TOTAL INGESTION	$mgCm^{-3}yr^{-1}$ (1993)	% OF TOTAL INGESTION
TOTAL PRODUCTION	21†-60*	30.4†-15.5*	26.5	46.8
SOMATIC	19†-54*	27.5†-14.0*	-	-
REPRODUCTIVE	2†-6*	2.9†-1.6*	-	-
RESPIRATION	33†-227*	47.8†-58.8*	14.0	24.7
DOC RELEASE	1.4†-22*	2.0†-5.7*	4.8	8.5
ASSIMILATION	55†-309*	80†-80*	45.3	80
INGESTION DEMAND[1]	69†-386*	100†-100*	56.6	100

TABLE 5.4.2 Comparison of the energy budget derived for *Aurelia aurita* at Cracknore during 1993, with the energy budget derived by Hansson and Norrman (1995) and Schneider (1989b) for a population in Kiel Bight, western Baltic for 1982 and 1983.

1 Ingestion demand calculated from assimilation demand utilising an assimilation efficiency of 80%.

However, in this area epi-benthic harpacticoids were not sampled although these were an important food source. The maximum biomass value during 1993 was at the Cracknore site where it reached 6.8mgCm^{-3}. This value greatly exceeds that of the calanoid copepod carbon, estimated from Zinger's (1989) study, for the same period, at around 0.077mgCm^{-3} (in 1985) to 0.671mgCm^{-3} (in 1986).

Energy budget:

Energy budgets have been constructed for *Aurelia aurita* within Southampton Water for 1993. Table 5.4.2 compares the budget derived at Cracknore with the only other complete population energy budget for a natural population published. This other study derived for *A.aurita* in Kiel Bight, Western Baltic (as constructed by Hansson and Norrman, 1995, who combined their own estimates of DOC excretion with the population data of Schneider, 1989b). One of the most striking differences between the budgets is the total production appears to make up a considerably greater proportion of total ingestion in the Southampton Water population than in the Kiel Bight population, growth being 46.8% of ingestion at Cracknore, but only 15.5 to 30.4% in Kiel Bight. One major reason for such a difference is that the somatic production for the Kiel Bight population was estimated by Schneider (1989b) using 'Total biomass change'. If production was estimated at Cracknore during 1994 using 'Total biomass change', rather than cohortic methods, then the annual production estimate would be 6.9mgCm^{-3}yr^{-1} rather than 26.5mgCm^{-3} yr^{-1}. Using a 'Total biomass change' method to estimate production rather than a cohort method may therefore result in production being underestimated by at least ~75%. This explains why production appears to make up such a small proportion of the ingestion in Kiel Bight, multiplying the production by 4 (in an attempt to correct for underestimation), results in production becoming 39 to 57% of ingestion (ie. growth efficiency) in Kiel Bight, the value of 46.8% for Cracknore being within this range. A gross growth efficiency of 37% (at 12°C) was given by Fraser (1969) for a single *A.aurita* kept in an aquarium. This gross growth efficiency was quoted as a comparison to their own data for *A.aurita* by Olesen *et al.* (1994). However, the figure was incorrectly quoted as a net growth efficiency (Production / Assimilation) when in actuality it is a gross growth efficiency (Production / Ingestion). Alldrege (1984) and Conover (1979) also quote this value in their reviews of production. However, the figure itself is in some doubt as it was estimated from dry weight rather than carbon. Recalculation using appropriate carbon weights (assuming *A.aurita* carbon to be 0.1634% WW: Larson (1986a), and that the prey had a carbon content of 4.81% of WW: taking the mid-range copepod values of Curl (1962)) gives a gross growth efficiency of 4.6%. This would appear to be remarkably low and unrepresentative of the gross growth efficiency found in the natural populations.

The percentage which respiration makes of total ingestion appears somewhat greater for the Kiel Bight population. If however the total production is once again multiplied by 4 then respiration makes up a much more similar percentage of total ingestion (ie. 22-37% in Kiel Bight compared to 24.7% in Southampton Water). Kremer and Reeve (1989) found that well-fed individuals of the ctenophore *Mnemiopsis mccradyi* respired only 16% of ingested food whereas individuals which were offered low amounts of food respired 32% of this food. In the present investigation the respiration equations were taken from Larson (1987a). A different equation for predicting respiration was used by Schneider (1989b) to that in the present investigation. Schneider (1989b) also used an RQ of 0.85 whereas a value of 0.8 was chosen as more appropriate in the present investigation. Using a larger RQ value has the effect of giving greater respired carbon estimates. Size differences between the populations in the two areas may also have a significant effect as may the temperatures at which the respiratory rate equation were made and environmental temperatures they were applied to.

DOC release was estimated by Hansson and Norrman (1995) for the Kiel Bight population by applying the release rate of 1.2mgC $ind.^{-1}d^{-1}$ to the abundance data of Schneider (1989b). Although Hansson and Norrman (1995) found no detectable relationship between *Aurelia aurita* size and DOC release rate only a small size range was examined (ie. 9.5-18cm). As such applying a single release rate, rather than a rate which is a fixed proportion of body weight (1.55% of body weight per day) as in the present investigation, would appear advisable. In both studies DOC release estimates were made upon medusae which were considerably smaller than those examined by Hansson and Norrman (1995).

It is important that prey selection by *Aurelia aurita* be described if an attempt to understand predatory effects of this species be completed. Hyman (1940) described the phylum Cnidaria as strictly carnivorous, this however may not entirely be the case, although carnivory may be the predominant metabolic source. Although algae and protozoa are poorly represented in the gastric cavities of *A.aurita* in terms of their mass in comparison to other organisms (Möller, 1980a), studies of this type cannot yield information on the ingestion of most protozoa or other soft bodied micro-zooplankton (Stoecker *et al.*, 1987a). Laboratory clearance rates have been used in an attempt to assess the importance of micro-zooplankton to *A.aurita* (Stoecker *et al.*, 1987a). In the present investigation daily carbon rations have been estimated from the data given in the literature, as well as estimated from the energy budget ingestion demand estimates made for *A.aurita* for 1993. All sources of data have been converted to daily ration in carbon terms to allow fair comparison (Hirst and Lucas, *in prep.*). The results are compiled into Table 5.4.3. and presented graphically in Figure 5.4.1 to allow comparisons and an assessment of the potential

importance of different prey types to *A.aurita*. Carbon required for respiration has also been estimated and are shown in Figure 5.4.1, these requirements were estimated using the same methodology as in the energy budget estimates utilising the respiratory equation of Larson (1987a), an RQ of 0.8, while medusae weight was calculated applying the dry weight equation and carbon contents given in Larson (1985).

Daily ration:

Båmstedt (1990) found in laboratory feeding experiments that *Aurelia aurita* medusae (ranging in size from 44 to 95mm bell diameter) did not utilize the phytoplankton *Isochrysis galbana* in concentrations ranging from 19.7-78.5μgCl^{-1}. Stoecker *et al.* (1987a) found that *A.aurita* of 25mm bell diameter did not clear the phytoplankton *Pyramimonas* sp. when at a concentration of 0.08μgCl^{-1}, and that the phytoplankton *Chaetoceros simplex* when supplied at 0.05μgCl^{-1} gave an estimated daily ration of 0.023% for *A.aurita* of 14mm bell diameter. Stoecker *et al.* (1987a) found that small medusae cleared only some types of phytoplankton, and in mixtures of ciliates cleared larger ciliates in preference to smaller ones. Non-loricated ciliates were preferred over similar sized tintinnids. While Båmstedt (1990) found that the ciliate *Strombidium sulcatum* was consumed by ephyrae and small medusae of 3-14mm diameter, but this supplied a carbon daily ration (DR) of less than 0.9%. Stoecker *et al.* (1987a) found that the smaller ciliate *Urotricha* sp. gave a daily ration of 0.024%, whereas larger ciliates gave daily rations between 0.57 and 5.36%. Stoecker *et al.* (1987a) found in predation experiments with natural assemblages of microzooplankton, that small non-loricate ciliates (30-50μm) were consistently cleared at very low rates compared to larger ones (>50μm). Båmstedt (1990) concluded that the small-sized ciliates may be of a much reduced importance as prey compared to larger ciliates. The ciliate *Urotricha* sp. was removed preferentially to the dinoflagellate *Heterocapsa triquetra*, even though the dinoflagellate was larger (Stoecker *et al.*, 1987a). They also found that *A.aurita* medusae selectively fed upon large, non-loricate ciliates over most metazoan microzooplankton, while copepod nauplii were selected over rotifers and polychaete larvae. Unfortunately Stoecker *et al.* (1987a) did not examine the importance of larger prey items including copepodites, adult copepods and barnacle nauplii. Of the microzooplankton examined the ciliate *Strobilidium* sp. gave the greatest value of daily ration at 5.36%. Rotifers have also been shown to be cleared by *A.aurita* (Båmstedt, 1990; Olesen *et al.*, 1994), *Synchaeta* sp. for example was consumed, but gave a daily ration of between 4.1 and 35.2% (Båmstedt, 1990). This may explain why in the study of Olesen *et al.* (1994), the saturated growth rate when fed high concentrations of rotifers was still apparently lower than has been found in many natural situations (see Table 5.4.3).

The relatively low daily rations estimated from ciliates, phytoplankton and rotifers may be compared to those for mesozooplankton including copepods and cladocerans. When feeding upon mesozooplankton daily ration may reach as high as 176.4% (Båmstedt, 1990). Indeed the daily rations found using mesozooplankton are well in excess of the respiratory requirements, while ciliates and phytoplankton appear often to barely meet such requirements (see Figure 5.4.1). These results give a strong indication that although many workers have cited microzooplankton as food sources for *Aurelia aurita* in their attempts to balance carbon demands and supply, this may typically not be the case, as they are an extremely poor source of carbon. It would appear from the comparisons of daily ration with the respiratory carbon requirements that these would possibly not sustain growth under the conditions of which they have been supplied. Such sources therefore are likely to be of minor importance, at least in terms of carbon and energy requirements in rapidly growing individuals. Stoecker *et al.* (1987) concluded that, given the clearance rate found for micro-zooplankton, even when the biomass of *A.aurita* was relatively great, medusae would remove less than 10% of the standing stock of large ciliates per day. Given the fast growth rates of large ciliates only extremely high densities of *A.aurita* could have any significant impact, the impact upon smaller ciliates would be even less than upon large ciliates (Stoecker *et al.*, 1987). The removal of copepods by *A.aurita*, which could lead to reduction in the grazing pressure on ciliates and also reduce their competition for algae foods with the copepods, may be a more important effect however (Stoecker *et al.*, 1987a).

Matsakis and Conover (1991) estimated the daily rations of *Aurelia aurita* in Bedford Basin, Nova Scotia, using gut content analysis of natural individuals together with digestion time. Unfortunately their estimates of daily ration of 400-750% are incorrect as their data for the carbon weight of medusae seem to be between 1 and 3 orders of magnitude too low (Hirst and Lucas, *in prep.*). This error could lead to orders of magnitude lower daily ration estimates. As such the daily ration estimates must be reduced by an equivalent amount. These values have therefore been excluded from the compiled data set.

Daily ration estimates made for the *Aurelia aurita* population within Southampton Water, through the energy budget approach already outlined, reveals that natural daily rations may be as high as 55% (see Figure 5.4.1). Laboratory investigations have shown mixed zooplankton (mainly copepods and cladocerans) allow the highest predation rates. Carbon daily rations are usually within the range of 11-85%, with highest rates at highest prey concentrations (Båmstedt, 1990). Båmstedt (1990) found that predation rate and daily ration were positively correlated with prey abundance, and that daily ration decreased with increasing medusae size. The energy-budget derived estimates however show an increase and then subsequent decrease.

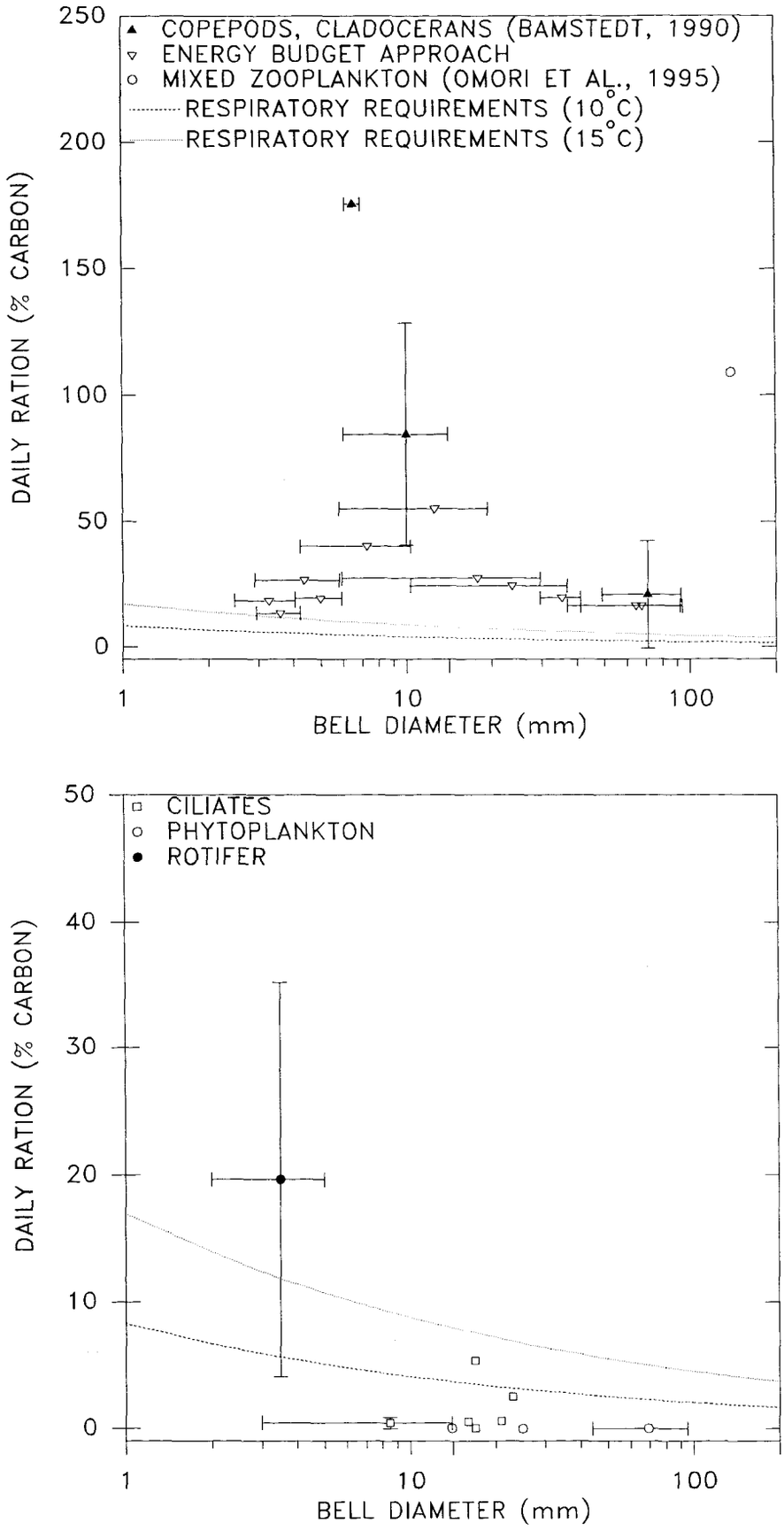


FIGURE 5.4.1 *Daily ration estimates for Aurelia aurita in laboratory clearance experiments and also estimated from ingestion demands for the population in Southampton Water during 1993 using results from the 'Energy Budget' approach. Estimated respiratory demands are given for comparative purposes. (Nore scale change).*

SIZE (mm)	TEMP (°C)	PREY TYPE	PREY WEIGHT (µgC ind.$^{-1}$)	PREY CONC. ind. l^{-1} (*µgC.l^{-1}*)	DR % (IN CARBON)	SOURCE
LABORATORY CLEARANCE EXPERIMENTS:						
44-95	15	*Isochrysis galbana* (Flagellate)	[1]2.4*10^{-6}	8.3*10^{6}-3.3*10^{7} ([1]*19.7-[1]78.5*)	[2]0.0	Båmstedt 1990
3-14	6.9	*Strombidium sulcatum* (Ciliate)	[1]8.16*10^{-4}	500-50000 ([1]*0.41-[1]40.8*)	[2]<0.9	
2-5	6-7	*Synchaeta* sp. (Rotifer)	30.30	100-605 ([3]*30.0-[3]181.7*)	[3]4.1-[3]35.2	
47-95	15	Mixed Zooplankton (mainly copepods and cladocerans)	[4]1.01-[4]1.36	12-125 ([4]*16.7-[4]128.6*)	[4]<1-[4]42.8	
6-14	15	Mixed Zooplankton (mainly copepods and cladocerans)	[4]0.92	273 ([4]*256.7*)	[4]40.7-[4]128.4	
6.1-6.9	15	Mixed Zooplankton (mainly copepods and cladocerans)	[4]0.92	323 ([4]*297.5*)	[4]175.5	
25	15	*Pyramimonas* sp. (Phytoplankton)	3.3*10^{-5}	2426 (*0.08*)	[5]0.0	Stoecker *et al.*1987a
14	15	*Chaetoceros simplex* (Phytoplankton)	2.8*10^{-5}	1886 (*0.05*)	[5]0.023	
17	15	*Urotricha* sp. (Ciliate)	5.1*10^{-5}	700 (*0.04*)	[5]0.024	
16	15	*Balanion* sp. (Ciliate)	1.75*10^{-3}	600 (*1.05*)	[5]0.571	
21	15	*Balanion* sp. (Ciliate)	1.75*10^{-3}	500 (*0.88*)	[5]0.595	

17	15	*Strobilidium* sp. (Ciliate)	$9.00*10^{-3}$	<1400 (*<12.6*)	[5]5.355	
23	15	*Favella* sp. (Ciliate)	$1.95*10^{-2}$	300 (*5.85*)	[5]2.486	
140	-	Mixed zooplankton (mainly *Acartia*)	-	'much higher than typical'	[6]108.8	Omori *et al.* 1995
ENERGY BUDGET APPROACH:						
N.W.Netley						
2.9-5.8	8.5-11.6	Natural Prey	-	Natural Conditions	26.6	Present Investigation
5.8-19.3	11.6-13.1				55.1	
Cracknore						
2.5-4.1	7.1-8.6	Natural Prey	-	Natural Conditions	18.3	
4.1-5.9	8.6-11.3				19.3	
5.9-29.7	11.3-13.0				27.4	
29.7-41.2	13.0-13.5				19.6	
41.2-94	13.5-17.5				16.3	
Bury Buoy						
3.9-4.2	8.7-11.0	Natural Prey	-	Natural Conditions	13.4	
4.2-10.3	11.0-13.0				40.2	
10.3-37	13.0-17.6				24.3	
37-92	17.6-17.4				16.4	

TABLE 5.4.3 *Aurelia aurita* daily ration (consumed prey mass (in carbon) per day as a percentage of the predator body mass (in carbon)) under laboratory conditions of varying prey types and concentrations, and estimated in the present investigation by applying energy-budget ingestion demands to body weight estimates of the natural population.

1 Carbon weight of ciliate and flagellate estimated using the ESD (equivalent spherical diameter) of 28.0μm and 4.0μm respectively (given in original paper) and a conversion factor where 1ml cell volume equals 0.071gC (as given for ciliates by Fenchel and Finlay, 1983). 2 Assuming ciliate carbon to be 40.8% of the AFDW (estimated from comparison with carbon estimates as given here with conversions given in original paper, where one cell has an AFDW of ~0.002μg ind.$^{-1}$) and *Aurelia* carbon to be 20.5% of AFDW (Larson, 1986a). 3 Estimated from DW daily ration by assuming rotifer carbon to be 55.55% AFDW (as carbon is 50% of DW (Duncan, 1989), and assuming ash to be 10% of DW), and *Aurelia* carbon to be 20.5% of AFDW (estimated from Larson, 1986a). 4 Assuming mixed zooplankton carbon to be 43.9% of the AFDW (as ash equals 8.9% AFDW (Laurence, 1976)) and carbon weight 40% of DW (Båmstedt, 1986)), and *Aurelia aurita* carbon to be 20.5% of AFDW (estimated from Larson, 1986a). 5 Calculated from Table II in Stoecker *et al.* (1987a), assuming carbon weight of medusae to be 0.1634% of Wet Weight (Larson, 1986a), and 1.44g WW to be equal to 1ml biovolume (estimated in this study by comparing volume to wet weight equations). 6 Estimated from authors' data assuming mixed zooplankton predominantly composed of *Acartia* had a carbon content of 40% of dry weight (Båmstedt, 1986), and that *Aurelia aurita* has a carbon content of 4.3% of dry weight (Larson, 1986a).

The daily rations achieved in the work of Båmstedt (1990) appear very similar to those estimated in the present investigation for the larger sized individuals but the smaller size do appear much greater in the study of Båmstedt (1990).

The daily ration estimates made by Båmstedt (1990) were at mesozooplankton prey concentrations of 12-273 ind. l^{-1}. Such concentrations are not typical from net catch estimates in Southampton Water, the highest value for zooplankton (100μm mesh net capture) at N.W.Netley being 75 ind. l^{-1}, although at Cracknore concentrations have been found to reach only 26 ind.l^{-1} (Zinger, 1989), and during much of the period of *Aurelia aurita* presence may be much lower. Indeed, rarely have mesozooplankton concentrations in any area been found to exceed 50 ind.l^{-1} (Reeve, 1980; Båmstedt, 1990). Båmstedt (1990) completed preliminary estimates of the food demand of *A.aurita*, concluding that the demands for food found in natural populations could not be satisfied by the recorded mesozooplankton concentrations. It was hypothesised therefore that the heterogenous distribution of zooplankton could lead to the occurrence of suitable food conditions even when the average prey abundance was low. Reeve (1980) stated that gelatinous predators appear to be much better at catching food in the environment than laboratory experiments would suggest. The most likely explanation for this phenomenon being that animals rely on encountering variable food densities on the scale of their own movement ie. micro-patchiness. Only when more is known about the actual food concentrations in space and time from the view point of the predator, can such problems be solved. Miller and Daan (1989) found that for *Pleurobrachia pileus* in Dutch coastal waters, there was no evidence that this predator was associated with high densities of prey, as has been hypothesised by many previous workers to explain apparent ctenophore food demands in relatively dilute prey conditions. Patches of zooplankton prey have commonly been found. Reeve and Baker (1975), for example, stated that 'It is certain that any environmental concentration [of mesozooplankton] estimated from a net tow is an average of several small-scale patches of higher and lower density. We have some information from direct observation by SCUBA (unpublished data) that patch densities at least an order of magnitude greater occur..' Larson (1987b) reported that patches of *Acartia* sp. in Link Port, eastern Florida, may have reached 15 times greater than the mean value. The dependence for *A.aurita* to find and stay in patches of prey which are much denser than the typical net sampled densities may also be the explanation for this phenomenon within Southampton Water, given the daily rations needed to sustain estimated ingestion demands. Bailey and Batty (1983) have demonstrated that *A.aurita* may alter its swimming patterns to facilitate efficient utilization of abundant prey and also minimize the costs at low prey abundance. The idea that gelatinous predators may require the presence of patches of high prey densities has also been put forward for other gelatinous species including ctenophores. Reeve (1980) concluded that ctenophores were

probably dependent upon high density micro-scale prey patches because laboratory-measured ingestion rates were too low at average prey densities to allow ctenophore growth.

Prey and predators:

Although gut content analysis cannot be viewed as a complete representation of the importance of each group, as a result of differential digestibility (Stoecker *et al.*, 1987a), it may give a good indication of relative importance. Such analysis has been completed upon *Aurelia* many times. Gut content analysis of captured *Aurelia aurita* have found the presence of many prey types including; crab zoea, copepods (calanoids and harpacticoids), cirripede nauplii, terebellid larvae, other gelatinous predators and fish larvae (Lebour, 1923). Van der Veer (1985) found that *A.aurita* collected from the western Wadden Sea had contents which included plaice and flounder larvae, but these were rare. Fraser (1969) found that *A.aurita* could feed on relatively large organisms from the plankton until it was about 50mm in diameter, and that some of these prey could be considerably larger than those taken by the adults. Shushkina and Musayeva (1983) drawing upon previous Russian work, stated that 'Zooplankton is the main food consumed by *Aurelia* and includes young and adult individuals of *Paracalanus*, *Pseudocalanus*, *Calanus*, *Acartia*, *Oithona*, cladocerans, and appendicularians...[they also] willingly consume *Sagitta*'. From examination of the stomach contents of *A.aurita* taken from Tokyo Bay, Omori *et al.* (1995) comment that 'they [*A.aurita*] ingest virtually any zooplankters in the field, including ciliates and copepods'. In laboratory predation experiments Arai and Jacobs (1980) also found no evidence for cannibalism even when ephyrae were placed with individuals 18-28mm in bell diameter. Möller (1980a) found that on a weight basis phytoplankton and protozooplankton made up much less than 5% of the stomach weight contents of *Aurelia*. The majority was made up by copepods, cladocerans, herring larvae, insects, amphipods, cumaceans and *Cottus* larvae. Matsakis and Conover (1991) found the average number of items in the gut of *A.aurita* collected in Bedford Basin, Canada, to sometimes exceed 20. Of these prey items less than 50% were copepods, the remainder including fish larvae, veligers and some microzooplankton (diatoms, other algae and ciliates). *A.aurita* was also found to consume the gelatinous species (and a potential competitor) *Rathkea octopunctata.*

Möller (1984) believed that the predation by *Aurelia aurita* may effect the recruitment of herring larvae in Kiel Bight. While van der Veer (1985) believed that in the western Wadden Sea it was unlikely that *A.aurita* had a strong impact upon recruitment of plaice, but could have a more significant impact upon flounder larvae. Lebour (1923) suggested that it may be the ephyrae or smaller individuals which take fish larvae rather than the larger medusae. Youngest ephyrae to

at least 30mm bell diameter individuals were found to prey upon fish, whereas individuals of greater than 60mm kept in plunger jars with fish did not prey upon them. Möller (1980a; 1984) found that *A.aurita* of up to 50mm size would take larval herring. On two occasions Lucas (1993) found fish larvae in the gut contents of *A.aurita*, on these occasions they made up 0.78 to 1.72% (by numbers) of the identifiable remains. It would certainly seem therefore that fish larvae are uncommon prey items for *A.aurita* within Southampton Water and there is little or no effect upon fish recruitment through larval predation.

Lucas (1993) examined the gut contents of ephyrae and small medusae (<50mm) collected at Cracknore. Copepods, polychaete larvae and cirripede nauplii dominated the diet of *Aurelia aurita* on a numerical basis, each of the prey items making up between 17-89% (copepods), 14-71% (cirripede nauplii), 11-57% (polychaete larvae), 0-7% (mollusc larvae) and 0-24% (decapod larvae). To conclude from examination of the information compiled from the literature and the study of Lucas (1993), together with daily ration estimates, it would appear that within Southampton Water *A.aurita* will gain its ingestion demands predominantly from copepods and other mesozooplanktonic meroplankton.

***Clytia hemisphaerica*:**

Population dynamics:

Cohort methods were not utilised in estimating the production of this species because no clear cohorts could be recognised given the rapid changes in density and size distribution. Although Lucas *et al.* (1995) attempted cohort separation and estimated production by utilising such partitioning, this was unadvisable and the results cannot be trusted. Daan (1989) also found great short term changes in *Clytia hemisphaerica* biomass, which was attributable to patchiness; while Larson (1985) also found no clear cohorts of *Phialidium* spp. in the estuarine Saanich Inlet, Canada.

The Hydromedusae group as a whole appears to have been very poorly studied in natural waters, and there are few quantitative examinations of abundance, biomass or production. Russell (1953) describes *Clytia hemisphaerica* as occurring all around the British Isles, being found in European waters from the Mediterranean to Iceland. *C.hemisphaerica* was found at various sites in Southampton Water from April to October, with maximum numbers generally during June and being absent from late Autumn to Spring. According to van der Baan (1980), *C.hemisphaerica* was very abundant from June to January around the Texel lightship. It was absent in this area for 2-3 months during Spring. Hamond (1957; 1963) found *C.hemisphaerica* to be present all year

around along the Norfolk coast, although it was scarce between November and March, this being similar to the situation in Southampton Water. Russell (1938) reported that off Plymouth it was absent from January to February. There appears therefore to be some difference in its pattern of abundance between studied areas, although it is commonly scarce or absent during late Winter / early Spring.

Larson (1985) found that recruitment of the young of the congenerics *Phialidium* spp. (*Phialidium lomae* and *Phialidium gregarium*) took place year round within Saanich Inlet, but mostly in spring and summer. The bell diameter of individuals in this area increased from 3mm in April to 16mm by June. Individual growth rates were higher than this, but were masked by the introduction of new recruits entering the population. The spring population reached larger sizes than the summer recruits, which hardly grew at all. He concluded that most *Phialidium* spp. growth occurred during spring. Larson (1985) found that *Phialidium* spp. mean bell diameter increased from 6.8mm to 12.5mm in 31 days, representing a growth rate of 0.18mm d^{-1}. During this period temperature was around 10 to 11°C (see his figure 4). In the subsequent year *Phialidium* spp. increased from 3.2 to 15.8mm in 52 days, a mean growth rate of 0.24mm d^{-1}. It is also possible to estimate growth rates from changes in the maximum size on subsequent sampling events from the data of Larson (1985). Indeed it can be seen that between 26/6/81 and 9/7/81 individuals grew from ~12mm to 18mm, equalling a daily growth rate of 0.5mm. From 8/7/80 to 22/7/80 individuals grew from ~4mm to 12mm, representing a growth rate of 0.57mm d^{-1}, and from 10/4/81 to 26/4/81 grew from 11mm to 19mm, giving a growth rate of 0.5mm d^{-1}. From Lebour (1922) it can be established that a single individual *Clytia hemisphaerica*, kept in the laboratory and fed fish larvae, grew from 6mm to 12mm between the 17th Feb and 15th March, which relates to a growth rate of 0.21mm d^{-1}. From the maximum size found on each sampling occasion it is possible to determine growth rates in Southampton Water. At Cracknore in 1991 on the 24th of May no individuals were found but by the 6th June 9mm ones were present, this relates to a daily increase of around 0.62mm d^{-1} (assuming recruitment into the samples at ~1mm). Between 28th June and the 2nd July individuals would appear to grow from 5mm to 11mm, a growth rate of 1.5mm d^{-1}. Such a rate is much greater than in any of the studies already detailed. Indeed it may indicate sampling problems associated with patchiness or lateral movements in this tidally dominated estuary. Such a discrepancy highlights the problem of cohort identification for this species in this area. Between the 24th July and the 5th of August individuals grew from 5mm to 10mm, this is a daily increase of 0.42mm d^{-1}, and between 21st of August and 28th of August by 0.43mmd^{-1}, between the 24th of September and 7th of October growth rates were 0.54mm d^{-1}.

Growth:

Larson (1986b) estimated that the maximum coefficient of daily exponential population biomass increase (K) for *Phialidium* spp. in Saanich Inlet was $0.17d^{-1}$ between April and May. At Cracknore the maximum K value for *Clytia hemisphaerica* was $0.36d^{-1}$, during July 1991. This represents a population biomass doubling time of 1.9 days. Larson (1985) estimated from the data of Kubota (1978) and Roosen-Runge (1970) that laboratory maintained *Phialidium edwardsi* and *Phialidium gregarium* (at 12°C) had maximum growth coefficients of $0.3d^{-1}$ and $0.2d^{-1}$ respectively, these being similar to those for Southampton Water. Maximum *in situ* results from his own work within Saanich Inlet were given as $0.2d^{-1}$. The highest value at Greenland was between July and August 1991 when it reached $0.3d^{-1}$, at N.W.Netley the maximum value was also $0.3d^{-1}$ during August 1991.

Prey and predators:

Clytia hemisphaerica has been described as a miscellaneous feeder: gut content analysis demonstrating the presence of *Sagitta* sp., fish and fish eggs, *Oikopleura* sp., copepods, crab zoea, crustacean larvae, young *Cottus*, *Obelia* medusae and young *Labrus* (Lebour, 1922), while laboratory studies have shown it to take and digest many other young fish when offered. Examination of gut contents of *C.hemisphaerica* collected in the southern North Sea by Daan (1989) found predominantly older copepod stages and copepod eggs but nauplii only 'very seldomly'. They were shown to ingest large numbers of copepod eggs, but these were very poorly digested and often appeared to be egested without damage. Unfortunately the gastric contents of *C.hemisphaerica* collected from Southampton Water have not been examined. Even so it is likely that prey will be dominated by copepodites, copepod adults and meroplanktonic larvae.

Phialidium sp. have been found to be preyed upon by other gelatinous predators including *Stomotoca atra*, *Eutonina indicans*, *Aequorea victoria*, *Rathkea octopunctata* and *Aurelia aurita*. Of these only the last occurs commonly in Southampton Water, while only one individual *Aequorea* sp. has been found (Lucas, *pers. comm.*). Lebour (1923) found under laboratory conditions that *Chrysaora isosceles* took *Phialidium* medusae, once again this species has never been found in Southampton Water. Given the apparent lack of major predators in Southampton Water, *Clytia* abundance may be controlled by prey abundance and physical factors, although *Aurelia* may have a control at higher sites.

Species	Max. Abundance (numbers m^{-3})	Max. Size (mm)	Max. Biomass (mgC m^{-3})	Max. Daily Production (mgC m^{-3} d^{-1})	Area	Source
Clytia hemisphaerica		Bell Diameter				
	5.41	-	-	-	Avon-Heathcote estuary, New Zealand	Roper *et al.* 1983
	467	-	2.8^{d}-6.8^{e}	-	Dutch coastal waters, North Sea (84^{d}-85^{e})	Daan 1989
	2.1^{c}	-	-	-	Calshot (93^{c})	This Study
	13.6^{a}-2.4^{b}-1.9^{c}	13^{a}-12^{b}	0.52^{a}-0.03^{b}	0.026^{a}-0.002^{b}	Hamble (90^{a}-91^{b}-93^{c})	
	1.0^{b}-3.0^{c}	16^{b}	0.06^{b}	0.002^{b}	N.W.Netley (91^{b}-93^{c})	
	15.7^{a}-1.2^{b}-1.5^{c}	15^{a}-16^{b}	0.55^{a}-0.11^{b}	0.020^{a}-0.005^{b}	Cracknore (90^{a}-91^{b}-93^{c})	
	5.2^{c}	-	-	-	Bury Buoy (93^{c})	
[1]*Phialidium* spp.						
	90	~23	25	0.5	Saanich Inlet, Canada	Larson 1985

TABLE 5.4.4 Comparisons of maximum recorded abundance, individual bell diameter, total carbon biomass and daily production of *Clytia hemisphaerica*, compiled from literature sources and for Southampton Water.

1 Identified as *Phialidium lomae* and *Phialidium gregarium* by Larson (1985).

NB. Values from 1993 are averaged from samples taken at 5 and 10 metres, while those in previous years are from samples taken at 5 metres alone.

Production and biomass:

A compilation of *Clytia hemisphaerica* and *Phialidium* spp. maximum reported abundances, sizes, biomass and daily production rates are presented in Table 5.4.4. Densities within Southampton Water being certainly much lower than those found in other areas including Dutch coastal waters, where densities were found to reach 467 ind. m^{-3} (Daan, 1989). In Saanich Inlet, Larson (1985) found *Phialidium* spp. at densities of up to 90 ind. m^{-3}. Maximum densities in Southampton Water were 15.7 ind. m^{-3} during 1990 at the Cracknore site. The maximum biomass values in Southampton Water are less than an order of magnitude lower than those in Dutch coastal waters (Daan, 1989), and around 50 times lower than the maximum of Saanich Inlet (Larson, 1985). Maximum daily production rates in Southampton Water are one twentieth to one hundredth of those in Saanich Inlet (in both cases production being estimated utilising the 'Total biomass change' method). Since density and biomass are so much lower in Southampton Water in comparison to these two other sites, this explains the much lower production rates in the present investigation.

Although Daan (1989) found much higher biomasses than in Southampton Water, from gut contents and digestion time he estimated that a maximum of only 2% of the copepod prey population was removed by *Clytia hemisphaerica* per day. Utilising a different method, namely by applying the specific daily rations of Larson (1987d) to density and carbon weights of medusae, Daan (1989) estimated a maximum demand of $3mgCm^{-3}d^{-1}$, ie. 4.5-6% of copepod biomass grazed per day. Ingestion demand by *C.hemisphaerica* within Southampton Water were estimated to reach a maximum during 1991 of $0.065mgCm^{-3}d^{-1}$ at the Greenland site. At the same point biomass of this predator was $517.3\mu gCm^{-3}$ and clearance rate may be estimated as $0.13mgC(mg\ medusae\ C)^{-1}d^{-1}$. Maximum ingestion demand during 1991 was at the Cracknore site, where it reached $0.014mgCm^{-3}d^{-1}$. Biomass of the predator at the same point was $111.6\mu gCm^{-3}$, thus a clearance rate once again of $0.13mgC(mg\ medusae\ C)^{-1}d^{-1}$ may be estimated. As such 13% of body weight was ingested per day by *C.hemisphaerica* on both these occasions. These rates may be compared to the daily rations estimated by Larson (1987d) for *Phialidium* spp. within Saanich Inlet. From gut contents analysis and digestion time, he found that for a medusae weight of ~40μgC (the mean weight of predators during the ingestion maximum in Southampton Water) the daily ration as a percentage of carbon weight was between ~25-70%, which is equivalent to a clearance rate of 0.25 to $0.7mgC(mg\ medusae\ C)^{-1}d^{-1}$. Given the assumptions in the present method of ingestion estimation for *C.hemisphaerica* within Southampton Water the results are similar to previously measured values. The full implications of the ingestion demands by this species upon prey populations within Southampton Water are

discussed later. This species reaches an estimated maximum ingestion rate of 65.4μgCm^{-3}d^{-1}, during unusually high abundance, which represents a removal rate of around 330 CI copepods m^{-3}d^{-1} (*Acartia* CI copepodites having a mean carbon weight of typically 0.2μgC).

***Pleurobrachia pileus*:**

Population dynamics:

Pleurobrachia pileus has been described as a cosmopolitan, neritic species (Mortensen, 1912; Fraser, 1970; Zelickman, 1972). It has however also been described as being intermediate between neritic and oceanic as it also occurs occasionally offshore (Kramp, 1913). *P.pileus* was reported as being allochthonous to the western Dutch Wadden Sea by van der Veer and Sadée (1984), who found it to be more abundant on the flood tide than the ebb. They suggested this was indicative of it being tidally transported in from outside the area. Schneider (1987) working in Kiel Bight found that comparisons of salinity and *P.pileus* abundance suggested that variations of the ctenophore stock were primarily caused by advection and did not reflect the biological population cycle of this species. Fluctuations in abundance which coincided with those in salinity were described as being demonstrative of advection processes, with density changes reflecting the different ctenophore loads in the water masses. Möller (1977) also found that mass occurrence of *P.pileus* appeared to be associated with wind induced currents, with individuals being 'concentrated' in Kiel Bight. Because of this apparent allochthonous nature of *P.pileus* in coastal waters, the 'Total biomass change' method was not utilised in this study. This method, however, was used by Larson (1985; 1986b) to determine the production of *Pleurobrachia bachei* in Saanich Inlet. Analysis of the data of salinity and *P.pileus* abundance from Lucas (1993) revealed no significant relationship between abundance and salinity (*personal observations*), however, such a result does not preclude the possibility of advection of the population. Schneider (1987) found no larvae or young juveniles during the study, and cited this as evidence of there being no reproductive recruitment in the area, and therefore in the locality studied the population must be transported in.

The diameter of the individuals caught by Schneider (1987) ranged from 5 to 15mm in winter and spring and 10 to 18mm in summer. Lucas (1993) found that individuals less than 3mm were only found in May and June, but not during the remainder of the year (even though large individuals were present later in the year and there were apparent positive and negative changes in their density). There may however be a problem regarding the fact that individuals were separated from the remaining sample using a 1mm mesh. During some periods it is probable that this species was reproducing in Southampton Water, and is not a true pseudo-

population. It has previously been postulated by Lucas (1993) that *Pleurobrachia pileus* may migrate into Southampton Water from the deeper water of the Solent, although over-wintering adults have been sampled in Southampton Water at Greenland (Lucas, 1993), and individuals were found throughout the estuary in December 1993 (although not in December 1992), and only at Calshot by January 1994. Given that in some years they occur in the estuary over the winter in very low densities, they may rapidly increase under favourable conditions giving rise to subsequent blooms. Such a situation was believed to occur in the case of the ctenophore *Mnemiopsis leidyi* in Narragansett Bay, U.S.A. (Kremer and Nixon, 1976). Over-wintering densities of 1-2 animals per 10^4 m^3 were found in this species (Kremer, 1976), although even these densities were believed adequate to explain later population increase. Given the relatively small volumes of water filtered in all the studies of Southampton Water it is likely that individuals at densities of this order could be missed. Others have shown recruitment to be entirely dependent upon offshore populations in ctenophores. Cronk (1982) believed that recruitment of the congeneric *Pleurobrachia bachei* in Newport Bay, California, occurred in February from offshore populations, given that no individuals were found in the several months prior to the population outbursts. Van der Veer and Sadée (1984) postulated that large individuals of *P.pileus* probably over-winter at depths of 50m on the bottom, and are transported into the west Wadden Sea by tidal currents. It is interesting to note that in Southampton Water the over-wintering specimens have been collected more commonly at more seaward sites, near to the deeper water areas in the Solent. Unlike most other studies, Yip (1981) found that small rather than large *P.pileus* individuals over-wintered in Galway Bay, Western Ireland. It is possible that over-wintering adults and newly introduced individuals may both contribute to the maintenance of this species within Southampton Water.

Temperature and salinity have both been shown to regulate the abundance of ctenophores, with salinity tolerance being temperature dependent in some species (Miller, 1970). Baker (1973) found no evidence to suggest that *Mnemiposis mccradyi* abundance or distribution was closely controlled by salinity *per se*. Indeed ctenophores appear to have very wide salinity tolerances. Baker (1973) found that in Biscayne Bay *M.mccradyi* was collected over a salinity range of 14-45$^{o}/_{oo}$, and *Mnemiopsis leidyi* has been reported to occur from 3.4 to 20$^{o}/_{oo}$ (Miller, 1970; as given in Baker, 1973). *Pleurobrachia pileus* has been reported to survive from 25 to 45$^{o}/_{oo}$ (Greve, 1972). Within Southampton Water salinities at which individuals were collected were well within this range. Wear (1965) reported critical temperatures for the occurrence of *P.pileus* to be between 15 and 16°C (Wear, 1965), at temperature below this *P.pileus* was present in great abundance, while at temperatures above 16°C they were rare or absent. In the present investigation this pattern is not demonstrated, peak densities occurring at most sites during June

coincide with temperatures in excess of 17°C. Hernroth and Ackefors (1979) found that *P.pileus* were only found in the Baltic when temperatures were below 10°C. This may be the result of them being able to only tolerate very low salinities in cold water. Greve (1972) found in the laboratory that this species may survive at temperatures ranging from -1 to 26°C.

Off Plymouth, Russell (1933) found *Pleurobrachia pileus* to occur in a bimodal seasonal distribution with a maximum peak in autumn (October), as well as an early smaller summer (May-June) peak. Fraser (1970) also found that in Scottish waters there was a maximum density in autumn (maximum in November) and a much lower second maximum in spring (June). In some years the maximum densities could be much earlier than the typical November peak, with values being greatest in July-August. In the North Sea near Helgoland this pattern was reversed with a May-June maximum at 10-15°C and a less distinct autumn peak (Greve, 1971). This is similar to the pattern found in Southampton Water during the 14 month abundance investigation, with a maximum peak during June and smaller, but more prolonged peaks in autumn, although at the more seaward sites the summer peak becomes less pronounced than the autumn peak. Collections in previous years by Lucas (1993) shows that this species is not restricted to spring and autumn however, rather it may occur during the summer. It is apparently however, always very rare during the first few months of each year. Yip (1981) found that in Galway Bay *P.pileus* reached maximum densities in late spring to early summer (May to June), with a smaller peak occurring in late autumn to early winter (October to December). Van der Veer and Sadée (1984) found a similar pattern in the western Dutch Wadden Sea, with maximum abundance in May and a second autumn peak in September to November. Möller (1972) found *P.pileus* in Kiel Bight all year round, but it occurred predominantly from September through to June, with maximum abundances from January to March. The seasonal occurrence of *P.pileus* would appear to be remarkably variable from site to site and also from year to year, and its potential impact would also appear to fluctuate between years. Highest abundances of post-larval *P.pileus* have been reported at 201.6 ind. m^{-3} (Daan, 1989) in the Southern Bight of the North Sea (see Table 5.4.5). In Southampton Water maximum integrated values reached 6.5 ind. m^{-3} at Bury, and only 0.5 ind. m^{-3} at Calshot during the 14 month investigation. The highest reported densities for this species within Southampton Water were reported by Zinger (1989), when in June 1985 integrated densities were found to reach 8.7 ind m^{-3} at the Cracknore site.

Vertical migration:

Vertical heterogeneity was encountered in the distribution of *Pleurobrachia pileus* population sampled by Frank (1986) over the Nova Scotian Shelf, with the great majority of

individuals being found in the upper 20 metres of the water column. Other workers have also noted a dominance in the upper 30 metres of the water column in the same area (Bigelow, 1926; Anderson, 1974), and for the genus *Pleurobrachia* in other areas (Hirota, 1974; Yip, 1981). *P.pileus* has been shown to change its vertical positioning in shallow areas on a diel basis. Rowe (1971) found it predominantly residing at greater depths during the day (>8 metres in a water column of 13 metres) and moving towards the surface at night. Cronk (1982) found in Newport Bay, California, that *Pleurobrachia bachei* showed strong vertical migratory behaviour. During late afternoon maximum densities were found at depth (in a water column of around 4 metres depth), while the reverse situation was found during the evening. Cronk (1982) found *P.bachei* to be absent from mid and shallow level during the day, however, night sampling showed moderate concentration at all depths. Sampling with a benthic sledge net demonstrated that during the day individuals could collect very closely to the bottom (Cronk, 1982). In Southampton Water samples during the 14 month abundance investigation were collected from 5 and 10 metres at all sites, it would appear that generally *Pleurobrachia* were more commonly present at 10 metres than 5 metres depth. When individuals were found at both depths the densities were generally similar (see Figure 5.3.16). There is a possibility that the abundance data available for this species may under represent its true abundance given its strong diurnal migration behaviour. This of course may have great implications to the estimates of its predatory impact, which is discussed in more detail later.

Growth rates:

Larson (1985) believed that most of the growth of *Pleurobrachia bachei* in Saanich Inlet occurred during spring. Small individuals were dominant in April (<3mm) but by late May maximum size had reached 10-17mm, with an average diameter of 8mm. Mean sizes were small during the summer and autumn, when Larson believed no significant growth took place. In the present investigation production was estimated as occurring between the months of May and October, although there were times during this period when they were absent and there was no production (see Figure 5.3.17). The abundance data from the 14 month investigation suggests that production may also extend beyond October through winter. Hirota (1974) found that *P.bachei* in La Jolla Bight had a mean (averaged over one year) daily P/B between 0.197 to $0.211d^{-1}$. Larson (1985) estimated that biomass increase by *P.bachei* was as great as 23% per day during April to June (K value of $0.21d^{-1}$), while daily mean P/B values are given as varying between 0.07 and $0.14d^{-1}$. It would be unwise to estimate K for the population in Southampton Water as changes in biomass may not be attributable to autochthonous production, rather they may be attributable to sampling problems through patchiness and migration. Daily P/B ratios may be estimated though,

at 0.003 to 0.023d^{-1}. These are much lower than those given by Larson (1985), although it should be noted that even utilising one of the other ratio methods (ie. a or c) relating respiration to growth would not increase these P/B values by more than a factor of 2. These results may indicate an underestimation of production, although this does not mean that ingestion is underestimated. It is possible to predict daily ration versus body size from the method used herein. Further, comparing such predictions with those measured by Larson (1987d) on *P.bachei* in Saanich Inlet, show very similar patterns (ie. decrease with size) in addition to similar values.

Pole length measurements of *Pleurobrachia pileus* in the area of Browns Bank, Southwestern Nova Scotia, averaged 3.8mm in March, 6.0mm in April, 7.7mm in early May, and 9.9mm in late May (Frank, 1986). Growth rates were given as increasing from 0.07-0.12mm per day during the late winter to spring period, and appeared to parallel changes in the surface water temperature (which rose from 3 to 6.5°C). These values may be compared to those produced by Greve (1972) for *Pleurobrachia* grown in the laboratory at 6°C when growth rates were 0.10mm per day. Van der Veer and Sadée (1984) found that mean *P.pileus* polar length increased from around 10mm in early May to 16.3mm by late June (polar lengths estimated by multiply equatorial diameters by 1.25 [ratio as determined by Van der Veer and Sadée, 1984]), thus increasing on average at a rate of ~0.13mm d^{-1}. Hirota (1972) found that *Pleurobrachia bachei* reached a maximum size of 17.5mm (converted from equatorial diameter to polar diameter by multiplying by 1.25) at 15°C, 80 days after hatching, while at 20°C they reached a diameter of 7.5mm in 35-40 days. This being some 10-15 days faster than at 15°C. Fraser (1970) found for specimens collected from Scottish coastal waters, that in April individuals were predominantly 4mm. By May they had grown to 5-6mm, and by June 6-9mm. A second period of spawning appeared to occur as in July, August and September, young specimens 2-4mm in length were found. These small individuals grew to 6-10mm by October and 7-15mm by November. Larson (1985) found that *P.bachei* increased from 1.5mm mean pole diameter to 8.4mm in 52 days. Although recruitment continued through this period, a growth rate of 0.13mm d^{-1} may be calculated. Temperature was around 8 to 11°C (see his figure 4) over this interval.

Between 12/8/91 and 23/8/91 at Cracknore (Southampton Water), *Pleurobrachia pileus* maximum pole length increased from 8mm to 16mm, representing a rate of increase of 0.73mm d^{-1} (at water temperatures of 19.5-21.2°C). While between 28/8/91 and 16/9/91 maximum pole length increased from 16mm to 20mm, giving a rate of increase of 0.21mm d^{-1} (water temperature 21.2-18.9°C). At N.W.Netley between 17/6/91 and 28/6/91 maximum size increased from 6mm to 16mm, representing a mean increase of 0.91mmd^{-1} (water temperature 14.5-15.8°C). Between 12/8/91 and 28/8/91 at N.W.Netley, maximum size increased from 8mm to 14mm, an

increase rate of 0.38mmd^{-1} (water temperature 19.5-20.2°C). At the Greenland site size increased from 4mm to 20mm between 6/3/91 and 29/4/91, giving a rate of increase of 0.30mmd^{-1} (water temperature ~10°C). Greve (1970) found in the laboratory (at 15°C), that the fastest rate of growth was show by individuals which grew from hatching to 3mm in 25 days, and to 13mm in diameter in 70 days. Between these two points growth may be estimated as 0.22mm d^{-1}. These were maximum growth rates however, and mean growth rates were much lower than these. Some of the faster growth rates found in Southampton Water may be elevated above those of Greve (1970) as a result of higher temperatures. However, many of the very high rates of increase in Southampton Water are not during periods when temperature is greater. This leads to the conclusion that the laboratory growth rates found by Greve (1970) and by others in natural situations are low, or more probably, that the changes in size within Southampton Water do not always reflect true growth processes. This may be indicative of patchiness and/or migration in this non-closed system. In either case these results confirm once more that cohort methods should not be used in the estimation of production in Southampton Water. Reeve *et al.* (1978) suggest that ctenophore population increase may at times be so strikingly rapid that it is tempting to attribute it to migration of already developed populations from elsewhere. However, using models of growth Reeve *et al.* (1978) and Kremer (1976) have both shown that in the areas they examined increases were well within the potential growth rates of the populations. In the present investigation migration was cited as a possibility as the growth rates compared to measured maximum rates were still too great.

The results of Lucas (1993) show that in 1990 *Clytia hemisphaerica* achieved higher biomass and production rates at all sites than it did in 1991. For *Pleurobrachia pileus* the reverse is true, 1991 being a year of much greater biomass and production than 1990. It is interesting to note that Larson (1985) comments that in Saanich Inlet during the year in which *P.pileus* production was at its highest *Phialidium* sp. production was at its lowest. Frank (1986) describes *Pleurobrachia* as a species in which significant inter-annual variability in the timing of events in its life cycle is a characteristic, indeed several studies have demonstrated not only great inter-annual differences in its abundance (Cronk, 1982; Frank, 1986) but also its predatory impact (Frank, 1986). Such a situation would certainly appear to occur within Southampton Water. Comparisons of maximum recorded abundance, biomass and daily production of *Pleurobrachia pileus*, compiled from literature sources, and for Southampton Water.are compiled from the current literature in Table 5.4.5.

Feeding and predators:

Fraser (1970) was among the first to recognize the ecological significance of ctenophores, suggesting that this group may act as important competitors for crustacean zooplankton with fish and their larvae. In many locations ctenophores have been observed to occur in strongly seasonal pulses (see Kremer, 1976), as is the case with *Pleurobrachia pileus* within Southampton Water. Baker (1973) found that the *Mnemiopsis mccradyi* population in Biscayne Bay, U.S.A., increased rapidly in autumn, and coincided with the period of maximum abundance of other zooplankters, which most likely served as prey. One of the most significant aspects of the feeding behaviour of ctenophores is their ability to ingest food proportionally to their concentration over an extremely broad range (Reeve *et al.*, 1978). *P.pileus* has been described as a non-selective carnivore, feeding on whatever is available in the plankton, predominantly crustacean, in particular copepods, cladocerans and cirripede nauplii (Fraser, 1970; Rowe, 1971; Greve, 1972). Fraser (1970) found that the gut content of *P.pileus*, collected from Scottish coastal waters, contained about 80% crustacea (by number) but reached 97%. The diets of individuals have also been shown to include; other *P.pileus*, *Sagitta* sp., mysids, cumaceans, euphausiids, *Oikopleura* sp., *Obelia* sp. and crab zoea (Lebour, 1923). Rowe (1971) found that the gut contents of *P.pileus* collected from Kaneohe Bay, Hawaii, included barnacle nauplii (43% by number), *Oikopleura* (27%), copepod nauplii (5%), copepods, crab zoea, gastropod veligers, cyprid larvae and *Lucifer* protozoea. Although they very rarely feed upon the larvae or eggs of fish (Fraser, 1970), at times prey items have been found to include; 10mm long *Gobius ruthensparri*, herring larvae, plaice eggs and larvae, young *Cottus*, young *Labrus*, *Gebia* larvae and *Bipinnaria* (Lebour, 1923; Fraser, 1970). Van der Veer (1985) found that *P.pileus* from the western Wadden Sea had gut contents which included flatfish larvae, although impact was deemed as relatively minor at least for flounder. *P.pileus* may have a more important impact upon fish recruitment and mortality through competition for food (Fraser, 1970; Frank, 1986). Hirota (1974) suggested that prey selection by the congeneric *Pleurobrachia bachei* may be determined by several attributes of the prey including: density, size, avoidance and escapement behaviour, strength and protective spination. Presumably palatability in chemical terms is additionally important. Hirota (1974) found *P.bachei* to have gut contents which included *Acartia tonsa*, *Euterpina acutifrons*, *Corycaeus anglicus*, *Evadne* spp., copepod nauplii, and copepod eggs.

Frank (1986) found that *Pleurobrachia pileus* had a non-selective, density dependent pattern of prey exploitation, with the size fractionated dry weighed gut contents reflecting closely the natural occurrence, in this case being predominantly calanoids. Fish eggs and *Oikopleura* sp. were found in less than 2% of the 600 individual gut contents examined, and fish larvae were

completely absent. Cronk (1982) working in Newport Bay, California, found that *Acartia tonsa / Acartia californiensis* made up the dominant portion of identifiable gut items (76% by number), the cladoceran *Podon polyphemoides* was the only other common prey item (making up 12% by number). Other prey included *Oithona oculata*, unidentified nauplii, mysids, *Sagitta euneritica* and the amphipod *Mayerella acanthopoda*. Crustacean zooplankton have been shown to be the major prey item for *Pleurobrachia* (Fraser, 1970; Anderson, 1974; Milne, 1984), copepodites and adult copepods making up the bulk of their carbon intake.

Hirota (1974) noted that on the rare occasions phytoplankton were seen in the gut of *Pleurobrachia bachei* they could have originated from the guts of ingested copepod prey. Deason and Smayda (1982b) found that although *Mnemiopsis leidyi* could clear phytoplankton, rates were well below the levels required for maintenance requirements, and individuals lost weight. Stoecker *et al.* (1987b) found similar results with larval stages of *M.leidyi* being unable to survive when offered phytoplankton alone. Indeed Reeve and Walter (1978) considered ctenophores to be strictly carnivorous. Baker (1973) found that *Mnemiopsis mccradyi* also lost weight when offered only phytoplankton or detritus, although these could be found in the gut. Reeve and Walter (1978) found that *P.bachei* lost weight when only barnacle nauplii were given as a food source, with the predator apparently unable to capture this prey. This appears in part to contradict the information available for gut content analyses of both *P.bachei* (Larson, 1985) and *Pleurobrachia pileus* (Lucas, 1993), where barnacle nauplii have both been found at times to make up large fractions of the gut contents. Hirota (1974) found that one of the more common prey items of *P.bachei* were barnacle nauplii, while Rowe (1971) found *P.pileus* to feed predominantly upon crustacea including barnacle nauplii. Stoecker *et al.* (1987b) found that planktonic ciliates were preyed upon by larvae and post-larvae of the ctenophore *M.leidyi*, while for the larvae of ctenophores, feeding upon ciliates could also be important. An optimal diet for newly hatched *M.leidyi* was described by Stoecker *et al.* (1987b) as being a mixture of ciliates and less abundant prey such as copepod nauplii. Sullivan and Reeve (1982) observed ciliates in the guts of small (<1mm) *Pleurobrachia*, and found that larvae fed natural plankton ingested ciliates and nauplii, with the larger food items contributing most of the ingested carbon. As these larvae grew their feeding preference shifted to larger items. It should be pointed out that gut content analysis by itself cannot be used to determine the role of ciliates in feeding as remains would likely not be visible (Stoecker *et al.*, 1987b). Fraser (1969) describes *P.pileus* as a species which prefers fish to copepods. Lucas (1993) found that fish were rarely found in their guts in Southampton Water, making up a maximum of 1.72% (by number). This result does not contradict that of Fraser (1969) however, as their virtual absence could be the result of the low abundance of fish larvae in this area.

Cronk (1982) found that feeding in *Pleurobrachia bachei* appeared to vary on a diel basis, much greater number of individuals whose guts were not empty were found at night compared to during the day. Hirota (1974) however found no variation in feeding on a diel basis in La Jolla Bight. The data of Rowe (1971) are equivocal as to whether feeding rates were greater during the night. The gut content information given by Lucas (1993) for *Pleurobrachia pileus* were derived from individuals collected during the day only in Southampton Water, no conclusions regarding diel feeding changes may be made for Southampton Water. Lucas (1993) found from gut content investigations upon this species, that copepods were usually dominant prey items (in terms of numbers of recognized prey), although on several occasions more cirripede nauplii were found. Copepods made up between 28.3 to 86.8% of the prey (by numbers), while cirripedes made up 0.0 to 71.7%. Polychaete larvae (maximum 10.5%), decapod larvae (maximum 10.5%), the genus *Oikopleura* (maximum 3.96%) and fish larvae (maximum 1.72%) were also found. The ingestion demands of the *P.pileus* population in Southampton Water would therefore appear to be met predominantly by copepods and barnacle nauplii, although other meroplankton were probably also of some importance.

The carnivorous ctenophore *Beroe gracilis* has been shown to prey upon *Pleurobrachia pileus*. Indeed Greve (1970) found under laboratory culture that this species fed exclusively on *P.pileus*. Greve (1971) found that the abundance of *B.gracilis* appeared to determine the abundance of *P.pileus* in the German Bight. Even when the abundance of *B.gracilis* is low it has been described as important in some areas at regulating the predation impact of *P.pileus* (van der Veer and Sadée, 1984). The congeneric species *Beroe cucumis* may also feed upon *P.pileus* (Greve, 1970). *Beroe* sp. has been recorded in other U.K. nearshore environments including the southern North Sea, western Scotland, the Bristol Channel, Lancaster Bay and the Irish Sea (Liley, 1958; Greve, 1975; Greve *et al.*, 1976) as well as in Southampton Water (Reubold, 1988; Lucas, 1993). During August 1974 Greve *et al.* (1974) found no *Beroe* in the central English Channel, but *B.gracilis* were found in the Bristol Channel, Irish Sea, German Bight and Northern North Sea during the same survey. Lucas (1993) reported it to be extremely rare in Southampton Water, with no individuals being found in 1990 and only two animals being captured at the N.W.Netley site in July 1991 and July 1992. None were found in the present 14 month abundance investigation (Chapter 2). With such low abundances it may be speculated that their influence as predators upon *P.pileus* is likely to be very small in the years examined here.

Infestation of *Pleurobrachia bachei* by the endoparasitic amphipod *Hyperoche mediterranea* has been reported in a population off California (Hirota, 1974), with over 40% of the post-larval population being parasitized at times.

Species	Max. Postlarvae* Abundance (numbers m^{-3})	Max. Size (mm)	Max. Biomass (mgC m^{-3})	Max. Daily Production (mgC m^{-3} d^{-1})	Area	Source
Pleurobrachia bachei		Oral-Aboral Length				
	~10	~16	1.3	0.5[2,3]	Californian coast, U.S.A.	Hirota 1974
	233	7.5	-	-	Newport Bay, California, U.S.A	Cronk 1982
	-	~8	7.6	3.7	Mesocosm, Saanich Inlet, Canada	Reeve and Walter 1976
	70[1]	17[1]	5[1]	0.6	Saanich Inlet, Canada	Larson 1985; 1986b
Pleurobrachia pileus						
	-	28	0.6[5]	-	Scottish coast, North Sea	Fraser 1970
	20	-	-	-	German Bight, North Sea	Greve 1971
	>100	15-20	-	-	German Bight, North Sea	Greve and Reiners 1980
	201.6	-	-	-	southern Bight, S.North Sea	Daan 1989
	-	-	5.4	-	Dutch coast, North Sea	Miller and Daan 1989
	81	-	3	-	Bristol Channel, U.K.	Williams and Collins 1985
	23	>13	-	-	Galway Bay, Ireland	Yip 1981
	75	-	-	-	Killary Harbour, W.Ireland	Ryan *et al.* 1986
	25	-	-	-	Kiel Bight, W.Baltic	Hillebrandt 1972
	10	-	0.07[4]	-	Kiel Bight, W.Baltic	Möller 1977; 1979
	0.55	-	-	-	western Kiel Bight	Schneider 1982
	0.55	-	-	-	Kiel Bight, W.Baltic	Schneider 1987
	20	20.3[6]	13	2.4[2]	western Dutch Wadden Sea	van der Veer & Sadée 1984
	-	-	0.6	-	Nova Scotian Bay, Canada	Anderson 1974
	2.1	21	3.7[5]	-	Browns Bank, Canada	Frank 1986
	249.17	-	-	-	Avon-Heathcote estuary, New Zealand	Roper *et al.* 1983

0.09[a]-1.00[b]-0.33[c]	16[a]-20[b]	0.3[a]-0.4[b]	0.001[a]-0.006[b]	Hamble 90[a]-91[b]-93[c]	This Study
1.97[b]-1.65[c]	26[b]	1.3[b]	0.015[b]	N.W.Netley 91[b]-93[c]	
1.47[a]-1.88[b]-3.22[c]	20[a]-26[b]	2.2[a]-3.4[b]	0.017[a]-0.012[b]	Cracknore 90[a]-91[b]-93[c]	

TABLE 5.4.5 Comparisons of maximum recorded abundance, biomass and daily production of *Pleurobrachia pileus*, compiled from literature sources, and for Southampton Water.

NB. Values from 1993 are averaged from samples taken at 5 and 10 metres, while those in previous years are from samples taken at 5 metres alone.

* Post-larvae abundance defined here as the abundance of ctenophores >0.5mm (Hirota, 1974), in studies where no distinction is made total abundance figure used. 1 Maximums in different years. 2 Values calculated by author/s applying laboratory growth rates to the field. 3 Calculated from authors' data assuming carbon to be 8.7% of AFDW (organic weight), and the mean water column depth to be 40 metres, all these estimates were made by application of natural mortality rates but growth rates at 15°C in laboratory with 35µgCl^{-1} prey. 4 Calculated from authors dry weight assuming carbon to be 3.68% of DW (Mean value from Schneider, 1989a). 5 As given by Miller and Daan (1989). 6 Equatorial diameter (ED) converted to Pole length (PL) assuming ED=80%PL (as determined for *P.pileus* by Oorthuysen and Sadée, 1982). 7 Calculated from authors' data assuming carbon to be 8.7% of AFDW (organic weight), and the water column depth of 100 metres.

Neither this species nor the gelatinous predator / parasitic amphipods *Hyperoche medusarum* and *Hyperia galba* (Evans and Sheader, 1972), have ever been found in Southampton Water (M.Sheader, *pers. comm.*), although these species are commonly found in the North Sea off Blyth, England (Evans and Sheader, 1972). Fish and other amphipod species may also act as predators upon *Pleurobrachia* (Mortenen, 1912; Jensen and Hansen, 1931; Hansen, 1949; Reeve and Walter, 1978), at times filling the guts of collected fish (Scott, 1913; 1924). In the North Sea *Pleurobrachia pileus* were parasitized by nematodes (Greve, 1971) and cercaria of the trematode *Opechona* (Fraser, 1970). Lucas (1993) found the presence of trematodes parasites, which were tentatively described as *Ophechona* sp., in the body cavity of *P.pileus* from Southampton Water. The majority of individuals did not contain parasites however. Lebour (1923) and Arai and Jacobs (1980) observed in laboratory experiments that several gelatinous species including *Aurelia aurita*, *Chrysaora isosceles*, *Cosmetira pilosella*, *Eutonina indicans*, and *Aequorea* spp. took *P.pileus* as prey. *A.aurita* have been commonly found at the higher estuarine sites during certain periods, while of the other species only a single *Aequorea* sp. has ever been found within Southampton Water (C.H.Lucas *pers. comm.*). The pelagic polychaete *Tomopteris* has also been found to prey upon *P.pileus* (Cargo and Scultz, 1967; Fraser, 1970), but this again is very rare in the area (*personal observation*). The top-down control of *P.pileus* within Southampton Water requires more attention before the possible control by predators may be accounted for. One may tentatively conclude however that only *Aurelia* has the potential in restricted areas of Southampton Water to be an important predator. Physical factors such as temperature and flushing in addition to prey abundance are likely to be of greater importance.

Reeve and Walter (1978) believed that since the bulk of production of many ctenophores occur over a short period of the year, it could be argued that ctenophores were not likely to be very food limited over this period of rapid population growth rate. Although at times this may be true (ie. the mesocosm experiments conducted by Reeve and Walter, 1976), there is certainly strong evidence that natural populations of ctenophores do not always grow at rates as great as those observed under food saturated laboratory conditions. Growth and fecundity rates may, however, become depressed when prey abundance becomes depleted (Kremer, 1976), therefore suggesting food-limitation. Van der Veer and Sadée (1984) found that the growth rates of *Pleurobrachia pileus* in the western Dutch Wadden Sea were almost always very much lower than those found in laboratory culture by Greve (1972). Hirota (1974) found that decreases in the abundance of *Pleurobrachia bachei* in November and December were associated with a five-fold decrease in the standing stock of prey. During other times in the year increases in food concentrations did not result in increases in ctenophore abundance. Food availability may be a major factor regulating the spatial and temporal variations in the ctenophore *Mnemiopsis leidyi*

abundance (Deason and Smayda, 1982a), although other factors also appear to be of importance. Frank (1986) for example found that in the southwestern Nova Scotia over 50% of the variation in a 10 year time series of spring *P.pileus* abundance was explained by sea surface temperature conditions prevailing during the previous January to April.

Miller and Daan (1989) found that *Pleurobrachia pileus* did not contribute to the very obvious spring-summer decline of copepod abundance near the Dutch coast. They questioned the apparently well 'described' predation impact of this species in natural conditions. Criticism was focused on the practise of using negative correlations between densities of ctenophores and their prey through time or space as evidence of the predatory impact of a species. *P.pileus* has often been implicated in regulation of copepods through negative density/biomass correlations (Bigelow, 1926; Fraser, 1970; Greve and Reiners, 1980; Frank, 1986), and although in some cases negative correlations and high predatory impact have been affirmed with supplementary feeding rates (ie. Frank, 1986), in other cases no other work has been completed (ie. Fraser, 1970). Other ctenophore and gelatinous 'blooms' including *Mnemiopsis* have also been described as coinciding with zooplankton reductions (see Baker, 1973). Because negative correlations between predators and their prey provide no controls, how populations would have changed with the removal of predatory impact is not established. Miller and Daan (1989) also pointed out that researchers who find positive or no relationship may simply not report such results. From clearance rate experiments using natural zooplankton densities and prey densities during late April to early July, Miller and Daan (1989) estimated that *P.pileus* in Dutch coastal waters removed between 0 and 1.6% of the copepod population per day. Although great declines in copepod densities were observed during this same period, in which biomass of *P.pileus* increased to 3.24mgCm^{-3} from apparently zero, the clearance results show that this decline could not be the result of *P.pileus* predation. In correlative terms alone one could mistakenly have assumed that *P.pileus* had an extremely great impact. However, this was shown through experimentation not to be the case.

Miller and Daan (1989) found weight specific clearance rates of *Pleurobrachia pileus* to vary between 0.35 and 0.78mgC (mgC ctenophore)$^{-1}$ d^{-1}, on the three occasions on which it was measured (over a 40 day period) under *quasi*-natural conditions. These results are derived from individuals with a mean size of around 4.6mm pole length (estimated from wet weight given, utilising a carbon wet weight conversion of wet weight (g) equals carbon weight (mg)/1.34, given by Hoeger (1983) in conjunction with the carbon to size relationship given in original paper). Applying these upper and lower weight specific clearance rates to the ctenophore biomass data for Southampton Water allows a comparison between the range predicted from the rates found by

Miller and Daan (1989) and the ingestion demands estimated in the present investigation. Such a comparison in fact demonstrates that on most occasions the ingestion demand estimates from Southampton Water lie between these clearance rates, for example at N.W.Netley the ingestion demands lie between the clearance rate range estimates on 6 out of the 11 occasions on which estimates are made. When *Pleurobrachia pileus* biomass reaches its maximum of 1.344mgCm^{-3} at this site, ingestion demand was estimated as 499.7μgCm^{-3}d^{-1}, the range predicted from Miller and Daan (1989) being 470-1,048μgCm^{-3}d^{-1}. When *P.pileus* biomass was at its lowest (non zero) value of 0.009mgCm^{-3}, ingestion demand in the present investigation was estimated as 7.0μgCm^{-3}d^{-1}, the range predicted from Miller and Daan (1989) being 3.15 to 7.0μgCm^{-3}d^{-1}. Comparisons of this nature are of course complicated by size distribution and temperature, although they are very similar given the different approaches are independent. Frid *et al.* (1994) examined the clearance rate of *P.pileus* under laboratory conditions. Weight specific clearance rates may be estimated from their work, assuming *Acartia* carbon to be 40% of dry weight (Båmstedt, 1986), at 0.029 to 0.039mgC(mgC ctenophore^{-1})d^{-1} at 400 copepods per m^3 (prey concentration 794-1,224μgCm^{-3}), and 0.128 to 0.224mgC(mgC ctenophore^{-1})d^{-1} at 2,500 copepods per m^3 (prey concentration 4,960-7,650μgCm^{-3}). Although these values are lower than those of Miller and Daan (1989), this could be the result of them being for larger sized *P.pileus*. In laboratory culture, Hirota (1972) found that *Pleurobrachia bachei* from 60 days onwards after hatching (maximum size around 17.5mm polar length, assuming equatorial diameter 80% of polar diameter [van der Veer and Sadée, 1984]), had a maximum recorded ingestion rate that was always less than 0.7mgC per individual when fed upon *Acartia tonsa*. Rates of carbon ingestion per unit carbon peaked at around 14mgC(mgC ctenophore^{-1})d^{-1}. However, values were generally below around 2mgC(mgC ctenophore^{-1})d^{-1}, and always below this rate when individuals exceeded 3.2mm pole diameter. The estimates from Hirota's work (taken from the graphs in Hirota, 1972), assuming that Hirota has over estimated ctenophore carbon weight by 10 times (Hirota (1974) having assumed carbon to be 50% of AFDW whereas in fact it is assumed herein to be 5% of AFDW [Mullin and Evans, 1974]), are greater than those found by Miller and Daan (1989) under natural feeding conditions, however, they are still relatively close, with less than a 2 fold difference.

There have been many problems associated with accounting for the ingestion demands of *Pleurobrachia pileus* in previous work. Van der Veer and Sadée (1984) found a maximum ctenophore biomass in the Dutch Wadden Sea during 1982 of ~11mgCm^{-3}. They applied maximum laboratory growth rates of Greve (1972) (which in fact appeared not to be met in the field), and a gross growth efficiency of 10% to estimate a potential daily ingestion demand of 24mgCm^{-3} d^{-1} (thus equating to an ingestion demand of 2.2mgC(mgC ctenophore^{-1})d^{-1}, which is interestingly

similar to the rates found under culture conditions by Hirota (1972)). Comparing this demand with the standing stock of zooplankton of 40-60mgCm^{-3} over the same period, and an observed zooplankton prey production of around 5 to 6.5mgCm^{-3}d^{-1}, it was estimated that mean daily consumption of about half the zooplankton standing stock could occur. Such predation rates could lead to an elimination of the crustacean zooplankton stock within a few days. However during this same period the copepod population was shown to increase (Fransz, 1981), which leads one to question their ingestion methodology. Applying the biomass data to the clearance rate estimates of Miller and Daan (1989) however, gives rates of 3.85 to 8.58 mgCm^{-3}d^{-1}. Most of this range lies below the prey production range and would allow the observed increase in prey biomass.

As already mentioned, increases in the numbers of *Pleurobrachia pileus* have been correlated with decreases in the population of copepods, conversely decreases in this ctenophores density have been shown to correspond to a recovery of the population of copepods (Greve, 1981). Such correlative events were demonstrated by Miller and Daan (1989) to potentially result in incorrect conclusions regarding predatory impact of *Pleurobrachia*. Stoecker *et al.* (1987b) postulated that the growth and survival of larval ctenophores should be favoured by low standing stock of adult copepods. Medium to large copepod species have been shown to cause damage to larvae and small individuals of the ctenophores *P.pileus* (Greve, 1972; 1977) and *M.leidyi* (Stanlaw *et al.*, 1981). Reeve and Walter (1976) even reported an adverse effect upon ctenophore larvae by *Acartia tonsa* when these copepods were at concentrations of 50,000 m^{-3}. Additionally copepod grazing probably reduces ciliate standing stocks (Stoecker and Sanders, 1985; Stoecker and Egloff, 1987). As such, could negative *Pleurobrachia*-copepod density relationships be the result of the influence which high copepod densities have upon larval ctenophore mortality? When copepod densities decline, the recruitment of ctenophores could be more successful and numbers increase. When copepod numbers increase, this could cause reduction in successful recruitment to post-larval stages in ctenophores and subsequent ctenophore increases. As such negative abundance patterns could be driven by the effects copepod density have upon larval ctenophore mortality rather than *Pleurobrachia* predation effects (Miller and Daan, 1989). Kremer (1979) for example found that the timing of the bloom of post-larval *Mnemiopsis* in Narragansett Bay was clearly proceeded by declining zooplankton abundance. Ctenophore larvae and post-larvae which would pass through a 1mm mesh net were not counted by Lucas (1993), this loss may result in an underestimation of the predatory impact of this group, particularly given their higher weight specific feeding rates. However, as their biomass is so low, and given their apparent ability to prey upon ciliates (Stoecker *et al.*, 1987b), then their impact upon mesozooplankton is probably small in comparison to those greater than 1mm.

***Sagitta setosa*:**

Feeding and predators:

Species within the genus *Sagitta* most commonly appear to feed upon copepods (Sevastopol Bay: Mironov, 1960; British Isle Seas: Rakusa-Suszczewski, 1969; Southern North Sea: Tungate, 1975; Northumberland Coastal Waters: Frid *et al.*, 1994), although they also prey upon cladocerans (Rakusa-Suszczewski, 1969), and may even take young fishes (Lebour, 1922; 1923; Kuhlmann, 1977), although they show a strong preference for copepods over fish larvae (Kuhlmann, 1977). They do not usually take fish eggs (Kuhlmann, 1977), probably because they only catch organisms showing swimming activity. Reeve (1966) found *Sagitta hispida* would not take phytoplankton or detritus, and apparently could discriminate between live prey and dead prey, only taking the former. This species was also found to have food preferences based on size and quality, as well as motility of the food, and was found to be cannibalistic under laboratory conditions. Tungate (1975) found cannibalism to be 'fairly common' in *Sagitta elegans* collected from the Southern North Sea, with large individuals being capable of taking individuals one half their size. The most common food items found in the stomachs of individuals were the copepods *Pseudocalanus elongatus*, *Acartia* spp., *Temora longicornis* and *Paracalanus parvus*. It was further postulated that the commonly found indeterminable gelatinous mass found in the guts were the remains of *Oikopleura dioica*. Rakusa-Suszczewski's (1969) examination of the gut contents of *Sagitta setosa* revealed that cannibalism was shown in animals 4 to 14mm in length. In the same study the limits to prey size which was taken, and the tendency of individuals to take larger prey with increase in the size of the predator, were both given as characteristics which influenced prey selection in naturally occurring *S.setosa*. Frid *et al.* (1994) examined the gut contents of *S.elegans* collected from Northumberland coastal waters and found that *Calanus finmarchicus*, *Acartia* and 'other small copepods' were dominant (by numbers), and individuals were once again cannibalistic. Of the 1,789 individuals they examined only one contained more than a single prey item, with 2 *Acartia* individuals. The greatest number of items found by Øresland (1987) in a single *S.setosa* collected from Gullmarsfjorden was 5, consisting of 2 copepods, 2 nauplii, and 1 unidentified item. This was less than the maximum of 9 items found in the guts of *S.elegans* found in the same area. Rakusa-Suszczewski (1969) reported that normally only one food item was found to be present in the gut of *S.elegans* in the North Sea, however, one individual of 19mm length contained 11 small *Pseudocalanus elongatus*. Frid *et al.* (1994) found that the size of prey items were linearly related to the size of the chaetognath, with stage 1 *S.elegans* never containing prey items greater that 1.3mm and stage 3 individuals never containing individuals less than 1.3mm. Pearre (1981) also found cannibalism to be common amongst *S.elegans* collected from Bedford Basin, Nova Scotia. The main identifiable dietary

components were found to consist of copepodites and adult copepods, copepod nauplii, other chaetognaths, polychaetes, tintinnids, rotifers and cladocerans. The copepodites and adult copepods, polychaete larvae, and other *S.elegans* were generally the dominant source of energy to the chaetognaths in the two months of study (July and August), although tintinnids and rotifers were important among the small (>4mm) individuals.

Lebour (1923) found in the laboratory that the gelatinous species *Chrysaora isosceles* and *Saphenia gracilis* both took *Sagitta*, *Saphenia gracilis* was also found to contain *Sagitta* when caught using net tows. *Stomotoca dinema* and *Steenstrupia rubra* were also found containing *Sagitta* in collections by plankton tows, as did *Cosmetira pilosella*, *Rathkea octopunctata*, *Willsia stellata* and *Obelia* sp. Of all these gelatinous species only *Obelia* has been found in Southampton Water (Lucas, 1993; *personal observation*), and only very rarely. It would appear that predation may be minor on this species. Reeve (1966) however commented that young *Sagitta hispida* could be taken by copepods including *Acartia*, while fish could prey also on adult individuals. Neither of these two impacts having been assessed in the present investigation.

Decrease in the feeding rate of *Sagitta setosa* during the day has previously been reported by many workers (Wimpenny, 1937,1938; Parry, 1944; Mirnov, 1960; Rakusa-Susczewski, 1969; Frid *et al.*, 1994). Øresland (1987) found that feeding increased around sunset and declined around sunrise. Øresland (1987) also found that the diets of *S.setosa* and *Sagitta elegans* differed considerably, with *S.elegans* taking almost only copepods, whereas *S.setosa* took small copepods, nauplii, appendicularia and other *S.setosa*. These differences were attributed to the size differences in the chaetognaths (with the larger *S.elegans* taking larger prey), and to their vertical positioning (with the shallower living *S.setosa* taking surface collecting small zooplankton). Cannibalism by *S.setosa* in this area was believed to contribute to the sharp decline in its numbers during autumn. Unfortunately no gut content analysis has been conducted upon *S.setosa* within Southampton Water, however, it is probable that such a study would find a dominance of *Acartia*, other copepods and meroplankton.

Population dynamics:

Hulsizer (1976) found that in Narragansett Bay, U.S.A., *Sagitta elegans* was present sporadically during winter and spring. Ryan *et al.* (1986) found that in Killary Harbour, Ireland, *S.elegans* was found between February and October, with low numbers in February, May and June. *Sagitta setosa* had a more prolonged abundance, being collected in every month of the year except March. Within Southampton Water maximum densities were found in the autumn and winter months from around September to February, although small numbers were also found

Species	Max. Abundance (numbers m^{-3})	Max. Size (mm) Head-Tail Length	Max. Biomass (mgC m^{-3})	Max. Daily Production (mgC m^{-3} d^{-1})	Area	Source
Sagitta hispida						
	250	14	-	-	Cedar Key, Florida, USA	Owre 1960
	80	10.5	-	-	Biscayne Bay, Florida, USA	Reeve 1966
	-	-	5.4	1.4	Biscayne Bay, Florida, USA	Reeve and Baker 1975
Sagitta elegans						
	-	20	-	-	Plymouth coastal waters	Russell 1932b
	-	21	-	-	Port Erin Bay, U.K.	Pierce 1941
	129	-	18	-	Bristol Channel, U.K.	Williams and Collins 1985
	-	26	-	-	North Sea	Rakusa-Suszczewski 1969
	-	31	-	-	Inner Oslofjord, Norway	Jakobsen 1971
	200	-	-	-	Kiel Bight, W.Baltic	Möller 1979
	-	-	1.4	-	North Sea and Kattegat	Möller 1980c
	-	37	-	-	Gullmarsfjorden Sweden	Øresland 1987
	-	~20	-	0.3	Ogac Lake, Canada	McLaren 1969
	-	32	-	-	St.Margaret's Bay, Canada	Sameoto 1971
	24	27	86.3	-	Bedford Basin, Canada	Sameoto 1973
	20	-	~1	-	Saanich Inlet, Canada	Larson 1985
	35	31	-	0.24	Bedford Basin, Canada	Zo 1973
	30	-	-	-	Bedford Basin, Canada	Matsakis and Conover 1991
	165	30	-	-	Georges Bank, U.S.A.	Clarke *et al.* 1943
	5	-	-	-	Narragansett Bay, U.S.A.	Hulsizer 1976
	106	22			Long Island Sound, U.S.A.	Tiselius and Peterson 1986

Sagitta sp.					
22	-	-	-	Southern Bight, S.North Sea	Daan 1989
Sagitta setosa					
-	22.5	-	-	Plymouth coastal waters, U.K.	Russell 1932b
-	19	-	-	Mersey Channels, U.K.	Pierce 1941
-	15	-	-	North Sea	Rakusa-Suszewski 1969
-	12	-	-	Inner Oslofjord, Norway	Jakobsen 1971
-	16	-	-	western English Channel	Øresland 1986
340	-	-	-	Eastern Irish Sea	Khan and Williamson 1985
-	15	-	-	Gullmarsfjorden, Sweden	Øresland 1987
4.38[c]	15[c]	0.20[c]	-	Calshot 93[c]	This study
2.93[a]-2.66[b]	12[a]-11[b]	0.05[a]-0.04[b]	-	Hamble 90[a]-91[b]	
3.69[b]	12[b]	0.06[b]	-	N.W.Netley 91[b]	
1.65[a]-1.98[b]	13[a]-12[b]	0.05[a]-0.04[b]	-	Cracknore 90[a]-91[b]	
1.17[c]	15[c]	0.06[c]	-	Bury 93[c]	

TABLE 5.4.6 Comparisons of maximum recorded abundance, biomass and daily production of *Sagitta*, compiled from literature sources, and for Southampton Water.

during the spring and summer. Russell (1932b) reported that there were at least six generations of *S.setosa* per year in Plymouth coastal waters. These results however, were later questioned by both Jakobsen (1971) and Øresland (1986), with these authors suggesting that there was only one generation per year in this area. Jakobsen (1971) also found one generation of *S.elegans* per year with one new brood per year in the inner Oslofjord. Although *S.elegans* was present all year round in this fjord, *S.setosa* presence was mainly confined to late summer and autumn. Although Jakobsen (1971) found that it was introduced from the outer fjord during a time when wind would cause outgoing surface movements, it was believed that compensatory currents in the water just below the surface caused the population to move inwards. Because of its seasonal occurrence in the inner Oslofjord few conclusions could be safely drawn, although it was suggested that spawning occurred from May to October, with two broods produced during this period. Øresland (1986) found that *S.setosa* numbers in the western English Channel were low during spring and summer but increased in late summer and autumn. This seasonal increase was attributed to reproduction in addition to advection. Given the rapid changes in density and size within Southampton Water it would certainly appear that either there is inconsistent sampling efficiency of the population and/or the population is very much non-closed. The advection of *S.setosa* in and out of the estuary would certainly seem likely, indeed Lucas (1993) described the population as allochthonous. Lucas (1993) also points out that *S.setosa* tends to be more abundant at lower estuarine sites, where it also appears earlier in the year. She suggested that this could indicate transport into the estuary from outside and therefore allochthonality. It has also found to be present in 'significant numbers' in the extreme western Solent during June, but only entered Southampton Water in the Autumn when hydrodynamic conditions were suitable.

Reeve *et al.* (1978) from comparisons of laboratory feeding experiments, postulated that ctenophores are at a competitive disadvantage to chaetognaths at low food densities, while at high food densities the reverse was true. They also found that negative growth of *Pleurobrachia bachei* occurred at a food concentration of less than 10^3 copepods m^{-3} (200µm net). Reeve and Baker (1975) postulated that ctenophores need a higher food concentration than chaetognaths to allow a population to grow. Often ctenophores have been found at times or in locations when food is more abundant while chaetognaths have been found when and where food is less abundant. *Sagitta hispida* was found in both Card Sound and Biscayne Bay, Florida by Reeve and Baker (1975), while *Mnemiopsis mccradyi* was only found in Biscayne Bay. This difference was attributed to the fact that there was a 10 fold difference in the mean annual standing stock of 200µm mesh zooplankton between Card Sound and Biscayne Bay. Within Southampton Water, ctenophores are found from April to October although sometimes through to February (see Figure 5.3.16). In some years they are missing in the summer months. The chaetognaths are

predominantly found between the months of September to March. Often highest numbers of copepods and meroplankton are found during August to December. There is therefore no clear distinction between food concentration and the dominance of one or the other of these groups. Physical processes including advection also have a role to play. The truly gelatinous predators are generally much less abundant in the winter months. This could be the result of flushing processes, temperature, turbulence or wave action, which may be particularly harmful to this group. The chaetognaths may be more abundant at these times as a result of their physical robustness and adaptation to more energetic environments.

Migration:

Sagitta migrates on a diurnal basis, spending daylight hours in deep water and migrating to the upper layers to feed during the night (Sameoto, 1971). Other workers have also shown chaetognaths to vertically migrate, and concentrate near the bottom during the day, rising to the surface at dusk (see review by Alvarino, 1965). Russell (1933b) also found that *Sagitta setosa* could collect in deeper water during the daytime. All the samples collected within Southampton Water have been taken during daylight hours. Night sampling or complete vertical integration would have been preferable, and it may be that biomass and density may have been underestimated during some parts of the year, particularly the older stages (see conclusions of Tiselius and Peterson, 1986). The data from the 14 month abundance investigation also show that abundance is greater towards the mouth of the estuary. Within Southampton Water large individuals sporadically appeared, these individuals may not have grown from the sizes sampled on the previous date, and probably indicating unrepresentative sampling within the estuary, or the influx of individuals from outside, as occurred for *S.setosa* in Oslofjord (Jakobsen, 1971), and in Long Island Sound (Tiselius and Peterson, 1986). Within Southampton Water numbers were often seen to decline as rapidly as they increased, this phenomenon was also seen by Jakobsen (1971) and once again may be attributable to water mass movements. It is likely that the 212μm mesh net used by Lucas (1993) could potentially under estimate *S.setosa* abundance as stage 1 individuals <4mm are only 200μm wide (King, 1979). Jakobsen (1971) also believed *Sagitta* to had the capacity to avoid nets, with larger individuals probably being more efficient at avoiding capture than small individuals. Both these effects will tend to cause quantification problems with underestimation of density.

Comparisons between maximum abundances, size, biomass and daily production, by Sagitta setosa and congenerics are presented in Table 5.4.6. Within Southampton Water these maxima are very much lower than in many other areas. Maximum head-tail lengths are very

similar between studies however. The presence of this species may be linked predominantly with its life-cycle in more offshore waters, however its abundance is certainly controlled by physical processes causing its advection in this region.

***Assessing the effects of the gelatinous predaotrs upon prey populations*:**

Gelatinous predators were ascribed by Lucas (1993), as having 'an important role in structuring the mesozooplankton community of Southampton Water, particularly at the Cracknore site'. Furthermore, *Aurelia aurita* was described as being the most important of gelatinous predators in terms of cropping and carbon demands by Lucas (1993). Indeed the importance of *A.aurita* was further assessed by Lucas and Williams (1995) and Lucas *et al. (in press)*. In the present investigation it is clear that at Cracknore, where *A.aurita* has its highest annual production, it also has by far the dominant carbon ingestion demand. While *Pleurobrachia pileus* has the greatest ingestion demand at both N.W.Netley and Hamble. At all sites *Clytia hemisphaerica* would appear to contribute only a small portion of the total annual gelatinous demands. *Sagitta setosa* is the only species to have a quantified ingestion demand at Calshot, as not all the species have been examined here. Although *C.hemisphaerica* and *S.setosa* would appear to be relatively minor predators, they are the dominant gelatinous predators at some points of the year.

Combined gelatinous predator ingestion demands in comparison to calanoid copepod production at Hamble are presented in Figure 5.4.2. It may be seen that the daily total ingestion demand over most of the year is a small fraction of the daily estimated calanoid production, typically around an order of magnitude less. In 1990 the calanoid copepod production estimated from the data of Lucas (1993) is exceeded during part of June and July by ingestion demand of gelatinous predators, this demand being made entirely by *Clytia hemisphaerica*, as no other gelatinous predators were present. In 1991 when ingestion exceeded production during July, total ingestion was dominated by *Pleurobrachia pileus*, although *C.hemisphaerica* contributed to this total. The demands never exceed the production estimates made from the abundance data of Zinger (1989). There are periods of rapid copepod decline apparent in the data of Zinger (1989). These declines do not appear to be attributable to gelatinous demands singularly, as given continuous recruitment and production, numbers should not decline. Calanoid copepod numbers decreased from 1584 ind. m^{-3} in May to 19 ind. m^{-3} by the start of June 1990 (ie. over a period of 13 days), representing a decline in numbers of 1,565 individuals m^{-3}. Over this 13 day period gelatinous demands were estimated to be 282μgC (with daily peak demand at 65μgC$m^{-3}d^{-1}$). This entire demand represents a removal rate over the period of around 1567 stage CI *Acartia*

(assuming CI weight of 0.18μgC), or 118 adult *Acartia* (assuming adult weight of 2.4μgC) (both these weights estimated from dry weight of *Acartia clausii* at similar temperatures as measured from Durbin and Durbin (1978), and assuming carbon to be 40% of dry weight). The declines could therefore potentially be the result of gelatinous predation if prey items were predominantly smaller individuals, and if the copepods were growing at a reduced rate. A lower growth rate than predicted is certainly likely given the apparent food limited growth which may occur in the estuary (see Chapter 3). The decline could therefore be attributable to gelatinous predation, although it could also indicate some form of food limited growth by the calanoid copepods.

In the assessment of predatory impact it has been assumed that the predation by gelatinous zooplankton is not concentrated upon a particular size range. If predators were to prey exclusively on a very small copepod size range then they could in effect have a demand which caused a prey decline even though the production of that prey species may be greater than that of they predator. This is because the life-cycle could effectively be broken. There is however, little evidence to suggest that gelatinous predators are so selective. Although, the gelatinous predator for which the decline in abundance may have been attributable is *Clytia hemisphaerica*, which has been shown to feed upon copepodites and adult copepods, and to have a gut contents which could be dominated by copepod eggs, ingested eggs have, however, been reported to be digested very slowly or not at all, and may most commonly be regurgitated, often appearing undamaged by the experience (Daan, 1989). It is interesting to note that over this same period *C.hemisphaerica* demands were very similar at Cracknore, and the initial abundance of copepods was also similar, yet no great reduction in calanoid copepods numbers were evident here. The general abundance patterns of copepods and meroplankton may be affected during very short periods of the year by the predation of gelatinous zooplankton. During isolated years it is possible that the ingestion by gelatinous predators may have at least approached the calanoid copepod production, or exceeded it over periods typically around one month. However, given that the other meroplankton may also meet these demands, the abundance patterns throughout the year may not be the result of the predation by gelatinous zooplankton. They are generally free of top down control, at least with regard to the gelatinous predation. The gelatinous demands may exacerbate the lows in abundance but are probably not the primary cause of these lows. As predation does not play a significant role, food availability and physical factors seem the most likely factor underlying their population dynamics.

Total demands of gelatinous predators together with calanoid copepod production estimates for N.W.Netley are given in Figure 5.4.3. Once again the demands exceed estimates of copepod production derived from the results of Lucas during June-July, and part of August,

SITE	INGESTION DEMAND $mgCm^{-3}yr^{-1}$ (% OF TOTAL QUANTIFIED)				
	A.AURITA	*C.HEMISPHAERICA*	*P.PILEUS*	*S.SETOSA*	TOTAL
CALSHOT	0.000 (0)	*	*	1.625 (100.0)	1.625 (100.0)
HAMBLE	0.006 (0.1)	1.037 (16.4)	4.005 (63.3)	1.283 (20.3)	6.331 (100.0)
N.W.NETLEY	1.273 (7.4)	0.223 (1.3)	14.505 (84.8)	1.099 (6.4)	17.100 (100.0)
CRACKNORE	56.589 (73.3)	1.140 (1.5)	18.523 (24.0)	0.942 (1.2)	77.194 (100.0)
BURY BUOY	9.630 (95.7)	*	*	0.431 (4.3)	10.061 (100.0)

* denotes no value available

TABLE 5.4.7 Summary of the estimated ingestion demand of the dominant gelatinous species within Southampton Water.

predominantly as a result of *Pleurobrachia pileus* predation but also contributed to in part by *Clytia hemisphaerica*. The decline in copepod numbers between the end of May and start of June is the period in which gelatinous demand begins to exceed copepod production. During this period calanoid numbers decline from 1,255 to 234 ind. m^{-3} (mean daily reduction of 92 ind. m^{-3} d^{-1}). A total decline of 1,021 ind. m^{-3}, or 2,450μgC m^{-3} (assuming all adults removed) may be estimated. Ingestion demand over the same period equals 3,816μgC m^{-3}. The most common sized individual *P.pileus* on the later of these dates was 8mm, Lucas (1993) estimated from laboratory digestion times and gut content analysis that individuals of 6-10mm took 90 prey items per day. Furthermore, Lucas (1993) also found that the dominant prey items for this species in Southampton Water were copepods. The demands of gelatinous predators do not however always exceed the production estimates made from the calanoid abundance data of Zinger (1989). Given that the *P.pileus* densities over this period were 1.02 ind. m^{-3} (averaged from 0.07 and 1.97 ind m^{-3}), then an average of 92 prey items per m^3 per day may have been taken. Remarkably this is identical to the rate of copepod decline of 92 ind. m^{-3} d^{-1}. It could therefore be a result of the ingestion demands of *P.pileus*. Once again numbers are rather low prior to the point where ingestion exceeds production, however, the demand could certainly be the cause of the subsequent depression in numbers which is found during some years and is observable in the data of Lucas and Zinger. Although there may be control over a very short period of around one and a half months in some years, throughout the rest of the year other factors will primarily cause abundance pattern change.

Figure 5.4.4 shows the combined ingestion demands of the gelatinous predators at Cracknore, together with estimated calanoid copepod production rates. The peak ingestion demands by the gelatinous predators at this site are much greater than at any of the other sites. Peak demands which exceed production occurring between April through June, although there is inter-annual variability. It is interesting to note from the data of both Zinger (1989) and Lucas (1993), that numbers may continue to increase during the period when the ingestion demands of the gelatinous predators appears to exceed the copepod production rates. However, more typically there are declines in abundance. Indeed July is the month of lowest abundance of calanoid copepods, and the meroplankton are often reduced. Around the time of there being a rapid decline in ingestion demands, caused by the extinction of *Aurelia aurita*, calanoid copepod abundances increase in all years. The declines, and rapid increases in calanoid copepod numbers tie closely in all years with the extinction of *A.aurita*. It is important to note that the decline in copepod numbers may be an important source of energy-matter used in meeting ingestion demands. There is a substantial decline in the copepod density between 13/5/91 and 24/05/91, with densities changing from 6,644 ind. m^{-3} to 745 ind. m^{-3}.

SITE	E.T.E. % (U.E %)				
	A.AURITA	*C.HEMISPHAERICA*	*P.PILEUS*	*S.SETOSA*	TOTAL
HAMBLE	0.001 (0.003)	0.22 (0.49)	0.07 (1.91)	* (0.61)	0.29 (3.01)
N.W.NETLEY	0.16 (0.24)	0.01 (0.04)	0.10 (2.75)	* (0.21)	0.27 (3.25)
CRACKNORE	7.66 (16.36)	0.10 (0.33)	0.19 (5.36)	* (0.27)	7.95 (22.32)

* denotes no value available

TABLE 5.4.8 Ecological transfer efficiency (ETE) and utilisation efficiency (UE) as percentages between gelatinous zooplankton production and ingestion respectively, and the calanoid copepod production within Southampton Water.

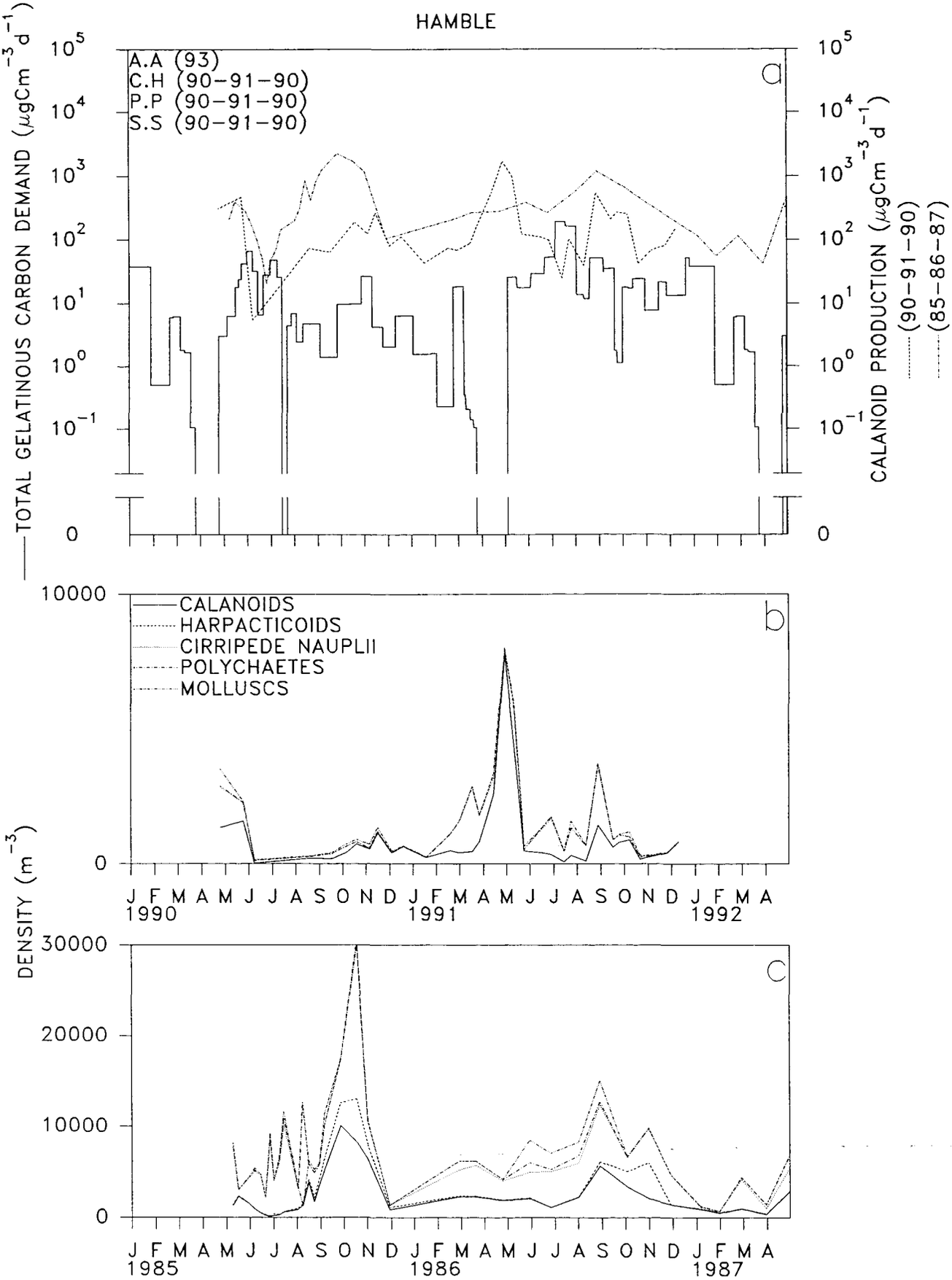


FIGURE 5.4.2 a. Comparisons of estimated copepod production with the ingestion demands of the gelatinous predators at the Hamble site (note different years of collection, years given for each species). b. Density measures of the dominant mesozooplankton at Hamble found by Lucas (1993) using a 212μm mesh net. c. Density found by Zinger (1989) using a 100μm mesh net.

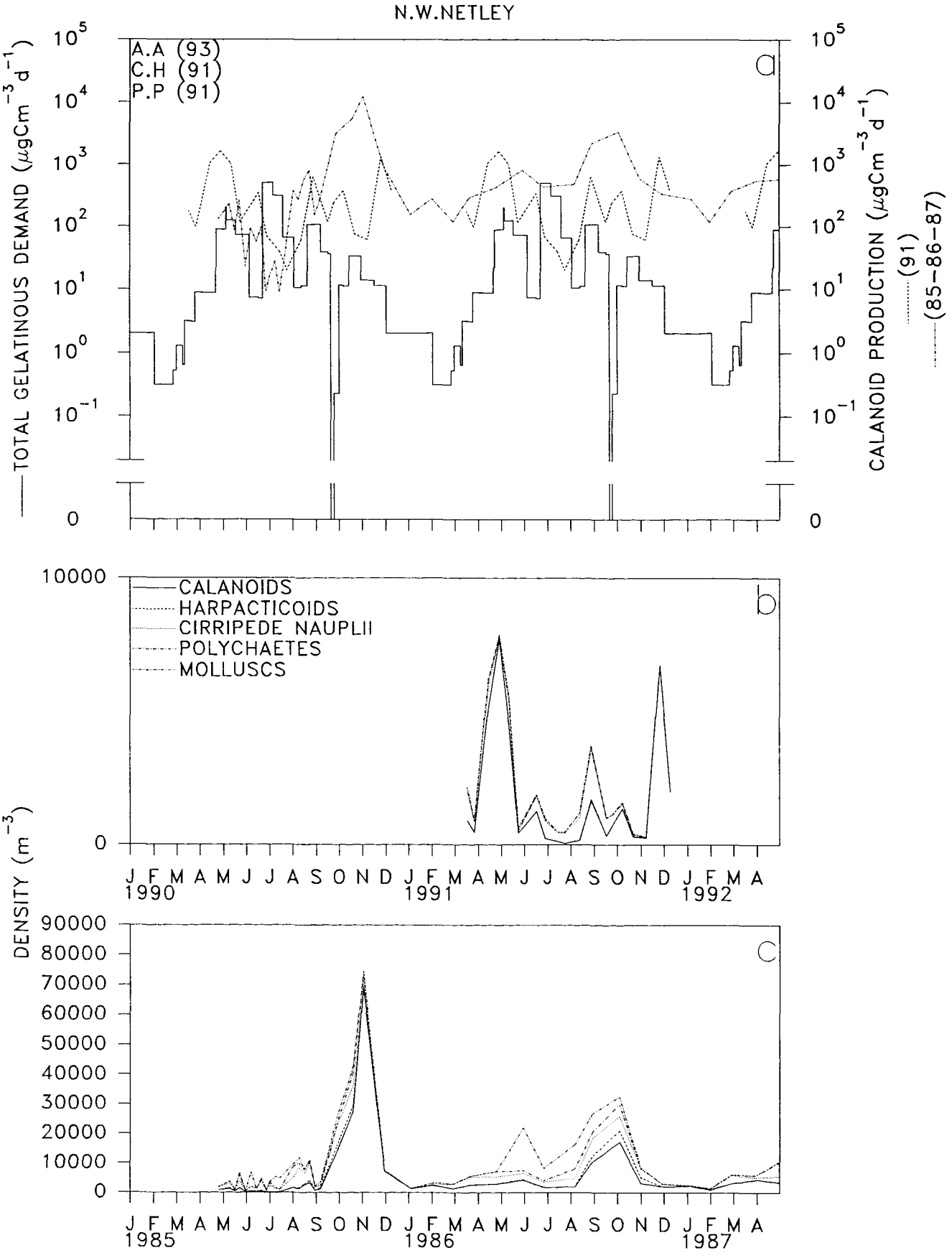


FIGURE 5.4.3 a. Comparisons of estimated copepod production with the ingestion demands of the gelatinous predators at the N.W.Netley site (note different years of collection, years given for each species). b. Density measures of the dominant mesozooplankton at N.W.Netley found by Lucas (1993) using a 212μm mesh net. c. Density found by Zinger (1989) using a 100μm mesh net.

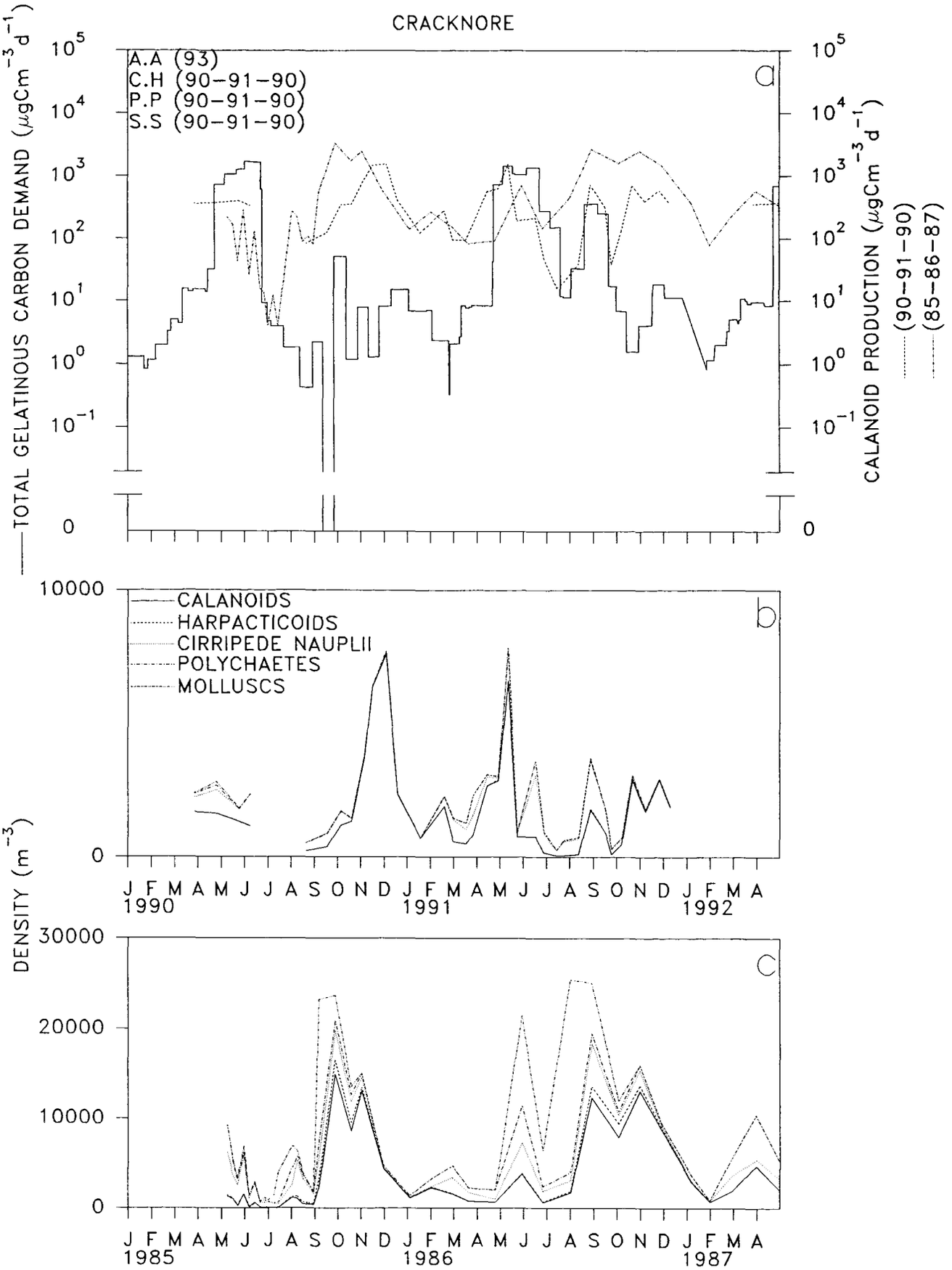


FIGURE 5.4.4 a. Comparisons of estimated copepod production with the ingestion demands of the gelatinous predators at the Cracknore site (note different years of collection, years given for each species). b. Density measures of the dominant mesozooplankton at Cracknore found by Lucas (1993) using a 212μm mesh net. c. Density found by Zinger (1989) using a 100μm mesh net.

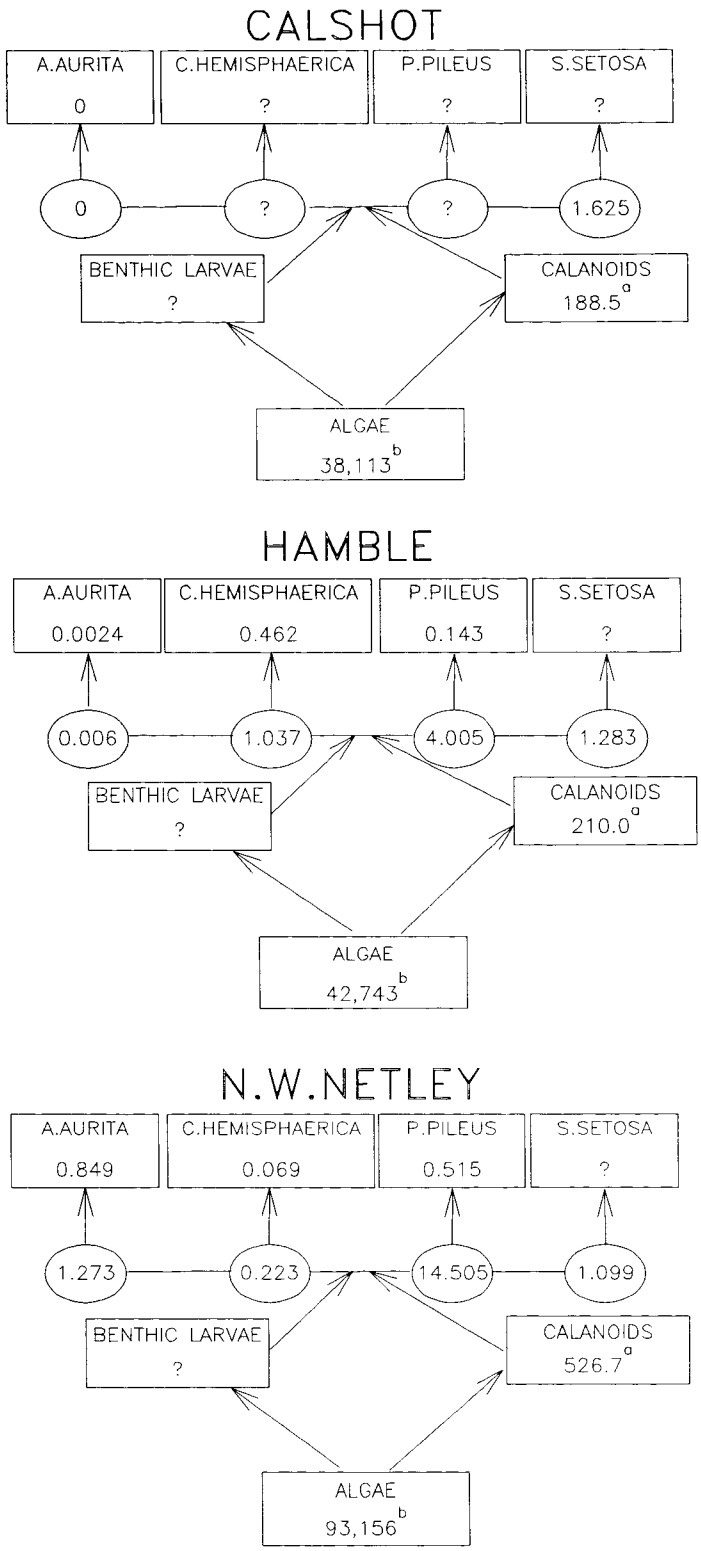


FIGURE 5.4.5 Estimated annual carbon flow (mgC m^{-3} yr^{-1}) through components of the planktonic and benthic community at Calshot, Hamble and N.W.Netley. Values in boxes are annual production estimates, those in circles are estimated annual carbon demands of the components above them.

a. Annual estimates derived from abundance data, see Chapter 8 for details.

b. Derived from chlorophyll a concentrations, see Chapter 8 for details.

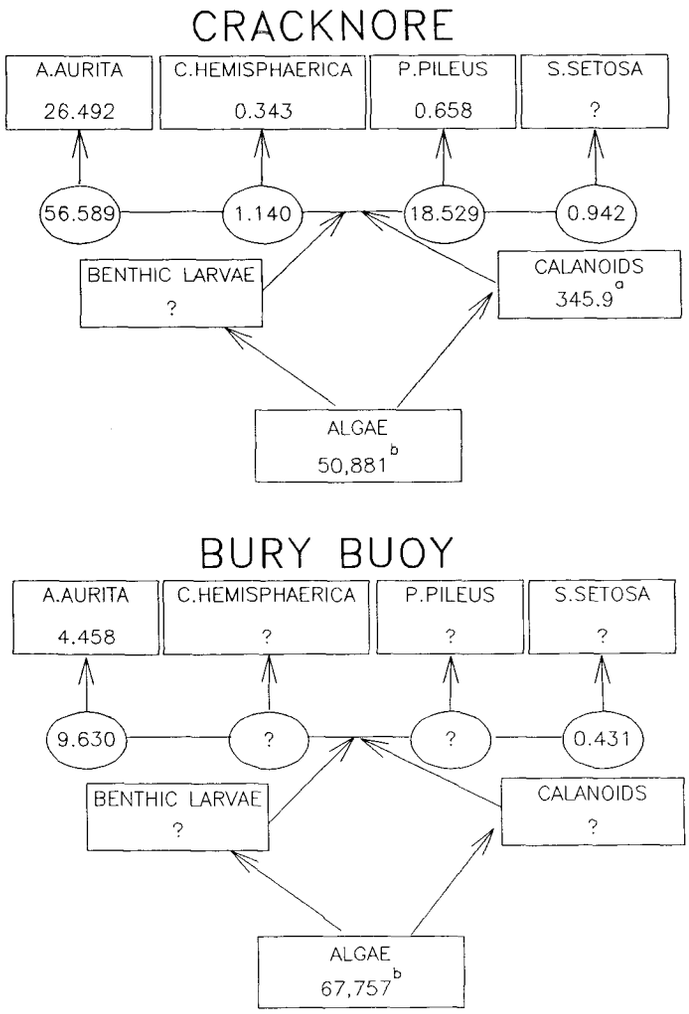


FIGURE 5.4.6 Estimated annual carbon flow (mgC m^{-3} yr^{-1}) through components of the planktonic and benthic community at Cracknore and Bury Buoy. Values in boxes are annual production estimates, those in circles are estimated annual carbon demands of the components above them. See previous figure for annotation.

This may help to satisfy the gelatinous predatory demands. Assuming a mean copepod weight of 2μg, this represents a decline of 983μgCm^{-3}d^{-1}. Over this same period gelatinous ingestion demands are greater than 1mgCm^{-3} d^{-1}. The decline in the copepod abundance does not continue at this rate however. A large proportion of the ingestion demand may also be met by the meroplanktonic larval production in addition to its 'new biomass'. This new biomass being transported into a region through lateral movements and being added from the benthic system. Aspects of meroplanktonic inputs, and the flow of matter in non-closed systems is examined in detail in Chapter 6.

Lucas (1993) demonstrated that *Aurelia aurita* collected at Cracknore had other components than calanoid copepods in their diet, with barnacle nauplii at times exceeding copepod numbers. Assuming a similar digestion time for these two components and similar carbon contents, then barnacle nauplii may certainly be as important or more so than copepods in satisfying the ingestion demand of *A.aurita* during certain parts of the year (see Chapter 6). It is feasible that the ingestion demand of a predator may exceed that of its prey, however in a closed system this would lead to the decline of the prey standing stock. It would appear that the ingestion demands of the gelatinous predators at most sites, and in most of the year, may be met without there being a depletion of their prey standing stock ie. ingestion demands of the gelatinous predators are almost always very much less than the production rates of calanoid copepods. Data from Zinger (1989) show there to be an estuarine wide low in mesozooplankton numbers during the months January to April, with highest abundances during August to December. Estuarine wide low abundance during the early months of the year are almost certainly not attributable simply to the predation pressure exerted by gelatinous predators, although at Cracknore *A.aurita* may certainly cause this low to be extenuated. Copepods and meroplanktonic larvae may be low because of food limitation in addition to predatory impacts.

Schneider (1989b) estimated that *Aurelia aurita* daily food intake in Kiel Bight during 1982 appeared to be as high as 15% of the mesozooplankton (>200μm), and 6% of both micro- and mesozooplankton (>20μm) standing stock per day. In the same study, during 1983 when *A.aurita* were less abundant, only 3% and 1% were consumed per day. In the same area Martens (1976) estimated that annual prey production was equal to 34gCm^{-2}yr^{-1} in a 20m deep water column, assuming 50% of this production to occur over the summer, Schneider (1989b) estimated that medusae consumed 42% of the summer secondary production in 1982 but only 8% in 1983. Schneider (1989b) also estimated that *A.aurita* medusae within Kiel Bight are not responsible for zooplankton decline in late spring, or the low values found during summer in Kiel Bight. This would superficially seem similar to Southampton Water in that mesozooplankton is low during

late spring and summer but this can not be attributed entirely to gelatinous consumption.

Table 5.4.7 gives the average annual average estimates of the ingestion demands of the dominant gelatinous species within Southampton Water. Annual ecological transfer efficiencies and annual utilization efficiencies in Table 5.4.8. Figures 5.4.5 and 5.4.6 give the annual production and ingestion demands of the gelatinous zooplankton in comparison to production by phytoplankton and copepods. Care must be taken in interpreting annual ETE and UTE values as low efficiencies do not necessarily infer that a predator population has no control over a population, rather it may be simply the result of a predator being absent through much of the year, but being important over only short periods. Furthermore, low ETEs do not necessarily mean low impact by a predator. A predator could have a high ingestion rate but a low gross growth efficiencies (or over-kill prey without ingesting them), having therefore low production in comparison to its prey, and yet important impacts upon them. Ingestion demands and application of clearance rates are generally much better methods of attempting to understand and quantifying energy flow.

The ingestion demands estimated for Southampton Water may be compared to those estimated by Larson (1985) for Saanich Inlet, Canada. Using tentative energy budgets he estimated that total gelatinous carbon demand between March to August (the dominant period) to be ~25mgCm^{-3}. The annual ingestion demands within Southampton Water are as little as 6.3mgCm^{-3} at Hamble, but are as great as 77.2mgCm^{-3} at Cracknore, over 70% of this demand being attributable to *Aurelia aurita*. Larson (1985) found gelatinous biomass in Saanich Inlet, Canada to be ~0.5mgC 100m^{-3} or less in winter, but increasing to a maximum in May-June at >5mgCm^{-3}. In Southampton Water during 1993 integrated carbon biomass of *A.aurita* reached 6.8mgCm^{-3} at Cracknore, with subsequent rapid declines as a result of *A.aurita* extinction. Larson (1985) also commented upon the rapid decline of gelatinous biomass but being attributable in part to advective processes, although this was not always the case.

Arai and Jacobs (1980) found that under laboratory conditions *Aurelia aurita* 8-18mm in size preyed on small (2-4mm) *Pleurobrachia pileus*, and 18-28mm *A.aurita* preyed upon larger (5-9mm) *P.pileus*. *A.aurita* may also preyed upon *Phialidium gregarium*. Direct predation by *A.aurita* is unlikely to be the reason why *P.pileus* and *Clytia hemisphaerica* both seem to appear predominantly later in the year after the number of *A.aurita* have declined. Indeed the same successional pattern was found at Greenland, even though *A.aurita* abundance is extremely low there. The succession effect noted by Lucas (1993) could be simply a reflection of the robustness of the predators to physical forces and flushing, shifts in prey type and availability, as well as

physical factors. Temperature may certainly be an important factor determining the seasonal occurrence patterns of gelatinous organisms (Kremer, 1994), and therefore also the pattern and predatory magnitude of this group. In the present investigation it would appear likely that flushing has an important effect upon the temporal and spatial patterning of ingestion demands. Other workers have also noted the importance of flushing in coastal areas to the decline in abundance and in some cases it would appear to be the principal factor in reducing the abundance of a population (*Sagitta elegans* loss from St. Margaret's Bay: Sameoto, 1971; *Aurelia aurita* loss from the Dutch Wadden Sea: van der Veer and Oorthuysen, 1985). The energetics of an environment may also have profound effects upon the distribution of fragile species. Given the apparent low gelatinous predator abundance in Southampton Water throughout most of the year, their abundance may be controlled physically. Of course water mass movements may also ensure the advection of gelatinous predators into an area.

Lucas (1993) described that 'a classic predator-prey interaction is apparent in Southampton Water, with almost coincidental peaks of gelatinous predator abundance/biomass and troughs of the total mesozooplankton population, particularly in May'. However, she also points out that the mesozooplankton population abundance during the course of her investigation were similar at all sites, regardless of the size of the gelatinous predator component, and showed similar temporal trends throughout the estuary despite the gelatinous component being greatest at the Cracknore site. Similar effects may be observed in the data of Zinger (1989), see Figures 5.4.2 to 5.4.4. Although gelatinous predation may have an important role in causing low abundance of copepods and meroplankton at times, throughout most of the year they would appear not to be dominant agents of control. Although there may also be a very limited control at the other sites it would appear that other factors are important throughout most of the year, and that these may be estuarine wide in their effect. Others, particularly food quality and availability and the affects these may have, need to be examined in closer detail if the controlling factors are to be determined, as must those controlling the production of benthic larvae by adults. The true impact of predators can only be assessed correctly when not only their demands, but the ability of the prey to withstand such demands, and also the other factors controlling the prey production have been assessed. Algae has previously been shown to be particularly important in determining the structure and abundance of prey copepods and meroplankton (Daan, 1989), and at times gelatinous predators may have their impact 'exaggerated' as a result of their prey being food limited (Kremer, 1979). Reeve and Walter (1976) showed ctenophores to suppress copepod densities in mesocosm experiments, and calanoids have been shown to be eliminated from enclosures (Grice *et al.*, 1980). The situation in such enclosures may arise because of herbivore food limitation (eg. Reeve and Walter, 1976). Chapter 3 has shown that growth rates of copepods

at Calshot may be lower than the model used herein to estimate growth and production. The impact of gelatinous predators may be particularly pronounced as a result of the sub-maximal copepod growth rates.

Hirota (1974) estimated a trophic transfer efficiency of 11% between zooplankton production and *Pleurobrachia bachei*, although this was calculated in terms of carbon, assuming that carbon was 50% of the AFDW of the ctenophores. This may be recalculated assuming, more correctly, that carbon is 5% of AFDW in *P.bachei*, which reduces the expected transfer efficiency to around 1.1%. Reeve *et al.* (1978) estimated that the ctenophore *Mnemiopsis* in Biscayne Bay removed copepods at a maximal rate of 10% of the population per day, although throughout most of the year removal would be below 1% per day. Siferd and Conover (1992) estimated that the ctenophore *Mertensia ovum* consumed between 4 and 10% of the standing crop of macrozooplankton per day in the Resolute Passage, Canadian High Arctic. Frank (1986) found that on Browns Bank, Southwestern Nova Scotia, *Pleurobrachia pileus* consumed on average 8.8% (range 0.2-28%) of the crustacean zooplankton standing stock per day in 1983, although this value fell to 0.7% (range 0.2-2%) in 1984. The year with much greater predation rates and also lower crustacean standing stocks (28% lower on average in this year than in the previous year) was described as being atypical for the area. At Cracknore, where ingestion demands were greatest, the peak ingestion rate in 1990 was 1.65mgCm^{-3}d^{-1}. This may be compared to estimated calanoid biomass from the work of Zinger (1989) at ~4.1mgCm^{-3} in 1986, and falls from 1.7 to 0.1mgCm^{-3} over this period in 1985. As such gelatinous demands were around 40% of the calanoid standing stock per day in 1986 but from 97 to 1,650% in 1985. Demands were of course met by other groups apart from the calanoid copepods, not accounted for here. Furthermore, comparisons are made more difficult as a result of inter-annual variability.

In a mesocosm experiment Reeve and Walter (1976) found that the production of *Pleurobrachia bachei* was equivalent to 4.3% of the primary production (in terms of carbon), while in a shore-based tank of comparable size, Mullin and Evans (1974) found an efficiency of 3% between *P.bachei* and primary production. Values from Figures 5.4.5 and 5.4.6 show that annual values would be very much lower than this. For example at N.W.Netley annual efficiencies of 0.002% were found, while at Cracknore it may be estimated as 0.054%. Of course on a daily basis this ration could rise, at Cracknore *Aurelia aurita* production reached around 0.5mgCm^{-3}d^{-1}, estimates of primary production during this period average at around 59mgCm^{-3}d^{-1} (Iriarte and Purdie, 1994), giving an efficiency of ~0.8%. There is no reason to expect a tight coupling between primary production and gelatinous production, although there are of course effects which primary production will have upon gelatinous production over more extended

periods.

Production rates have been estimated for the species *Aurelia aurita* by utilizing the natural *quasi*-cohortic behaviour of the population in the present investigation. Similar patterns of near synchronous development have been found in *A.aurita* populations elsewhere (Hamner and Jenssen, 1974), and in some cases have been utilized in estimating *in situ* growth rates and production (van der Veer and Oorthuysen, 1985). Population patterns which allow cohort methods to be utilized are rare in natural pelagic populations although some species have populations which have allowed cohort separation (McLaren, 1969; Zo, 1969; 1973; Sameoto, 1973; García, 1990). Often laboratory growth rates have been applied to data of natural abundance (Hirota, 1974; Reeve and Baker, 1975; Reeve and Walter, 1976; van der Veer and Sadée, 1984). Laboratory methods have many draw backs, particularly with respect to mimicking natural zooplankton abundance and type and their true representation of *in situ* growth rates. For ctenophore species there is certainly still some question as to whether laboratory rates are representative of natural growth rates given the fact that much higher food concentrations have to be used even to meet basal metabolic requirements (Walter, 1976).

Cohort methods applied to natural populations displaying truly cohortic behaviour is almost always desirable to most other methods. Non-cohortic field methods such as the 'Total biomass change' method have also been applied by Lucas *et al.* (*in press.*) and Schneider (1989c) for *Aurelia aurita* in Horsea Lake and Kiel Bight respectively. Larson (1985) also applied this method for a variety of gelatinous predators in Saanich Inlet, and McLaren (1969) used it to estimate the production of *Beroe ovata.* This method gives near minimum production values, they do not allow for any mortality (which would give higher production values if allowed for), although it is also possible to miss negative production (which would give lower production values). Gelatinous organisms may also be lost from coastal regions not only by mortality but also by washout of individuals (Larson, 1985;van der Veer and Oorthuysen, 1985; this study). Such methods should only be applied to closed or near closed populations, when biomass accrued may be attributable to an area without the import or export of matter to bias results. Many gelatinous species have however, been shown to be accumulated by physical or behavioural patterns in coastal areas (*Cyanea capillata* drifting from Kattegat into Kiel Bight: Möller, 1977; *A.aurita* and *Pleurobrachia pileus* brought into Kiel Bight by wind induced upwelling: Möller, 1977; *P.pileus* brought into Kiel Bight by water advection: Schneider, 1987; *P.pileus* brought into Wadden Sea from the Southern North Sea by tidal currents: van der Veer and Sadée, 1984; *Sagitta setosa* introduced from outer to inner Oslofjord through surface currents: Jakobsen, 1971; *Sagitta elegans* breeding stock brought from offshore waters into St. Margaret's Bay: Sameoto,

1971; *S.setosa* advected into sampling sites in the western English Channel: Øresland, 1986; *S.setosa* brought into Southampton Water by tidal currents, Lucas, 1993). There are also many indirect indications that patchiness of gelatinous predators may be the result of physical/behavioural processes rather than the biomass and densities found being the result of growth and mortality processes (eg. *A.aurita* patches in Japanese coastal waters: Kuwabara *et al.* 1969; see Alldredge, 1984; *Stomolophus meleagris* patchiness in NE Gulf of Mexico waters: Larson, 1991). Not only diurnal but seasonal vertical migration of gelatinous species may occur (eg. *A.aurita* in deep fjords, Hernroth and Gröndahl, 1985a). Vertical migration of gelatinous species, unless accounted for, may also bias estimates if sampling is not complete. For species with alternation of generations some of the body weight of pelagic individuals may be strictly attributable to benthic production, although this is typically very small. Unless both horizontal and vertical patchiness is accounted for then biomass measures in even so called 'closed systems' may not give true representations of production.

Results from the present investigation may in fact be used to demonstrate the poor estimates made using the 'Total biomass change' method. If such a method were to have been used to estimate the production of *Aurelia aurita* at Cracknore during 1993, then it would have been estimated to be $6.8 mgCm^{-3}yr^{-1}$. However, using the cohort technique we know that production is around $24.4 mgCm^{-3}yr^{-1}$, therefore an underestimation of 72% of annual production would have occurred. Schneider (1989b) also used the maximum biomass achieved as a measure of the production of *A.aurita* in Kiel Bight, energy-budgets were later constructed from this work. As a result of probable great underestimation of somatic production, subsequent estimations of assimilation demand was probably an underestimate, as has already been commented upon. Van der Veer and Oorthuysen (1985) found production rates of up to $1.1 mgCm^{-3}d^{-1}$ for *A.aurita*. They also reported that zooplankton occur with a carbon biomass of 40 to $60 mgCm^{-3}$, and that during the period of greatest predation pressure (May to June) the zooplankton standing stock increases. They did however probably overestimate *A.aurita* production by around 1.9 times, since they assumed carbon was 8.4% of dry weight whereas it is more likely to be around 4.3% of dry weight (Larson, 1986a) given the salinity (Hirst and Lucas, *in prep.*). In the same area, van der Veer and Sadeé (1984) estimated that *P.pileus* production reached $2.4 mgCm^{-3}d^{-1}$. Once again this was probably an overestimate, as laboratory growth rates were applied, although appeared not to be achieved.

Estimated daily production rates of *Aurelia aurita* during the 14 month investigation were maximally $0.48 mgCm^{-3}d^{-1}$. Maximum daily production reached $0.03 mgCm^{-3}d^{-1}$ for *Clytia hemisphaerica*, and $0.02 mgCm^{-3}d^{-1}$ for *Pleurobrachia pileus*. Daily production by the ctenophore

Mnemiopsis mccradyi, in the Biscayne Bay Region (Baker, 1973), ranged from 0.00036 to 2.63mgCm^{-3}d^{-1} (0.001 to 7.89mgCm^{-2}d^{-1}), with a daily average over a 17 month sampling programme of 0.357mgCm^{-3}d^{-1} (1.07mgCm^{-2}d^{-1}). Reeve and Baker (1975) estimated annual production of *M.mccradyi* in Biscayne Bay to be 61-123mgCm^{-3}yr^{-1} (equivalent to 183-369mgCm^{-2}yr^{-1}), with a daily P:B ratio between 0.06-0.20. These results being based upon application of laboratory growth rate data to the natural population. The ash-free dry weight production estimates for *Pleurobrachia bachei* off the coast of California as estimated by Hirota (1974) can be converted to units of carbon by assuming carbon to be 8.7% of ash-free dry weight (calculated from Reeve and Baker, 1975). This gives an annual estimate of production at 11.7mgCm^{-3}yr^{-1} (470mgCm^{-2}yr^{-1}, water column depth being 40m), and a mean daily P:B ratio of 0.2. Production of the carnivore *Sagitta elegans* has been estimated by Sameoto (1971) to range between 0.9 to 0.55 mgCm^{-2}d^{-1}, in St. Margaret's Bay, Nova Scotia. This represents consumption of between 0.07 and 1.1% of the annual copepod production. Sameoto (1973) found that the production of *S.elegans* in Bedford Basin, Nova Scotia, was 9.0% of the yearly copepod production. Furthermore, he estimated that the percentage of total yearly production of copepods consumed by *S.elegans* was 36%. In the present investigation, total annual ingestion by all gelatinous predators was 28.5%, and production transfer efficiency was 10.1%, at the Cracknore site, with values much lower at the more seaward sites. Both these values were estimated from calanoid production alone however. Mullin and Evans (1974) obtained a secondary production estimates for a population of *Pleurobrachia* raised in a deep tank to be equal to 12.6% of prey production and 2.6% of primary production. Reeve and Baker (1975) estimated that the production of *Mnemiopsis* equalled 9.5 to 19.2% of the production of other zooplankton, while the daily net production of *Sagitta hispida* was 11.7-47.7% of that of copepods. This transfer ratio was however, calculated in terms of AFDW which gives a somewhat biased result. Recalculating the values in terms of carbon weight (assuming carbon to be 47% of AFDW, estimated from mid-value range for copepods, as given by Curl, 1972; and using gelatinous carbon values given in original text), the transfer efficiency would be 1.8-3.6% for *Mnemiopsis* in Biscayne Bay, while for *S.hispida* the figure changes only minimally being 11.1 and 45.6% for Biscayne Bay and Card Sound respectively.

Table 4.4.2 is a compilation of gelatinous species production values available from the current literature, corrections have been applied and are detailed where it was believed incorrect conversion factors were utilised. Annual production estimates for Southampton Water have been included, and these show that the values given in the present investigation for total gelatinous production are within the limits of the other studies. The maximum total annual gelatinous production of 27.5mgCm^{-3}yr^{-1} within Southampton Water, which was estimated at Cracknore, is

SPECIES	PRODUCTION (mg C)			DAILY	ANNUAL	LOCATION	SOURCE
	DAILY (max)	YEARLY		P/B range	P/B range		
	(m^{-3})	(m^{-3})	(m^{-2})	(max*)			
Hydromedusae							
[C]*Aglantha digitale*	0.3	0.65-8.8	13-263	-	3.4-10.2	Ogac Lake	McLaren 1969
[B]*Phialidium* spp.	0.5	8		0.01-0.2	10-30	British Columbia	Larson 1985
[B]*Clytia hemisphaerica*	0.026-0.002	0.87-0.05	8.7-0.5	-	-	Greenland (90-91)	This Study
[B]*Clytia hemisphaerica*	0.002	0.07	0.56	-	-	N.W.Netley (91-92)	This Study
[B]*Clytia hemisphaerica*	0.020-0.005	0.57-0.12	5.7-1.2	-	-	Cracknore (90-91)	This Study
Scyphomedusae							
[B]*Aurelia aurita*	1.0[6]	120.4[6]	-	-	-	Mediterranean	Papathanassiou *et al.*, 1987
[B]*Aurelia aurita*	-	48-138[6]	-	-	-	Tokyo Bay, Japan	Omori *et al.* 1995
[B]*Aurelia aurita*	0.8[6]	47.3[6]	378	-	-	Kiel Bight, W.Baltic	Möller 1980b
[B]*Aurelia aurita*	1.5-2.2-1.91[6]	54.8-18.8-34.9[6]	-	-	-	Kiel Bight (82-83-84)	Schneider 1989c
[C]*Aurelia aurita*	1.1[7]	9-12[7]	~68-90	-	-	W.Wadden Sea	van der Veer & Oorthuysen 1985
[B]as above	0.6	6-12	~45-90	-	-	as above	as above
[B]*Aurelia aurita*	1.11	75.6	491	0.006-0.09	-	Horsea Lake	Lucas *et al. in press*
[B]*Aurelia aurita*	22.7[6]	351-450[6]	702-900[6]	0.08	-	Kertinge Nor, Denmark	Olesen *et al.* 1994
[C]*Aurelia aurita*	0.05	0.8	6.4	-	-	N.W.Netley, Southampton	This study (during 1993)
[B]as above	0.01	0.2	2	-	-	as above	as above
[C]*Aurelia aurita*	0.48	26.5	212	-	-	Cracknore, Southampton	This study (during 1993)
[B]as above	0.38	6.9	55	-	-	as above	as above
[C]*Aurelia aurita*	0.12	4.5	36	-	-	Bury Buoy, Southampton	This study (during 1993)
[B]as above	0.07	2.7	22	-	-	as above	as above

[B]*Cyanea capillata*	-	0.8-2.5	25-50	-	-	Baffin Island	McLaren 1969
[C]*Phyllorhiza punctata*	0.35[13]	18.3[13]	273.5[13]	-	-	Puerto Rico	García 1990
[B]as above	0.24[13]	14.1[13]	21.1[13]	-	-	as above	as above
Ctenophores							
[B]*Beroe ovata*	-	3.3-5	100	-	-	Baffin Island	McLaren 1969
[A]*Mnemiopsis mccradyi*	2.4	61-123	183-369	0.059-0.20	23-35[4]	Biscayne Bay, Florida	Reeve & Baker 1975
[B]as above	0.9	28-21	83-62	-	-	as above	as above
[B]*Mnemiopsis leidyi*	3[1]	44[8]	-	-	-	Narragansett Bay, R.I.	Kremer 1976
[B]*Mnemiopsis leidyi*	1.9[8]	53-99[8]	-	-	-	North Carolina	Miller 1974
[A]*Pleurobrachia bachei*	0.5[5]	11.7[5]	469.8[5]	0.2[3](mean)	-	California	Hirota 1974
[A]*Pleurobrachia bachei*	3.68	57.0 over 34days	-	0.35-0.57	-	Saanich Inlet[2]	Reeve & Walter 1976
[B]as above	0.88	7.50 over 34days	-	-	-	as above	as above
[B]*Pleurobrachia bachei*	0.28[12]	-	-	0.13	-	Scripps 70m^3 Deep tank	Mullin and Evans 1974
[B]*Pleurobrachia bachei*	0.6	2-6	-	0.07-0.14	7-20	British Columbia	Larson 1985
[A]*Pleurobrachia pileus*	<2.4	<90	<675	<0.26*	-	Dutch Wadden Sea	van der Veer and Sadée 1984
[D]*Pleurobrachia pileus*	0.0001-0.006	0.042-0.243	0.42-2.43	-	-	Greenland (90-91)	This study
[B]as above	0.007-0.017	0.31-0.80	3.1-8.0	0.03-0.18	-	as above (90-91)	as above
[D]*Pleurobrachia pileus*	0.004	0.515	4.12	-	-	N.W.Netley (91)	This study
[B]as above	0.12	2.56	25.6	0.11-0.18	-	as above (91)	as above
[D]*Pleurobrachia pileus*	0.017-0.012	0.489-0.827	3.9-6.6	-	-	Cracknore (90-91)	This study
[B]as above	0.10-0.24	2.29-5.22	18.3-41.8	0.065-0.25	-	as above (90-91)	as above
Chaetognaths							
[A]*Sagitta hispida*	1.4	244	732	0.20-0.41	109	Card Sound, Florida	Reeve and Baker 1975
[A]*Sagitta hispida*	1.4	584	1752	0.20-0.41	109	Biscayne Bay, Florida	Reeve and Walter 1975
[B]as above	0.48	14.5	43.5	-	-	as above	as above

[C]*Sagitta elegans*	0.24	8.6 over 106 dys	585 over 106 dys	0.0006-0.037	-	Bedford Basin, Canada	Zo 1969; 1973
[B]as above	0.44	8.3	563	-	-	as above	as above
[C]*Sagitta elegans*	-	82.8	2400	-	-	Bedford Basin, Canada	Sameoto 1973
[C]*Sagitta elegans*	-	4	200	-	2.0-2.1	St.Margaret's Bay, Canada	Sameoto 1971
[C]*Sagitta elegans*	0.35	1.6-10.6	49-318	-	1.0-2.1	Ogac Lake, Canada	McLaren 1969
[B]*Sagitta elegans*	-	31.5 over 33 dys	1100 over 33 dys	-	-	Long Island Sound, USA	Tiselius and Peterson 1986
Appendicularia							
Oikopleura sp.	-	97-219[9]	2902-6579[9]	-	-	Lime Cay, Jamaica	Clarke and Roff 1990
Oikopleura dioica	22.1	953	7150	-	-	Fukuyama Harbour, Japan	Uye and Ichino 1995
[B]as above	-	50	375	-	-	as above	as above
Fritillaria spp.	-	63-143[9]	1883-4298[9]	-	-	Lime Cay, Jamaica	Clarke and Roff 1990
Salpidae	-	21[11]	633[11]	-	-	Lime Cay, Jamaica	Clarke and Roff 1990
Pteropoda							
Creseis acicula	-	1.0[10]	29[10]	-	-	Lime Cay, Jamaica	Clarke and Roff 1990
Total gelatinous predators							
[B,C]Total gelatinous predators	-	8.5-24.3	231-731	-	-	Ogac Lake, Canada	McLaren 1969
[B]Total gelatinous predators	0.2[1]	6[1]	-	-	-	British Columbia, Canada	Huntley 1976
[B]Total gelatinous predators	0.6[1]	20[1]	1000[1]	-	-	British Columbia, Canada	Guest 1976
[B]Total gelatinous predators	0.5	5-10	150-400	0.01-0.2	9	British Columbia, Canada	Larson 1985
[B,C,D]Total gelatinous predators	-	0.6	6	-	-	Greenland	This Study
[B,C,D]Total gelatinous predators	-	1.4	11	-	-	N.W.Netley	This Study
[B,C,D]Total gelatinous predators	-	27.5	220	-	-	Cracknore	This Study

TABLE 5.4.9 Compilation of gelatinous and semi-gelatinous zooplankton production rates and P/B measurements obtained from the current literature and determined in the present investigation.

1 Calculated by Larson (1986b) from data in original work using 'Total biomass change' method. 2 $68m^3$ mesocosm experiment. 3 Misquoted by Reeve and Walter (1978), Alldredge (1984), Larson (1986). 4 Approximated from authors' data. 5 Calculated from authors' data assuming carbon to be 8.7% of AFDW (organic weight), and the mean water column depth to be 40 metres, all these estimates were made by application of natural mortality rates but growth rates at 15°C in laboratory with $35\mu gCl^{-1}$ prey. 6 Calculated from authors' data using 'Total biomass change' method (and appropriate conversions for carbon, ie.Carbon Weight = 4.3% of Dry Weight (from Larson, 1986a), Carbon Weight = 0.1204% of Wet Weight (combination of two factors Dry Weight = 2.8% of Wet Weight (mid-range figure from Hirst and Lucas *in prep.*) and Carbon Weight = 4.3% of Dry Weight (from Larson, 1986a)). 7 Recalculated from authors' data instead of assuming Carbon 8.4% of DW, assume Carbon 4.3% of DW (Larson, 1986). 8 Calculated from author's wet volume data, where 1ml live volume equals 0.958mgWW, DW is 4.43% WW, AFDW is 21.90% DW, and Carbon is 8.72% AFDW (All from Reeve and Baker, 1975). 9 Converted from kJ to carbon assuming 20.9kJ gDW^{-1}, (used originally by Clarke and Roff (1990) to convert DW to kJ), and assuming carbon to be 46.3% of DW (as determined by Uye (1982) for *Oikopleura dioica* in the Inland Sea of Japan). 10 Converted from kJ to carbon assuming 20.9kJ gDW^{-1} (used originally by Clarke and Roff (1990) to convert DW to kJ), and assuming carbon to be 23% of DW (mid-range from the results of Beers (1966) for Pteropods collected in the Sargasso Sea). 11 Converted from kJ to carbon assuming 19.6kJ gDW^{-1} (used originally by Clarke and Roff (1990) to convert DW to kJ), and assuming carbon to be 7.9% of DW (mid-range from the compiled results of Schneider (1989d)). 12 Estimated from their being 1.5gC of ctenophore harvested over a 75 day period. 13 Converted to AFDW assuming carbon to 2.46% (mean scyphomedusae value estimated from whole medusae values compiled by Larson, 1986a, Table III). 14 'Total biomass change' method applied for a cohortic population by removing initial egg weight from adult weights.

Methods:

A Laboratory growth rates applied to field data.

B 'Total biomass change' method.

C Identification of natural cohorts.

D Metabolic/physiological methods applied.

E Separation of population into cohorts and subsequent contained *in situ* incubation.

higher (on a per volume basis) than estimates of total gelatinous production in several other studies, although values may also commonly exceed this too (see Table 5.4.8). It is less for example, than the production of *Aurelia aurita* in Horsea Lake (Lucas *et al.*, *in press*). Comparisons are made more difficult as the methods applied have varied. When possible the 'Total biomass change' method has been applied to the original data to give a second absolute minimum (in the case of representative sampling and closed systems) estimate for comparison. As the table shows the methods may make remarkably large differences in the values produced.

Sameoto (1971, 1972) found that during winter in St. Margaret's Bay, Nova Scotia, *Sagitta elegans* biomass equalled that of the copepods, and that they consumed up to 50% of the winter's production of copepods, but only 0.7 to 1.1% or 2.2 to 3.3% of the total annual estimated yearly copepod production (depending upon calculation; see Sameoto 1973). Sameoto (1973) estimated that within Bedford Basin, *S.elegans* had an annual ingestion demand (including demand for respiration and production) of around 9,830mgC$m^{-2}yr^{-1}$ or 339gC$m^{-3}yr^{-1}$. While production was estimated at 2,400mgC$m^{-2}yr^{-1}$, or 82.8mgC$m^{-3}yr^{-1}$. Annual primary production in the Basin was given as 220gC$m^{-2}yr^{-1}$. As such production of *S.elegans* was 1.1% of primary production, and consumption was equivalent to 4.5% of the primary production. Sameoto (1973) attempted to estimate production and consumption of *S.elegans* in relation to the copepod population by assuming that the production of the copepods was 10% of primary production. As such production would be 11% of copepod production and consumption was estimated as 45% of copepod production. In coastal waters off Northumberland, Frid *et al.* (1994) estimated from gut contents, daily ration, and abundance, that *Sagitta* cropped a maximum of 0.04% of the copepod standing stock per day. In the same study they estimated that *Pleurobrachia* cropped a maximum of 0.06% per day, while the amphipod *Themisto* cropped a maximum of 0.84% of the biomass per day. Larson (1987) estimated that in Saanich Inlet, Canada, the medusae and ctenophores mostly cropped less than 1% of the mesozooplankton biomass per day (in the upper 25 metres), although in the upper 5 metres this increased to 5-10% of the biomass per day. Furthermore specific predation on *Euphausia pacifica* eggs and nauplii was much greater, with 10-40% of the stock cropped per day. Most literature rates give values between 5-20% of prey stock removed per day (Alldredge, 1984). Of course how important this cropping may be will depend upon the growth or input rates of the prey species. If prey growth rates exceed the cropping rates then the biomass of the prey may still increase. Kremer (1979) estimated that >1cm sized *Mnemiopsis leidyi* cropped maximally from 5 to 10% of *Acartia tonsa*'s standing stock daily (bay average) in Narragansett Bay, USA, although localized maxima could increase to 30%. Although these rates were substantial they were not sufficient to account for the summer decline in zooplankton. She noted that the observed decline in summer may not be exclusively the result of predatory

demands, as food limitation for herbivores could have occurred. Mean zooplankton removal rates by adults and larval ctenophores were subsequently estimated to be 20% per day, with localized maxima of 90% per day (Deason and Smayda, 1982a). Miller (1970) used water clearance rates in the laboratory to compute total water clearance rates for *M.leidyi* population of Pamlico River, USA. At the maximum biomass level for this ctenophore, clearance rate was estimated as being 48% of the copepod biomass per day. Values were generally much lower than this, and rarely exceeding 10% removal per day. When averaged over the year, Miller (1970) estimated that ctenophores could obtain only 23% of their energy requirements from zooplankton, which does of course lead to a questioning of the results.

Reeve and Walter (1976) found that *Pleurobrachia bachei* cleared a maximum of 3.6% of the water column per day in a mesocosm experiment in which at this same point production of *P.bachei* was estimated as being $3.68 mgCm^{-3}d^{-1}$. Reeve *et al.* (1978) estimated that the ctenophore population of Biscayne Bay, U.S.A., achieved maximum clearance rates of 62 to 99 litres $m^{-3}d^{-1}$ when biomass peaked (ie. 6.2 to 9.9% of the water column cleared per day). However throughout much of the year it was below 1%. Purcell (1982) examined the siphonophore *Muggiaea atlantica* and concluded that based upon gut content analysis and digestion time, along with prey abundance and data, that this species consumed 0.1 to 0.2% of the available prey copepods per day. While Parsons *et al.* (1969) reported growth of copepod production to be 6.5% of the standing stock during spring near the location examined by Purcell (1982).

In Link Port, eastern Florida, Larson (1987b) found that *in situ* clearance rates of *Mnemiopsis mccradyi* (5cm mean length) may be estimated as 2.4-31.2 litres $ind.^{-1}d^{-1}$. Laboratory measures of *Mnemiopsis* sp. clearance have been found to vary between 16.8-52.8 litres $ind.^{-1}$ d^{-1} (Larson, 1987b), for similarly sized individuals. Larson (1991) found that the scyphomedusa *Stomolophus meleagris* in NE Gulf of Mexico had estimated *in situ* clearance rates which ranged from <24 to 3240l $ind.^{-1}d^{-1}$ depending upon prey and medusa size. Unfortunately as no data were available on natural abundance of this predator and it was therefore not possible to estimate its predatory impact.

The compilation of production estimates in Table 5.4.8 gives an indication of the upper limits of daily and annual production by gelatinous zooplankton. In the present investigation the scyphozoan *Aurelia aurita* was estimated as having a gross growth efficiency of around 47% at Cracknore. Reeve *et al.* (1978) and Hirota (1974) found gross growth efficiencies which fell between 3 and 11% in the ctenophore *Pleurobrachia bachei* for laboratory kept individuals of

6mm length at various food concentrations. While they report gross growth efficiencies for *Mnemiopsis mccradyi* of between ~1.5 to ~6.5%, depending upon food concentration supplied. Kremer *et al.* (1980) however, found values for *M.mccradyi* to be as high as 40%. In chaetognaths a gross growth efficiency by *Sagitta hispida* has been reported to be maximally ~50%, this measurement being in the elemental terms of nitrogen rather than carbon (Reeve, 1970). These measures lead one to conclude that the annual production estimates of the cnidaria, chaetognaths and ctenophores given in Table 5.4.8 may probably be multiplied by at least two to give estimates of annual ingestion demands.

The aims of this work were not to produce a definitive work on the impact of gelatinous predators, and their impact within Southampton Water. Time was not sufficient to allow close examination and detailed quantification. The present investigation however, is an important step forward in the balancing of gelatinous demands against predatory sources. Not only are there problems in the present work regarding the host of assumptions which were made, or went relatively untested, but these problems are commonly encountered in the field of gelatinous zooplankton. General methodological problems and improvements have been suggested in the main body of this chapter. There are however fundamental problems which need to be highlighted as they are not only problems for this study but in this field of research generally. There are still significant inroads which need to be made regarding gelatinous production and the abundance and patchiness of their prey to allow achievement of a comprehensive understanding of energy-matter flux is to be achieved. To conclude this chapter it was therefore felt necessary that a brief statement of the direction which future work and improvements which should be next made be detailed in a 'Future Improvements' statement.

FUTURE IMPROVEMENTS

It is often the case that laboratory growth and fecundity rates measured in the laboratory are applied to natural abundances. Cohort methods are generally ideal, but rare in nature, whereas 'Total Biomass Change' methods would appear from this study to underestimate production tremendously. Attempts at estimating growth and clearance under more representative conditions therefore need be made. Artificial cohort work may prove fruitful with respect to growth rates.

Although there is a broad understanding of the prey of many gelatinous species, assessments of prey abundance in the field are often far from ideal. It is common for 200μm mesh nets to be used to assess the prey abundance, or to make bulk weight measurements from smaller mesh sizes. Baker (1973) for example collected zooplankton with a 200μm mesh net,

while Miller and Williams (1972) assessed zooplankton prey biomass through displacement volume of samples collected in a 370μm mesh net. Such large size meshes may seriously underestimate the abundance of prey, and bulk weights of finer mesh caught samples may be biased in some areas through contamination by living and non-living material which are not sources of energy-matter for the predator. Biomass of prey must be more thoroughly examined and also production rates of mesozooplankton (which have barely ever been examined) must simultaneously be more thoroughly assessed.

The role of advective process upon prey and predators must be examined with the aim of accounting for predator loss and the inputs of benthic larvae examined more thoroughly. Indeed an examination of predatory demands in non-closed systems is undertaken in the following chapter, which highlights some of these problems.

Body elemental weight of not only truly gelatinous but semi-gelatinous predators (see Sameoto, 1971) appear to differ remarkably between studies. Some of these differences are the result of investigator error (eg. Matsakis and Conover, 1991), while others may be attributable to salinity changes upon dry weight, and carbon conversions from dry weight at other salinities. Not all of these differences are attributable to salinity however. If the production of gelatinous zooplankton is to be assessed meaningfully in elemental terms, then more work is needed in the clarification of these weights or appropriate conversion. Using other carbon conversions which do not rely upon dry weight may still produce carbon values which differ between studies by more than 100%. The estimation of carbon biomass and production of course is linked to the accuracy of such weight:length equations. It would appear that estimates of gelatinous impact, when these rely upon such conversions, may in some cases be questioned at the ±100% level or greater. Until biomass quantification is cleared up then there will continue to be problems. Fortunately much of the ingestion and clearance rate literature has been conducted using methods in which the weight of the predator need not be known.

Allowance must be made not only for type of prey but size or stage of prey. If all predation were concentrated within particular ranges then the impact could be more severe than the ingestion would appear to suggest. There is evidence that *Pleurobrachia pileus* does not selectively prey more upon any specific copepodite sizes of *Acartia* than upon any other (Frid *et al.*, 1994), although *Clytia hemisphaerica* may be highly selective (Daan, 1989). In the present study ingestion demands were compared against total calanoid production, although prey have a production rate which exceeds that of gelatinous zooplankton the gelatinous zooplankton may cause the decline in abundance of prey through size selective predation.

In future studies of energy-matter flux of the gelatinous species within Southampton Water, there are several improvements which should be made to sample design. Firstly sampling should be conducted to allow for vertical heterogeneity. Diel vertical migration should also be assessed by sampling over a 24 hour period. In the present investigation day and night sampling would help in determining the abundance of *Pleurobrachia pileus*, as there is certainly a strong possibility that *P.pileus* populations have been consistently under sampled. Larger volumes of water, possibly several hundred cubic metres filtered would also help to overcome some of the patchiness problems, although efforts would have to be made to determine the amount of net clogging, particularly during algal blooms. Further measurements of prey growth (see Chapter 3), and estimates of production also need to be undertaken throughout Southampton Water. Estimates of clearance rates and daily rations need also to be conducted rather than relying upon some of the indirect methods as has been necessary in this work.

CHAPTER 6

PREDATORY DEMAND FOR ENERGY-MATTER IN A NON-CLOSED SYSTEM

6.1 INTRODUCTION

There are many problems associated with attempting to correctly construct and balance energy-matter budgets in marine systems. One major problem concerned with balancing such flows in estuarine and coastal areas is their non-closed nature. In completing the ingestion estimates of *Aurelia aurita* within Southampton Water, some problems were encountered by Lucas (1993) in balancing the energy-matter demands of these pelagic predators with the 'apparent' production of the pelagic mesozooplankton. Much of this discrepancy disappears after allowance is made for incorrect production estimation, and by making trophic level comparisons which are not biased by water of hydration. Indeed, in most cases gelatinous production and ingestion demands would appear to be generally very low in comparison to the 'pelagic production' of their mesozooplankton prey (see Chapter 5). At the Cracknore site within Southampton Water, where the highest ingestion demands of the gelatinous predators occur, preliminary calculations in this study would appear to suggest that the gelatinous predators have an ingestion demand which may exceed the production of prey over short periods. Including zooplankton missed by the typical sampling regime as a source of energy-matter would however reduce this apparent discrepancy. Ciliates are a potential source of energy-matter for *Aurelia aurita* (Stoecker *et al.*, 1987a), and within Southampton Water this group has a production of around 2 orders of magnitude greater than that of the calanoid copepods (see Chapter 8). The true importance of ciliates as a dietary item under natural conditions, particularly for *Aurelia aurita*, is still questionable (Båmstedt, 1988), and work in the previous chapter suggests they may be relatively unimportant. The aim of this chapter is to demonstrate other sources available to predators in this ecosystem, as well as in other similar systems. Benthic larval inputs and the lateral movement of prey have commonly been ignored or incorrectly accounted for, although these sources may be important in satisfying the demands of gelatinous predators in real systems.

When examining production in a marine area, for practical reasons it must be delimited. In the marine environment these limits may commonly be spatial, and include water column (pelagic) or non-water column (benthic). Such a division would appear a relatively intuitive

division to make. In addition to the great difference in many of the organism life histories, the techniques used to examine these two environments are very different. Delimited study areas are rarely closed systems however, rather the organisms may be open to exchange with other areas; the benthos, and through lateral exchange. Before introducing these two forms of movement, let us first highlight the problems associated with the 'traditional' definition of production when applied to non-closed systems. Production (P) in a closed system may be defined by:

$$P = (B_t - B_o) + B_e \qquad (1)$$

Where B_t is the biomass at time t

B_o is the biomass at time 0

and B_e is the gross biomass eliminated during the period 0 to t

This equation is used in the definition of production, and describes the accrual of biomass, regardless of its subsequent fate (Winberg *et al.*, 1971). Problems may arise if this equation is applied in certain non-closed systems, although not always. Difficulties do not arise for example if internal biomass is exported. This is because the equation allows for all losses, ie. is fate independent. Utilising the above equation in conditions of import however would result in error. Under these circumstances biomass may increase between sampling events without any individual growth, and therefore no 'real' production. Application of equation 1 to a system with biomass import would result in unrepresentative production estimation, ie. values which are contrary to both the definition and interpretation of production. A new equation to allow the definition of production to remain, even in non-closed systems, may be given as:

$$P = [(B_t - B_o) + B_e] - B_i \qquad (2)$$

Where production (P) is still biomass accrued regardless of its fate, but with compensation for the gross biomass imported (B_i) during the period 0 to t. For this study the definition of production has not been altered. What must be examined however, is that now the source of energy-matter available to a predator may be uncoupled from the rate of production, even in a steady-state system. Now we have a new equation to describe production in non-closed system, we can explore the production available to predators inhabiting them.

6.2 ALLOWING FOR BENTHIC-PELAGIC MOVEMENT

Energy-matter is commonly accepted as flowing to the benthic system from the pelagic

system, indeed benthos in offshore areas may rely entirely upon the pelagic system for its primary energy-matter inputs. The flow of energy-matter from the benthic environment to the pelagic environment however may also be significant. Many species, including fish and crustacea obtain their food through grazing on benthic animals. The output of meroplanktonic larvae from benthic organisms, and the numerical dominance of such larvae have been extensively noted in coastal and shallow areas, and represents another potential source for pelagic predators. The numbers and biomass of these transient larval individuals may greatly exceed that of the holoplankton (eg. in Biscayne Bay, Florida: Baker, 1973; in Southampton Water: Zinger, 1989). Meroplanktonic larvae at times will undoubtedly also have production rates which greatly exceed those of the holo-mesozooplankton, although actual measurements of *in situ* growth or production estimates appear to be virtually non-existent (although see Incze, 1984). The importance of various meroplankton as prey for planktonic gelatinous predators has been demonstrated in a multitude of studies of gut content and prey selection. Cirripede nauplii were found by Lucas (1993) to make up to 72% (by numbers) of the identifiable food items in the gut contents of *Aurelia aurita* from Southampton Water. The larvae of polychaetes, molluscs and decapods were also found to be numerically important, making up maximally 55%, 7% and 24% of the gut contents respectively. *Pleurobrachia pileus* collected from Southampton Water were found to have gut contents comprising up to 72% (by numbers) cirripede nauplii, and 11% polychaete larvae (Lucas, 1993). Gelatinous organisms collected from coastal areas have commonly been found to contain large numbers of meroplanktonic larvae in their guts. Olesen *et al.* (1995) found that *Aurelia aurita* from Kertinge Nor, Denmark, had gut contents including gastropod larvae, this group making up to 29% (by numbers) of the total. Larson (1987c) reported a variety of gelatinous predators within Saanich Inlet to contain meroplanktonic larvae, with 39% of the diet (by carbon mass) of the gelatinous predator *Proboscidactyla flavicirrata* to be veliger larvae. Walter (1976) found that barnacle nauplii were one of the dominant forms in the guts of *Mnemiopsis mccradyi* collected from Biscayne Bay. Rowe (1971) reported that *Pleurobrachia pileus* collected from Kaneohe Bay, Oahu, had gastric contents which were dominated by nauplii (predominantly barnacle), making up 47% of the total number of individuals, while crab zoea made up 7.6% and cyprid larvae 2.8%. Larson (1991) recorded that individuals of the scyphomedusa *Stomolophus meleagris*, taken from the N.E. Gulf of Mexico, had gut contents dominated by bivalve veligers, making up an estimated 47% of their total daily ration. Gastropod veligers were also important, contributing around 10% of the daily ration. Larson (1987b) found that *Mnemiopsis mccradyi* collected from Link Port, central Florida, had gut contents in which barnacle nauplii and bivalve veligers numerically made up 21% and 19% respectively. Other meroplanktonic larvae were also present, including brachyuran zoea, polychaete larvae and gastropod veligers. Deason and Smayda (1982b) reported that copepods, cladocerans and larval

annelids, molluscs and barnacles were frequently found in the stomodaeum of *Mnemiopsis leidyi*. *Mnemiopsis leidyi* were reported by Burrell and Van Engel (1976) to preferentially prey upon some meroplankton, with bivalve veligers, barnacle nauplii, and polychaete larvae being more abundant in their diet than in relation to the relative *in situ* densities of prey. Furthermore, Hirota (1974) recognised that *Pleurobrachia bachei* relied upon benthic produced larvae for its ingestion requirements in the region of La Jolla, coastal California.

Not only have meroplankton been found in the gastric cavities of gelatinous predators, but important impacts by gelatinous organisms upon these prey have also been found, this possibly being indicative of their role as an important source of energy-matter. Olesen *et al.* (1994) believed diurnally migrating epi-benthic harpacticoids could satisfy the short fall in the daytime measured food concentration, which was below those necessary to allow the *in situ* growth rates of *A.aurita* in a Danish fjord to continue, with their high abundance at night (20 fold increase in density compared with daytime values), and their increased abundance in stomachs of *A.aurita* over the same period. Greve (1971) found that the annual mass occurrence of *Pleurobrachia pileus* was coupled with pulses in copepod and larval meroplankton abundance in the German Bight. While Nelson (1925) observed *M.leidyi* to graze voraciously on bivalve larvae in Barnegat Bay, U.S.A., and described a close correlation between *Mnemiopsis* abundance and the intensity of oyster sets. In 1921 and 1922 heavy sets of *Ostrea*, *Teredo* and *Bankia* occurred when *Mnemiopsis* was rare or absent in the region. Hulsizer (1976) found that during a bloom of *Mnemiopsis leidyi* within Narragansett Bay, U.S.A., there was a substantial decline in both total zooplankton numbers, total zooplankton biomass, and also in the abundance of benthic larvae. Burrell's (1968) work on the significance of *M.leidyi* in York River Estuary, U.S.A., demonstrated that the number of copepods, annelid larvae, mollusc larvae, and barnacle nauplii varied inversely with the number of ctenophores present.

It is quite reasonable to expect that a predator may have an ingestion rate which is greater than the production rate of its prey, even when (as will be assumed in this study) un-assimilated egested matter is never re-ingested. However, a situation of ingestion exceeding production cannot continue for an indefinite period of time in a closed system, and in such circumstances the prey biomass must inevitably decline. What has apparently been left unexplored however, is that in a non-closed systems the ingestion demands of a predator may exceed the pelagic production of its planktonic prey for an indefinite period of time. When examining the functioning of a non-closed system, the demands of the predators within that system do not, and probably often are not, met internally by the system. Instead they may be dependent upon input into that system. In the case of Southampton Water the gelatinous predators

do not simply have to rely upon the planktonic production of their prey (ie. holoplanktonic production in addition to meroplanktonic pelagic production), as was apparently believed by Lucas (1993). Rather they may be dependent in part on the supply of 'new' biomass into the system in the form of the recruitment biomass of meroplanktonic larvae. This input term is correctly ascribed to the benthic system (reproductive) production. This point can be described with the following equations for a case where there is no lateral movement, the system is not vertically stratified, and the biomass of pelagic prey is not being reduced. Rather than stating that gelatinous ingestion demands cannot exceed planktonic prey production. ie.

$$I_{PRED} \leq (P_h + P_m) \qquad (3)$$

Where I_{PRED} is the ingestion demands of gelatinous predators (units of energy-matter per unit volume over a unit time)

P is the production of the prey component over the same unit of time; h represents that of holoplankton and m that of meroplankton (P definition given in equation 2 for systems with an import)

Instead the ingestion demands of the gelatinous predators cannot exceed the production of planktonic prey plus the gross input of benthic energy-matter (eg. benthic larvae), this can be given as:

$$I_{PRED} \leq [P_h + (P_m + B_{mi})] \qquad (4)$$

Where B_{mi} is the gross energy-matter input of meroplankton from the benthic system to the pelagic system over a unit time

Applying equation 2 this reduces to the from:

$$I_{PRED} \leq [P_h + (B_{mt} - B_{mo} + B_{me})] \qquad (5)$$

The production of holoplankton can be estimated through one of the common methods, where elimination including mortality or loss from the pelagic system may or may not need be estimated (Kimmerer, 1987). If the meroplankton population/s were cohortic, with instantaneous recruitment, then the rate of biomass increase and elimination could be followed simply through time, sampling over the appropriate time interval. However, this may not be the case, and under such circumstances a non-synchronous approach would have to be utilised. For this, instantaneous

growth could be estimated through one of the typical growth estimating methods including; growth/molting rate methods (Burkill and Kendall, 1982; Kimmerer and McKinnon, 1987; Peterson *et al.*, 1991), elemental ratio method (Le Borgne, 1977; 1978; 1982). One could also apply one of the growth rate estimation models (Ikeda and Motoda, 1978; Huntley and Lopez, 1992; see Chapter 4). In this case the biomass available from meroplankton could be solved through the measurement of their instantaneous growth multiplied by biomass (Kimmerer, 1987), and adding to this a rate of biomass input from the benthos into the de-limited area.

With this improved concept of energy-matter flow other important points are brought to light. If a predator removes a percentage of the total standing stock which exceeds the replacement rate through growth, then there is no reason to believe that prey standing stocks must decline, indeed with continuous input of benthic larvae it may increase.

Care should be taken in the construction of models of energy-matter flux in coastal and estuarine areas, as benthic reproductive production has been ignored in the construction of many past models. Examples of possible cases where the supply of energy-matter flow from the benthic system to the pelagic system has been incorrectly accounted for can be found in the literature. Baird and Ulanowicz (1993) compare the trophic structure of four tidal estuaries. In their construction of the energy-matter networks they include the production of benthic organisms and mesozooplankton, however, no direct link from the benthic organisms to the planktonic organisms is given, except via a non-living P.O.C. component and as grazing by fish. Mesozooplankton were shown as being fed upon by other mesozooplankton, invertebrate carnivores and fish, but there was no direct feeding link between living mesozooplankton and the benthic organisms. Jean and Thouzeau (1995) produced a model of carbon flux through the benthic community of the Bay of Brest. Although the model provided a supply of organic carbon from the pelagic system to the benthic system, no pathway by which benthic production may pass in the reverse direction, to the pelagic system, was included. Many studies fail to account for the fact that much of the meroplankton biomass may be consumed, and yet not be attributable to pelagic production. This recruitment biomass may form an important energy-matter source in the satisfying of pelagic predators. Although there appears to have been no previous estimates of this supply, it is possible to apply data from various sources in an attempt to complete such a calculation for Southampton Water. Soares (1958) estimated densities of staged barnacle nauplii within Southampton Water. The 4 most common species in this area; *Balanus balanoides*, *B.crenatus*, *B.improvisus* and *Elminius modestus*, have stage II carapace lengths which vary between 0.19 and 0.31mm (lengths taken from various sources: Bassindale, 1936; Pyefinch, 1948; Soares, 1958 and Geary, 1991, when only total length provided converted to carapace length

assuming it to be 60% of the total, this being a typical ratio in sources given). Applying the carapace length to carbon weight regression of White and Roman (1992) allows estimation of carbon weights for stage II individuals. Stage II individuals typically made up the vast majority of the total number of barnacle nauplii (Soares, 1958), therefore if there were no stage specific selection of barnacle nauplii by the gelatinous predators examined herein, then it is possible that the dominant fraction of the prey taken would generally be of this stage. Further, as the weight of this stage will be almost entirely 'recruitment' weight, then the greatest fraction of barnacle nauplii taken would appear to be benthic production. This would not be included for in pelagic prey production measurements if these simply included individual growth rates applied to *in situ* abundance (ie. as applied by Lucas, 1993). Using the length-weight conversions already detailed, stage II barnacle nauplii may weigh as much as 20% of stage VI nauplii, and as such, predation of even the last stage nauplii could be made up of a considerable proportion of benthic reproductive production. Lucas (1993) found that up to 72% (by numbers) of the gut content of *P.pileus* could be barnacle nauplii. Assuming these to be stage II *Elminius modestus* with a mean individual weight of 0.6μgC (estimated from sizes and length-weight regressions detailed above), and the other components in the gut to have a mean individual weight of 2μgC (typical late stage copepod weight), then it would appear that as much as 44% of the identified contents were of benthic reproductive production on this occasion. Lucas (1993) also found the maximum percentage of cirripede nauplii in the gut contents of *A.aurita* from Southampton Water was also 72%, so a similar percentage of benthic production could contribute to the gut contents in this instance also. Remarkably this may be the first approximation of the possible importance of benthic production to a gelatinous species. Although others have shown the relative importance of meroplankton through gut contents, no previous attempts have been made to estimate the proportion which is represented by the benthic produced weight of the larvae.

Determining the possible importance of meroplanktonic prey in satisfying the ingestion demands of gelatinous predators will be a reasonably simple step. A predators energy-matter demands have often been assessed through gut content analysis and digestion time to allow estimation of daily ration. This could be divided into that supplied by pelagic production and benthic reproductive production if input weights of meroplankton were known. The equation for daily ration (in carbon) supplied in total, from pelagic production and benthic reproductive production may be solved by the following equations. Total daily ration is given in the generally used form (see Larson, 1987d):

$$DR = \frac{GC \times 24}{DT} \qquad (6)$$

Where DR is the daily ration (μgC individual per day)

GC is the mean weight of the gut contents (μgC)

and DT is the digestion time (hours), ie. the time from ingestion to an empty gut

The daily ration supplied by pelagic produced biomass (DR_P) may be described as:

$$DR_P = \frac{(GC - GC_r) \times 24}{DT_h} \qquad (7)$$

Where GC is the total gut contents (μgC)

GC_r is the gut contents made up of the recruitment weights of the meroplanktonic larvae (μgC)

and DT_h is the digestion time of pelagic produced biomass (for practical reasons however, it may be impossible to separate the digestion of recruitment weights)

Finally, the daily ration supplied by benthic reproductive production (DR_R) may be estimated as:

$$DR_R = \frac{(GC_r) \times 24}{DT_m} \qquad (8)$$

Where DT_m is the digestion time of meroplankton in gut

In estimating the daily ration supplied by the benthic system it is assumed that there is no de-growth of the input biomass of each individual.

In the assessment of the impact of prey removal by a predator, removal rate are generally compared with the rate of prey production. In non-closed system with inputs in the form of benthic larvae this is more difficult to solve using typical sampling regimes. Input from the benthic system needs to be measured to take account of the affects of removal rates.

6.3 ALLOWING FOR LATERAL MOVEMENT

Van der Veer and Oorthuysen (1985), in their attempt to balance the carbon demands of

A.aurita and *P.pileus* in the western Wadden Sea, do not consider the possibility that the meroplankton, which are co-dominant along with copepods (Fransz, 1981), may be continually recruited from the benthic system, supplying gelatinous demands from outside the pelagic system. They do however suggest that zooplankton prey may be replenished continuously from the coastal (external) area where gelatinous predation is less. This brings us on to the next source of energy-matter in non-closed systems. Movements of plankton may not only occur vertically between the benthic and pelagic systems, but also horizontally through lateral water movements. Such movements can be particularly pronounced in tidal estuaries, and coastal regions. The lateral movements of prey should be considered in attempts to balance energy-matter demands of predators with supply by their prey. Lateral inputs of energy-matter may be incorporated into the previous definition of the limits to the ingestion demands of a predator as follows:

$$I_{PRED} \leq [(P_h + L_h) + (P_m + B_{mi} + L_m)] \quad (9)$$

Where L is the gross prey energy-matter imported laterally into the spatially delimited study area per unit volume per unit time

It should be noted that lateral export is already allowed for in the elimination of matter term, and therefore no extra term need be added for this.

It is well known that some species may maintain their geographical position in an area which is flushed, or where there are lateral movements of water. This of course clearly applies to benthic organisms, but may also apply to some organisms in the pelagos. The position of predator and their prey may change differentially with respect to one another through passive or active transport. Under such circumstances the predator is not limited to preying upon items typically defined as being within a de-limited study area/volume, rather it may take prey as they move through its apparent contained volume. Discriminating between biomass which is consumed by a predator which has been produced within a de-limited area, and that imported laterally would appear to be extremely difficult. Of course removal rate estimates made for predators still apply, however, assessing the impacts of these removal rates upon the size of the prey population, when the two move at differential rates, will be difficult. Solving such problems will involve study of physical and biological parameters, with reference to physical replacement rates.

Movements into and out of non-closed systems does not necessarily change the form of the ecological transfer efficiency (ETE) or utilisation efficiency (UE) equations if their definitions remain the same. Ecological transfer efficiency is a measure of the transfer of production of prey

(presumably within a defined de-limited volume/area) to predators in the same area, and utilisation efficiency is a ratio of ingestion by predator of prey to the production of the prey. The derivation of production for non-closed systems may be applied (equation 2). All inputs should therefore not be included as production, and simply applying instantaneous growth to biomass (Kimmerer, 1987) would allow prey production to be derived. A discrepancy does arise however, in that these efficiencies may theoretically exceed 100% when the system is non-closed (even when biomass of prey does not decline), and the predator takes prey which are imported. This is because predators may consume energy-matter which is not produced, rather which is imported and therefore not allowed for as a production term. The only possible way of overcoming such a problem would be to redefine transfer efficiencies to allow for imported biomass.

6.4 CONCLUSIONS

The described sources of energy-matter to planktonic predators, in the form of benthic inputs and lateral movements, need to be examined in much more detail in nature, to allow a fuller understanding if their implications are to be quantified and correctly assessed. The purpose of the present investigation was simply to demonstrate some of the potential problems, often ignored, in examining energy-matter flux in non-closed systems. The importance of benthic production to the natural diets of predators should be relatively easy to assess through existing gut content analysis and digestion time work, combined with measures of the known release rates of meroplankton. Assessing the percentage standing stock of meroplankton removed by predators may also be easy to determine through the usual methods, measuring prey concentrations and prey-specific removal rates. The importance of benthic reproductive production to predators may be fairly simple to estimate. What may be more effort demanding in its assessment, is the effects which predator removal rates will have upon mero- holo-planktonic prey densities when inputs are particularly pronounced. The true impact of a predator on its prey, in terms of their control of prey density and biomass, may only be able to be fully appreciated once the cross-boundary movements are taken account of.

CHAPTER 7

EXTENDING THE THEORETICAL ANALYSIS OF ENERGY-MATTER RECYCLING

7.1 INTRODUCTION TO PRODUCTION RECYCLING

Important developments in our understanding of food web structure and functioning have been made over the last few years. In the first part of this chapter a model of production recycling, with particular respect to defining the limits to the production of a heterotrophic species, is presented. This model departs from the most recent model of energy-matter recycling in that the number of times energy-matter is recycled is an integral part of the production estimation. In a previous model by Higashi *et al.* (1993) it was assumed that once a recycling loop was in place recycling must continue by mathematical abstraction to infinity, this is questioned in the second section of this chapter 'Compartmentalization and its implications to production and energy-matter recycling'. The new model and the subsequent rationale behind its development bring to light important points regarding real food webs, particularly over-simplification of systems, and their theoretical interpretation.

Production recycling is the process whereby energy-matter which was incorporated into a trophic compartment (compartment being, for example, a species population or other de-limited group in a food web) leaves that compartment, or an individual in that compartment, and eventually via other compartments, or directly, re-enters and becomes once again incorporated (ie. becomes body tissue within the compartment once again). Recycling of energy-matter has important implications to the way that ecosystem design and function are viewed, affecting traditional 'trophic level' definitions and the complexity of systems, and also implications to the ingestion demands and production which heterotrophs may have. In attempting to model food webs Pimm (1982) set limits to random food webs which were generated using what were termed 'biologically reasonable constraints', with the objective of ensuring that 'patently absurd webs are eliminated'. Included within the biologically reasonable constraints were those that prohibited loops of the kind sp.A eats sp.B eats sp.C eats sp.A, and loops of the kind sp.A eats sp.A (cannibalism). The reasoning behind these exclusions were that 'loops of these kinds are rare in the real world'. Other theoreticians of food webs have often dismissed loops as 'unreasonable structures' (Gallopin, 1972; Cohen, 1978; Pimm, 1982; May, 1983; Cohen *et al.*, 1990; as given

in Polis, 1991). While such loops may be uncommon, they may also often be overlooked (Polis, 1991), usually as a result of oversimplification or study constraints. One of the major recycling pathways is likely to be the result of cannibalistic activity, which is a regularly observed phenomenon. It has been reported to occur in a great number of fresh water and marine copepods including; *Cyclops bicuspidatus thomasi* (McQueen, 1969), *Rhincalanus nasutus* (Mullin and Brooks, 1967), *Labidocera trispinosa* (Landry, 1978b), *Acartia clausi* (Landry, 1978a; Ayukai, 1986), *Oithona nana* (Lampitt, 1979), *Acartia tonsa* (Lonsdale *et al.*, 1979; Heinle, 1970), *Tortanus discaudatus* (Mullin, 1979), *Centropages furcatus* (Paffenhöfer and Knowles, 1980), *Centropages abdominalis* (as reported in Liang *et al.*, 1994), *Calanus pacificus* (Landry, 1981), *Oithona davisae* (Uchima and Hirano, 1986), *Temora longicornis* (Daan *et al.*, 1988) and *Sinocalanus tenellus* (Hada and Uye, 1991). Furthermore, it may be an important source of energy-matter; Heinle (1970) found 20 to 60% mortality per day in the first 9 stages of *Acartia tonsa* in laboratory cultures, and suggested 'cannibalism to act as a mechanism for regulating populations where (alternative) food is scarce and densities of populations are high'. Others have also suggested that cannibalism in copepod populations may have a strong impact upon survival rates (Liang and Uye, 1996). McQueen (1969) found that copepodites IV, V and adults of *Cyclops bicuspidatus thomasi* were estimated to have consumed 31% of the nauplii stock in Marion Lake in the summer of 1967 through cannibalism. Cannibalism has been shown to be advantageous to cyclopoid copepods, both in environments which are constant (Gabriel and Lampert, 1985) and also in environments with fluctuating food conditions (Gabriel, 1985).

Intra-specific feeding may be an important energy-matter source for other pelagic predators, and has commonly been observed in many species of *Sagitta* (Feigenbaum and Maris, 1984). *Sagitta setosa* (Rakusa-Suszczewski, 1969; Øresland, 1987), *Sagitta elegans* (Tungate, 1975; Pearre, 1981; Frid *et al.*, 1994) and *Sagitta hispida* (Reeve, 1966) have all been shown to be cannibalistic, with 'self-feeding' at times playing an important role in structuring populations (Pearre, 1981; Øresland, 1987). Øresland (1987) reported that cannibalism by *S.setosa* in the Gullmarsfjorden could result in a sharp decline in numbers during autumn. Polis (1981) discussed the evolution and dynamics of intra-specific predation, and described cannibalism as being 'a significant and widespread process...The nutritional benefits of cannibalism may be large, and in many species conspecifics are one of the most frequent prey items. When prey species are ranked by weight or volume, conspecific may represent an important food source'. Polis (1981) reviewed over 900 papers describing such intra-specific predation in over 1,300 species. Citing other works Polis (1981) stated that a large proportion of either the entire population or a vulnerable age class may be eaten, often in a short time: eg. 31-50% of copepod nauplii (Landry, 1978; McQueen, 1969), >80% of all prawns (Forster, 1970), 30-75% of dragonfly nymphs in eight days (Fischer,

1960), >50% of first instar *Notonecta* (Fox, 1975a), 80-90% of two species of bass fry in 11-14 days (DeAngelis *et. al.*, 1979; Rhodes *et. al.*, 1973), >90% of *Anabis* fish in 60 days (Banerji *et. al.*, 1975), 23-46% of herring gull chicks and eggs (Parsons, 1971), >90% of crow chicks and eggs (Yom-Tov, 1974). Furthermore, in a review of cannibalism in natural populations, Fox (1975b) described cannibalism as being a normal phenomenon in many natural populations, one which is not confined to highly stressed populations, but is a normal response to many environmental factors. Where intra-specific predation makes up a considerable proportion of the diet of a component of a population, then a large part of their measured production will be made up of recycled production. Loops of the form sp A eats sp A, can occur not only as a result of cannibalism but also as a result of any activity which causes a species to feed directly upon dead material resulting from its own production. When cannibalism occurs, or when a species (e.g. a detritivore) feeds upon non-living material derived directly from that species population, for example; moulted exoskeletons, organic secretions, or dead individuals, then there will effectively be only one transfer stage in the recycling loop. As such, the overall efficiency of transfer will be much greater than when several feeding stages are passed through in the loop. Since the material ingested in the intra-specific loop may generally be of a similar biochemical composition to the consumers or its body products, the tissue growth efficiency in utilising such material may be higher. It is also possible that such material may be ingested with greater efficiency as a result of spatial and temporal proximity of the predator and prey. Although cannibalism is not always size dependent, it very often is, with smaller individuals being taken by larger individuals (Gabriel, 1985). This brings an important point to light. If a compartment is constructed at the species level then production recycling in this compartment will show discrimination between the first time it is recycled and possible subsequent recycling event, this would appear to directly contradict the model of recycling produced by Higashi *et al.* (1993).

Production recycling loops of the type sp.A eats sp.B eats sp A may also occur, and may often be a result of ontogenetic changes in diet in relation to age and/or size. For example, Sheader and Evans (1975) found that fish larvae (mainly *Clupea harengus*) composed around 20% of the diet of the amphipod *Themisto compressa*. Previously, Hardy (1924) had found that *T. compressa* formed around 18% of the annual diet of *Clupea harengus* off the North East Coast of England. The herring and amphipod generate a recycling loop within the pelagic food web of the area. Force (1974) also gives an example of a production recycling loop in the trophic structure of an insect community. He examined a system where the midge *Rhopalomyia californica* (Diptera: Cecidomyiidae) was parasitised by a variety of wasp species (Hymenoptera). Of these parasitizing species *Amblymercus* fed on *Zatropis*, and vice-versa, thus forming a production recycling loop. The young of *Sagitta hispida* have been found to be taken by

copepods such a *Acartia* (Reeve, 1966), while the adults of this chaetognath take this copepod species. In a very extensive analysis of trophic relationships in the desert system of Coachella Valley, Polis (1991) found that recycling was a common feature. It would appear that when studies extend beyond superficiality, recycling loops are commonly discovered. Once again recycling loops which do not involve cannibalism are often dependent upon size or age structure within real populations, and if a compartment is defined at the species level then the concepts of Higashi *et al.* (1993) that once production has been recycled once it will continue to be recycled, without discrimination as to the number of recycling events, would appear to be violated.

Not only may energy-matter be recycled back to a species population via other species but also in part via a non-living component ie. through dead organic matter. Such material may consist of dead particulate organic or dissolved organic matter. Those species in which food comprises dead particulate or dissolved forms are likely candidates in which production recycling may be important. Such systems are often also the most complex where loops may have often been ignored. Heal and MacLean (1975) recognized that, 'Two or more less distinct trophic systems exist in virtually all ecosystems - a herbivore system based on living autotrophic tissue, and a saprovore system based on dead organic matter'. Similar divisions may also occur in freshwater and marine environments. Heal and MacLean (1975) showed how the two systems are separated by a stage through which the material passes from a herbivore system to a saprovore system in the form of dead organic matter. However, some species are not only detritivorous but are also biophagic (ie. they feed on both dead and also living items of food), and in the marine systems metazoan grazing of the microbial loop may be significant (Turner and Roff, 1993). This complicates the simple system discussed, and could result in recycled production contributing to the productivity of species which would not traditionally be considered as part of the saprovore system. In Scavia's (1988) schematic diagram of carbon flow through a lake community, organic carbon would appear to be recycled through bacteria, micrograzers, as well as through the larger consumer organisms in the plant-herbivore-carnivore chain, via an organic carbon pool.

It is frequently stated or inferred that the carbon demand and secondary production of heterotrophic consumers within an ecosystem cannot exceed the organic inputs to that system (e.g. Scavia and Laird, 1987). However, in an important work on the limits to secondary production, Strayer (1988) demonstrated that both the summed carbon demand (ie. assimilation) and the summed production of consumers may both greatly exceed the original organic input to a closed system.

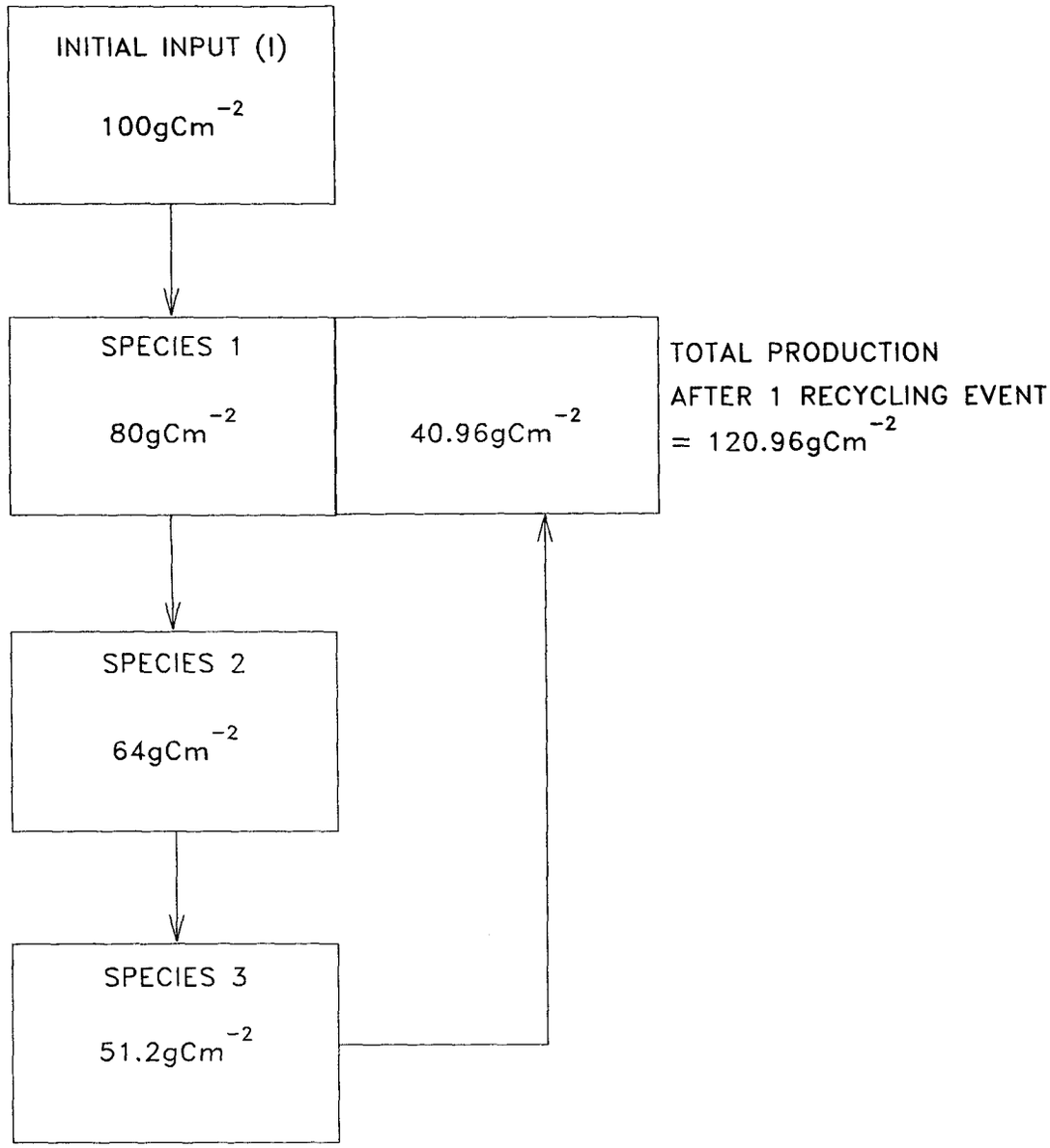


FIGURE 7.1.1 The transfer of energy–matter between successive species populations in a food chain. Species 1 occupies a position on the the 1st and 4th trophic level. Trophic level production efficincies are assumed to be 80% at each level. As a result of the recycling of energy–matter the secondary production of Species 1 is greater than the input (I).

The summed respiration of consumers in a steady state closed system cannot exceed the autotrophic inputs. This work focused on defining the limits to the overall secondary production of a system where material passed from trophic level to trophic level, continuing to the point where the organic material was completely utilized or lost. The purpose of the present study is to further extend our understanding of the limits of secondary production, but with reference to single heterotrophic species populations, rather than entire heterotrophic food chains.

Because organic material may be recycled through food chains (Heal and MacLean, 1975; Rigler, 1975; Polis, 1991), an apparent paradox arises in that not only may the summed carbon demand and the summed production of all the consumers within an ecosystem exceed the organic input, but also the carbon demand and the production of a single species population may exceed the organic input to that system, which is contrary to the situation inferred by Odum (1971). A hypothetical example which demonstrates the effect that organic material recycling may have upon the secondary production of a species population is illustrated in Figure 7.1.1. In the example given, Species 1 occupies two positions (trophic levels) in a single food chain, and organic carbon passes through the same species population more than once. Species 1 has a production of $121 gCm^{-2}yr^{-1}$, which is greater than the original organic input ($100 gCm^{-2}yr^{-1}$), showing that in theory the secondary production may exceed the organic input. If this is so, then we need also to appreciate what the limits to secondary production of a species population are.

It is possible for a species to occupy many trophic levels simultaneously, and in systems where feeding loops occur, trophic distinctions become blurred and the complexity of even simple food webs are greatly increased. In this example organic carbon has been recycled back to Species 1 only once, with a termination in the passage of organic carbon at this point. In the natural environment it is possible that when such recycling events take place termination may or may not occur at this point. An organic carbon molecule could pass through such a cycle repeatedly, and be included in a species' production many times before being lost from the system, being respired, or becoming unavailable for further recycling. Although this example is hypothetical, and uses a remarkably high ecological efficiency value of 80%, it nevertheless demonstrate the importance which carbon recycling may have on the production of heterotrophic species. For species populations in ecosystems where organic material is not readily lost, where the efficiency of transfer between feeding levels in the recycling loop is high, and/or where the material recycles many times, production values will be very much increased as a result of the recycled component.

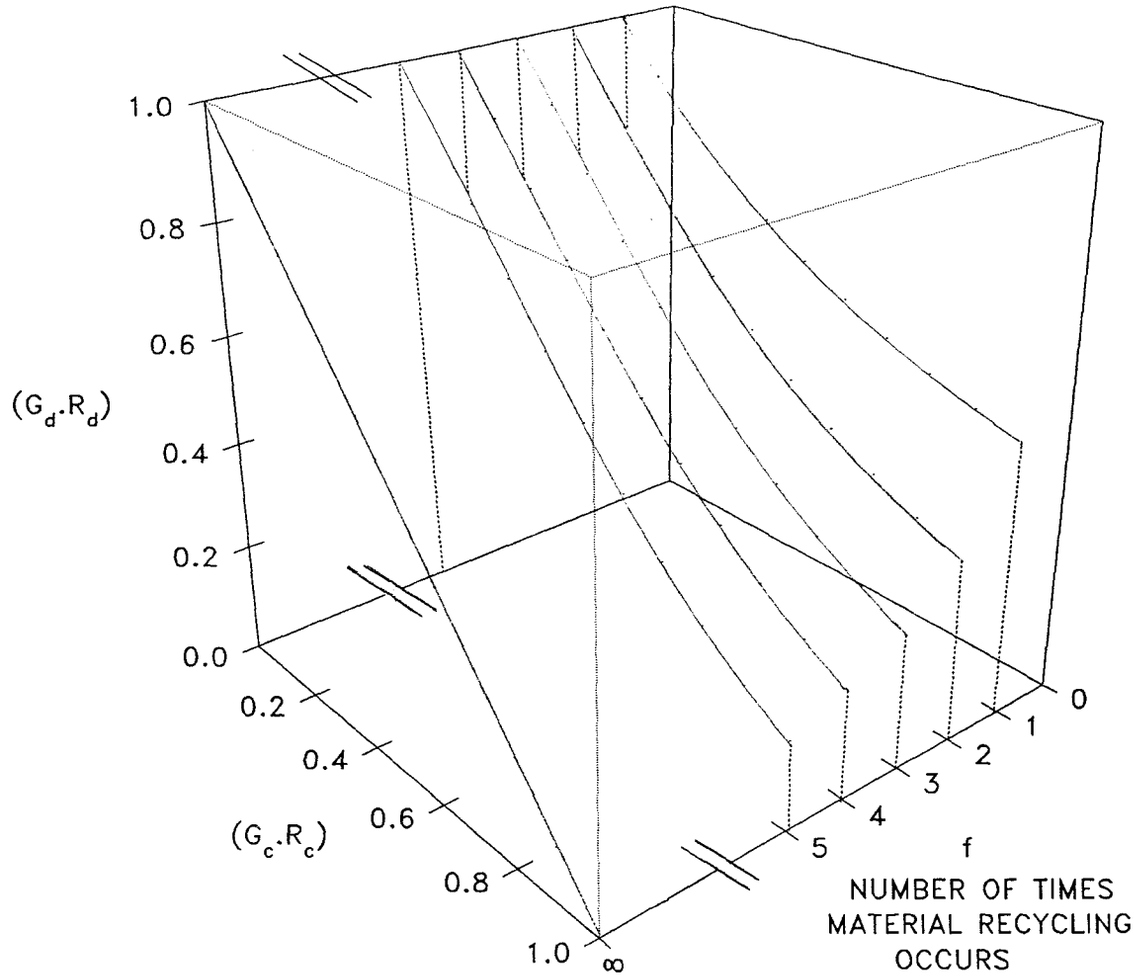
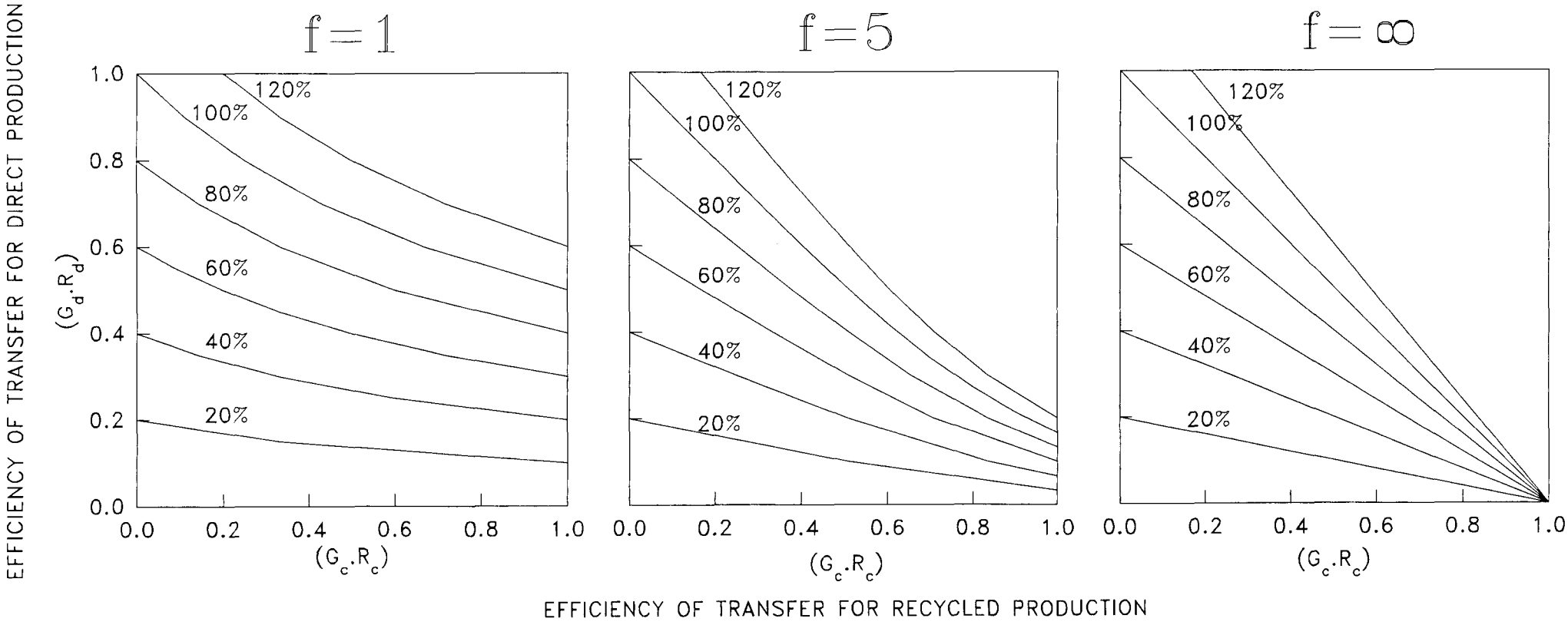


FIGURE 7.1.2 Demonstration of the values of efficiency of transfer, for both direct production ($G_d.R_d$) and recycled production ($G_c.R_c$), and the number of times which material is recycled (f), which give production values for a species population equal to the initial input term (I).



7.1.3 The secondary production of a species population as a percentage of the inital input (I), for the range of possible values for Direct and Recycled transfer, where recycling occurs once (f=1), five (f=5) and an infinite number of times (f=oo).

The total secondary production (P) of a species population occupying a feeding level (n), may be calculated from the organic energy inputs (I) to the system and the efficiencies at which this organic material is transferred between successive feeding levels. The energy-matter inputs do not necessarily represent the net primary production of the community, and may not have been produced within the ecosystem in question (e.g. deep-sea communities may obtain all their organic inputs from external sources). For the purposes of this model it may be useful to examine small sections of a larger food web and define the input (I) as being the production of a prey item. The production of a higher order consumer/predator may then be calculated in the following way. The transfer efficiencies which will determine the overall secondary production of a species are not only those involved in the transfer of organic energy from the input source to the species, but also the efficiency at which the material is recycled back to the species. The efficiency of transfer of production from one feeding level to the next is defined as:

$$EFFICIENCY\ OF\ TRANSFER = \frac{P_t}{P_{t-1}} = R_t.G_t \qquad (1)$$

Where P_t is the production at feeding level t, and P_{t-1} is the production at the preceding feeding level (t-1). The efficiency of transfer can also be calculated from the 2 components R and G. R_t is a measure of the retentiveness and usage of the material as it passes from being the production at one level (in this case t-1) to form the assimilated matter on the next (level t), and is demonstrated in equation 2. This utilization measure takes into account all non-respiratory losses of organic matter as material passes from being production at one feeding level to being assimilated on the next. This term includes material lost from the community, and all organic matter which is not utilized as assimilation on the next feeding level for whatever reason:

$$UTILIZATION\ EFFICIENCY\ (R_t) = \frac{A_t}{P_{t-1}} \qquad (2)$$

Where A_t is the amount of material assimilated on level t. The second component, the tissue growth efficiency G_t given in equation 3, is a measure of the efficiency with which material upon assimilation becomes production within the species, this takes into account metabolic demands, and is defined by:

$$TISSUE\ GROWTH\ EFFICIENCY\ (G_t) = \frac{P_t}{A_t} \qquad (3)$$

R_tG_t is therefore a measure of the exact proportion of the production passing from one species

population in an ecosystem to the species population at the next feeding level. An R_tG_t value of 0.1 for example represents a 10% transferal of production from level t-1 into level t. The direct production of a single species population may be calculated from the energy-matter input (I), and the efficiencies of transfer of this input to the species (Direct production, P_D):

$$P_D = [(I \times (G_1R_1) \times ..(G_nR_n)] \quad (4)$$

In this equation, n is the feeding level on which a species population is situated relative to the input source (the input occupying level 0). The amount of production due to the first recycling loop (P_1) is:

$$P_1 = P_D \times [(G_{n+1}R_{n+1}) \times ..(G_{n+r}R_{n+r})] \quad (5)$$

and subsequent loops:

$$P_2 = P_1 \times [(G_{r+1}R_{r+1}) \times ..(G_{r+r2}R_{r+r2})] \quad (6)$$

Where r is the number of trophic transfer stages in first recycling loop (for example if the production recycling loop were a result of cannibalistic activities then r would equal 1), and r2 is the number in the second recycling loop etc. Thus total production is:

$$P_n = [\ P_D\ ] + [\ P_1 + P_2 + P_3 + ... + P_f\ ] \quad (7)$$

Where f is the number of times material passes through recycling loops. These equation applies to linear feeding chains and simple loops, but could be adapted for use with more complex feeding webs.

Furthermore if the term G_dR_d is defined as the overall efficiency at which organic matter passes from the input (I) to the species population of interest (in the Direct Production food chain), and the term G_cR_c as the overall efficiency at which material passes through the feeding loop (the Recycled Production food chain) on each discrete cycle, assuming it does so with the same efficiency on each occasion, then the production of a species population may be explored with respect to the number of times that material recycles (f) before termination. Figure 7.1.2

demonstrates the values of (G_dR_d) and (G_cR_c), necessary for the production of a heterotrophic species population to equal the initial input for various values of *f*. Even when the efficiencies of transfer of organic matter from the input source to a species population is low, if the efficiency of material recycling is high, and if the recycling event occurs several times then production of a single species may be very high (possibly larger than the input). Figure 7.1.3 shows a range of production values (as a percentage of input) for a species population, calculated for a range of possible values of (G_dR_d) and (G_cR_c), for the cases where recycling occurs one, five, and an infinite number of times (*f* = 1, 5, and oo).

The production P of a species occupying feeding level n is greater than the total organic carbon input (I) when:

$$1 + [\ (G_cR_c)^1 + (G_cR_c)^2 + ...(G_cR_c)^f\ ] > \frac{1}{(G_dR_d)} \qquad (8)$$

The absolute upper limit to production of a single species population will effectively be determined not only by the efficiency of transfer of material from the input source to the species population, but also by the number of times the organic material is recycled and the efficiency at which this recycled transfer of material occurs. If no recycling occurs then the efficiency at which material is transferred to the species population from the input source will determine the upper limit of production of a species population (ie. maximum possible production will occur when G_dR_d is 1, and the secondary production of the species would be equal to I). If recycling occurs once then the maximum upper limit for production will be 2I, if it occurs twice then the maximum upper limit will be 3I and so on. Calow's (1977) best possible conversion efficiencies for organisms are ignored in these upper limit estimations. The maximum possible production of a species population (P_{max}) as a percentage of the input, can be calculated as follows;

$$P_{max} = 100 \times (f+1) \qquad (9)$$

It is important to note that if a predatory species preys solely upon a species which has elevated production as a result of a recycling process, then if the predator is not itself involved in a separate recycling loop or in the recycling loop of the species upon which it preys, then the maximum potential production which it could ever show would be equal to the 'Direct Production' value of its prey species (assuming 100% transfer efficiency). This has implications in the analysis of production transfer efficiencies between two species.

Material recycling loops maintain energy within a population, and there is theoretical evidence to suggest that cannibalism may have an advantage to the predator and the prey (Bobisud, 1976). The intention of this argument is not to propose that recycled production is quantitatively important in all ecosystem types, but to draw attention to this process and to the probability that recycling may be particularly important in certain systems or in parts of some ecosystems. This major diversion from previous examinations of energy-matter recycling by Higashi *et al.* (1993) is that in this model the number of time energy-matter is recycled is an integral part of the calculation. The reasons that the inclusion of this argument was necessary and the problems associated with understanding recycling processes are brought to light in the following section.

7.2 COMPARTMENTALIZATION AND ITS IMPLICATIONS TO PRODUCTION AND ENERGY-MATTER RECYCLING

The implications of the compartmentalization of ecosystem is examined with respect to the process of energy-matter flow, compartment production and recycling. In examinations of real systems the identification and definition of compartments is of fundamental importance to the results produced, and also their subsequent interpretation and analysis. The theoretical descriptions of how energy-matter flows through natural systems has to some extent developed at such a rate as to leave the measuring of such processes behind. Indeed disparity between system descriptions derived from theoretical analysis of under studied, over-simplified, food webs, and those from real complex unsimplified systems may be extremely common (Polis, 1991). In the present study one of the gaps which has developed between theoretical modelling and the examination of natural systems is explored. Demonstrating that the decisions of compartment identification and separation are extremely important, and that models of energy-matter recycling (as already given in the previous section) should accommodate the idea that termination of recycling even in steady-state models is necessary, and does not continue to infinity by mathematical formulation as previously suggested (Higashi *et al.*, 1993).

In an important and major development of understanding energy-matter flow through food networks, Higashi *et al.* (1993) identified and examined two distinct modes and corresponding pathways of energy-matter utilization. Their work further developed the idea that the trophic structures of real ecosystems may not simply be linear and of the classic 'food chain type', but may be of a more complex network nature, with accompanying non-linear cyclical flows of energy-matter. Such non-linear flows have been increasingly recognised and examined in real systems (Polis, 1991). It is the aim of the present work not to diminish the importance of the

work of Higashi *et al.* (1993), rather to highlight that the marriage of the theoretical face of tropho-dynamics with practical and field measurements of energy-matter flow through ecosystems is as yet far from complete and many problems have yet to be resolved. Problems specifically associated to compartmentalization and its effect on production and energy-matter recycling in continuous time models of food networks are examined here, and these have been then extended with regard to concepts of energy movements through studies of real systems.

As Rigler (1975) makes clear, ecosystems are generally far too complex to be able to quantify or predict the behaviour of each and every component, in fact, we can neither describe nor recognize every component. To make the system examinable it must be simplified, this is done in the case of energy-matter flow by creating groupings or compartments. These compartments are extremely important as they reflect the way in which the behaviour of the system is eventually understood or described. Compartments defined for the purpose of energy-matter examination may incorporate living and / or non-living components. The smallest compartment taken in descriptions of the pathways of energy-matter could be at a sub-individual level (ie. separate body compartments etc.), an array of compartment types and sizes may occur from this level up through species specific age-class groups, individual species populations ie. fish species[b], feeding types/activity ie. grazing zooplankton[a], carnivorous zooplankton[a], mucus net feeders[a], heterotrophic microflagellates[b], invertebrate predators[a], suspension feeders[b], crustacean deposit feeders[b] (a Burns *et al.*, 1991 after Pace *et al.*, 1984: b Baird and Ulanowicz, 1989), as well as into feeding guilds.

Trophic compartments are also defined on the basis of the size of the individuals in an ecosystem ie. meio-benthos[a], macro-benthos[a], meio-fauna[b], micro-zooplankton[b]. The microzooplankton component of Baird and Ulanowicz (1989) for example (defined as 20-200μm in size) includes taxa as diverse as tintinnid ciliates, rotifers, sarcodinians, and copepod nauplii stages. Classification also occurs on the basis of habitat types such as pelagic, benthic, infauna, epifauna, particle associated, free-living etc. (separation of this form including; pelagic bacteria (free and/or attached)[ab], benthic bacteria[a], planktonic protozoa[a], pelagic fish[a], demersal fish[a], planktonic protozoa[a]). 'Food-web segments' have also been used (Szyrmer and Ulanowicz, 1987; originally from Tilly, 1968), these dividing the system into blocks of autotrophic plants, detritus, bacteria, detritus feeders and carnivores, this divisioning being justified on the basis '...that the analysis of populations, tedious and cumbersome as it is, would have been too detailed; whereas limiting the study to a trophic chain would have deleted some important information'. The sampling or sorting methodologies used in examinations are typically size or habitat type specific. The lowest compartment resolution could encompass the entire ecosystem, examples which are

highly simplistic where two compartments occur (heterotrophic consumers and autotrophic producers) are in evidence in the literature.

Workers have therefore divided their ecosystem components on the basis of a great variety of stated or unstated reasons. The important question 'At what level should compartment boundaries for examination of tropho-dynamics and energy-matter flow be drawn?' has not been answered. Further, the resolution to this question has varied dramatically between individual studies and workers. It is common for the level of grouping or classification to vary considerably even within single individual ecosystem models, ie. Ulanowicz, (1984) includes an example taken from Homer and Kemp (unpublished manuscript), which details carbon flow through a marsh ecosystem, Crystal River. Within this model many single species of fish are included, yet also a single compartment entitled 'zooplankton' is also included. Do fish act as homogenous trophic units at the species level, while zooplankton function, and are acted upon, as a single homogenous unit? Large metazoan organisms may be compartmentalized at the species level generally with less effort than smaller or taxonomically more difficult groups such as the ciliates and microbial components. The intertidal oyster reef community described by Dame and Patten (1981) have a microbiota and meiofauna compartments, these two diverse feeding types being grouped at this level because 'little if any detailed information is available on their relations'. Often since energy-matter flow studies involve great amounts of time and effort complete models have been produced which assimilate the information from many workers collected at very different points in time. This leads to compartment definition being commonly of different taxonomic, size, and diversity of form or function resolution within single or compiled studies.

One of the more favoured units for compartment identification and isolation must be that of the species population, ie. a single identified species within the area of study, although it is common for this not to be the case. Indeed cannibalism has always been regarded as somewhat of a separate and special type of feeding. However, individual compartments in tropho-dynamic investigations have not always been so restrictive and compartments may be composed of whole suites of organism types, sizes and/or feeding guilds (eg. filter feeders, deposited detritus, microbiota, meiofauna, deposit feeders and predators are the compartments within the oyster reef food web model of Dame and Patten, 1981) as well as non-living components. Compartments which contain more than a single species are certainly the norm, rather than the exception, with resolution of measurements often being restricted by time, effort, or present understanding constraints.

The problems with compartment definition and the artifacts it may create have not gone

without examination. Polis (1991) comments that most analysis upon empirical food webs has been conducted on webs which are totally unsuitable for this purpose, with inadequate representation of species diversity, dietary information, age structure and looping (including recycling). Concern has previously been expressed about whole system analysis and how robust conclusions remain in the face of changes in the level of system aggregation (Pahl-Wostl and Ulanowicz, 1993). Baird and Ulanowicz (1989) point out that 'In interpreting the importance of recycle in a system one should constantly bear in mind that the perceived amount of recycle tends to rise as the degree of aggregation increases'. In a group 'other polychaetes' they attribute the high recycling of energy-matter back to this compartment as purely a consequence of scale of aggregation, and so appreciate that energy-matter is more likely to pass back to a compartment, in this case as a result of detritus feeding, the larger the compartment construct. Compartments however may also have direct internal movements not resulting from detritus feeding, as well as re-introduction via other compartments or detritus feeding. As a compartment's boundaries are enlarged the probability of energy-matter re-introduction and internal self-feeding may increase.

Higashi *et al.* (1993) do not clearly define what a compartment may consist of, although they imply that the terms 'chain of compartments' and 'trophic levels' are equivalent, and that transfer of food between trophic levels requires assimilation. Their only apparent factor which determines a compartment as a single unit is that, if material passes back to it once, the cycle established is one in which energy matter will continue to travel around (it is not recognized as being any different on its first passage than on its second third fourth etc..) to the point where it is lost from the system or completely utilized. Thus by mathematical abstraction the formulation of number of recycling times is extended to infinity. Such compartment definition is however unworkable. Indeed their definition has never been used in decisions regarding compartmentalization of real systems (and not even in the examples which they utilised), as such confusion may arise. The infinite cycle types are not the most applicable to investigations of carbon flow through real systems, infinite recycling is however the basis of flow analysis. Other workers have also misinterpreted cycles in a similar way to Higashi *et al.* (1993), in the sense that they must run to infinity. Braner (1985) states that 'If there are cycles, there are also, in principal, an infinity of level (*Meaning trophic transfer levels*)'. Let us be clear on this point, all recycling loops come about as a result of compartment definition, the definition of the compartment being inextricably linked to the loop itself, and the number of times material is recycled may vary depending upon the level of compartmentalization.

Recycling may be the result of internal movements within a defined compartment or

movements of energy-matter externally and subsequent re-introduction back into the compartment of origin. In abstractions of real systems both of these processes may be cyclical, in the sense that they will continue indefinitely, or acyclical, in that they will not continue indefinitely. Higashi *et al.* (1993) state 'Whether the energy is first passage or recycled, and its age distribution within and between these two categories, are irrelevant to the receiving organism'. This however is not the case in compartments which arise in real studies. First passage and reincorporated (recycled) material may be segregated because of the apparently hidden structure of compartments constructed for real systems. Compartments are not an undifferentiable mix of energy-matter receivers, but have internal structure. Although studies frequently ignore potentially important internal structure, this may not be justified. If there has been a lack of data produced on the subject of recycling, then there is an even greater lack of information on recycling loops with regard to segregation within compartments.

Virtual amplification, the phenomenon where compartments further from a source of energy-matter may receive more of this energy-matter than those closer, can simply be the result of compartment definition. In the following hypothetical examples energy-matter is passed from an initial compartment (always terms a), when these groups belong to a single species they are given the same identifier (ie. b, c and d). For simplicity, all trophic transfers in the initial model (ie. in part i), prior to grouping at the species level (ie. in parts ii an iii), have been set at 90%. Figure 7.2.1 demonstrates the importance of the compartmentalization of a single food network. Model 7.2.1 i demonstrates the flow from a feeding source (a), with a production of 100, into three theoretical groups, all of which belong to the same species (ie. b'). Individuals in compartment b3 however, cannibalize those in compartment b2, which in turn cannibalize those in compartment b1. It is evident from model 7.2.1 i that energy-matter passes non-cyclically between all the instar compartments, however if the compartment boundaries are re-grouped at the species level (see Figure 7.2.1 model ii and iii), then production in compartment b' becomes greater than production in compartment a, and recycling must be occurring. Although at the sub-species level (Figure 7.2.1 i) there is no production recycling between components, at the species level there is recycling (energy-matter passing into compartment ii is utilised more than once). However, this recycling occurs a finite number of times in Figure 7.2.1 (iii), and does not go to infinity by mathematical formulation as derived by Higashi *et al.* (1993).

Figure 7.2.1 clearly shows that when compartments are constructed there may be internal structures in terms of the energy-matter pathways. Such internal structure may occur even at the species level.

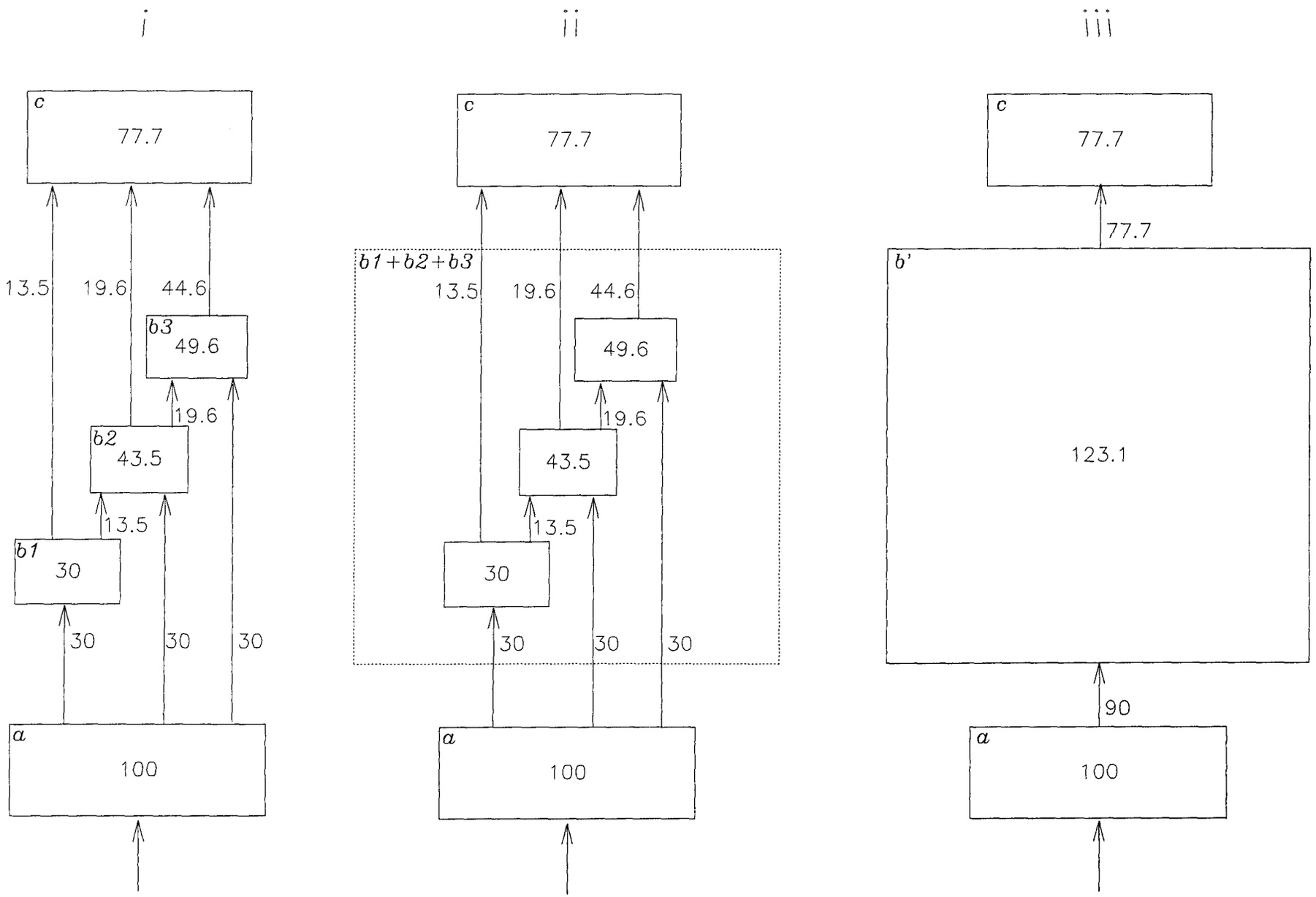


FIGURE 7.2.1 Comparisons of food web models at different levels of aggregation, and resulting production for each compartment at each level. i. Unaggregated model of production, ii. New aggregation boundaries, iii. New model of aggregated production.

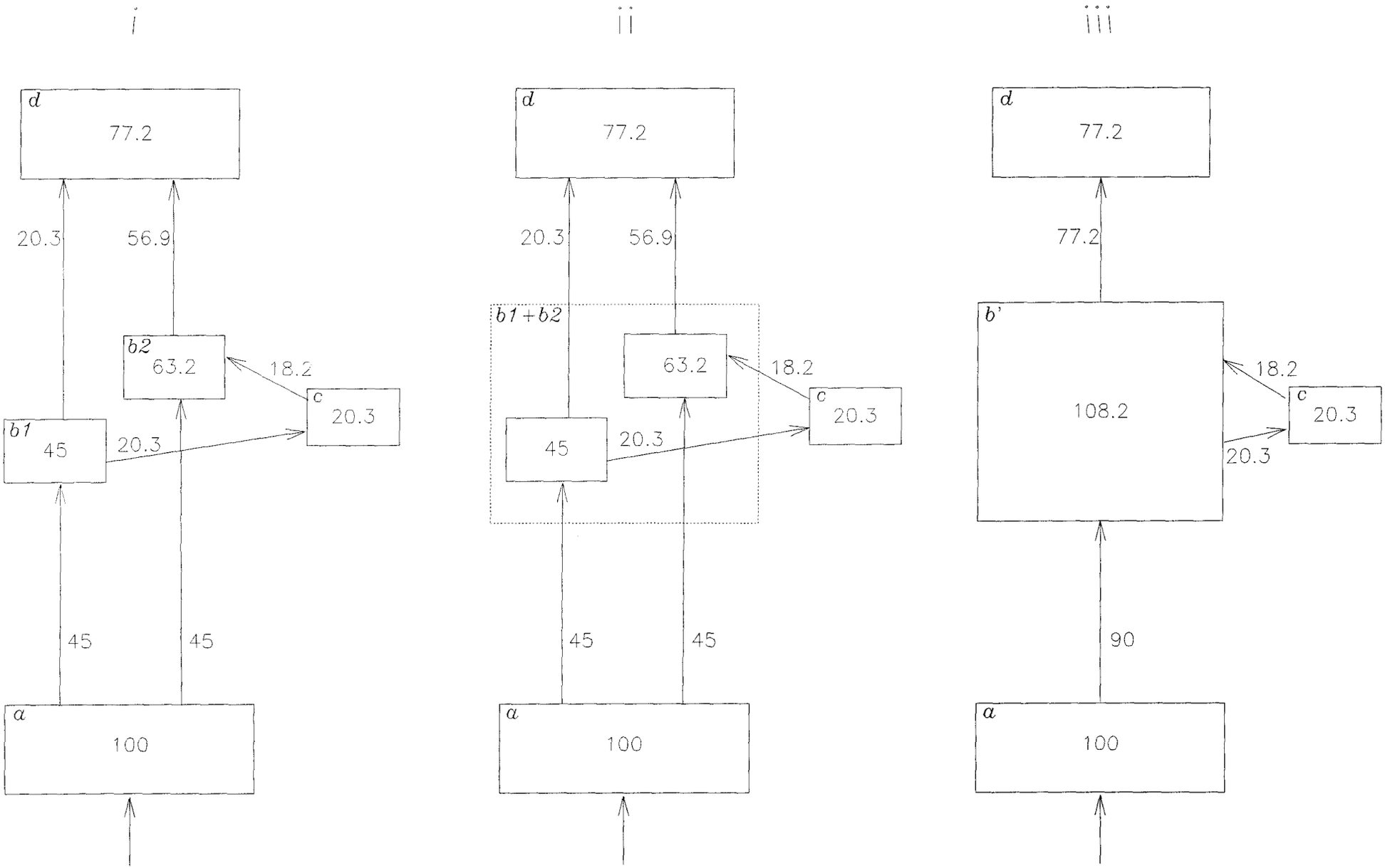


FIGURE 7.2.2 Comparisons of food web models at different levels of aggregation, and resulting production for each compartment at each level. i. Unaggregated model of production, ii. New aggregation boundaries, iii. New model of aggregated production.

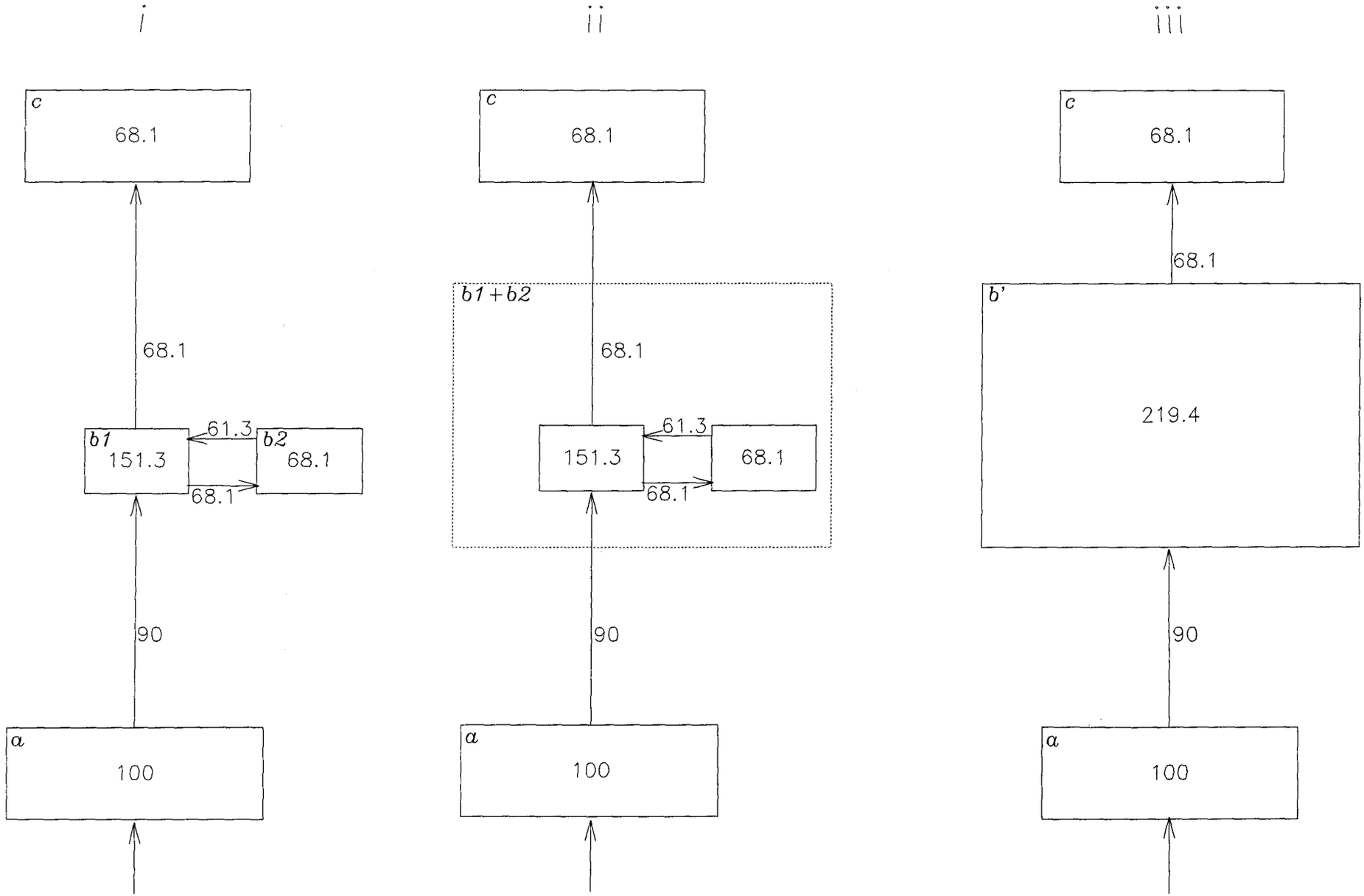


FIGURE 7.2.3 Comparisons of food web models at different levels of aggregation, and resulting production for each compartment at each level. i. Unaggregated model of production, ii. New aggregation boundaries, iii. New model of aggregation production.

If individual compartments are taken to consist of single species populations there is internal heterogeneity in processing and functions, age or stage or size classes of species may take different food articles, have different predators and may be differently cannibalistic. Such selection differences are well documented, particularly qualitatively although often not quantitatively. In fact each individual within a single age group or cohort may show different preferences. Cannibalism is an important and common process in natural systems, and is predominately the result of the feeding activity of large individuals on smaller individuals, for example the predation of later instar stages of crustaceans on younger stages or inter-cohort feeding in teleost fishes. At one level of aggregation there may be production recycling or virtual amplification, while at another there is none. Thus cyclical paths are determined by the very divisioning of the system and not simply by the pathways of energy and matter themselves.

An important assumption that Higashi *et al.* (1993) make is that energy-matter passes out of a compartment, and is then cycled, upon re-entry into a compartment on the first cycle it is not separate and will continue to recycle. The second example (see Figure 7.2.2) demonstrates a case where energy-matter is passed out of a species population, enters a second compartment and then is returned to this first. When compartments are enlarged (ii), this leads to the apparent identification of a cycle, however the energy-matter passing through such a cycle is discriminated and separated on the first and second time it enters. Although production recycling is measurable at the macro-compartment level it will be of a non-infinite cycle type, thus conflicting once again with the ideas of Higashi *et al.* (1993). Acyclical paths may become apparently cyclical by the process of compartment redefinition, and these recycling processes do not continue indefinitely. The process of the creation of apparent recycling loops is demonstrated in Figure 7.2.2. In this example energy-matter is transferred from compartment b1 to b2 via compartment c. If the two compartments b1 and b2 are merged then a loop is produced. However, once again this loop violates the rule that once energy-matter is recycled back to a compartment then it will continue to cycle. In this case cycling terminates after one return. Figure 7.2.2 iii demonstrates how the production after merging results in a compartment which shows virtual amplification, this being the result of compartment merging. When the compartment b and d consume an amount of c this material can only be first time cyclical.

Example 7.2.3 demonstrates a case where production recycling occurs between the two compartments b1 and b2, this being cyclical and continuing to infinity with energy-matter not being separated after its first loop. However, upon merging compartments b1 and b2 the resultant energy-matter model (Figure 7.2.3 iii) would give an unclear account of the actual recycling processes.

Three categories of paths and flow were identified by Higashi *et al.* (1993), namely:

1. First passage, acyclical.

2. First passage, with medial cycles.

3. Subsequent passage, recycling.

The present investigation has however, clearly demonstrated that in real systems which have been compartmentalized it is possible that cycles occur which take material back to a compartment where re-utilization within the compartment occurs, however this cycle may be terminated at this point and not continue *ad infinitum*, thus terminating apparently prematurely. The returning of energy-matter to a compartment after previously being part of it may therefore continue to cycle through this same pathway as discussed by Higashi *et al.*, (1993), or it may then pass along another cyclical or acyclical pathway and will not necessarily return. The third category in the list (3. Subsequent passage, recycling), may therefore be divided into two:

3a. True Cycling, in which energy-matter is re-routed back to a defined compartment. The established cycle continuing with no segregation or separation on each subsequent cycle. This is defined by the equations given in Higashi *et al.* (1993).

Alternatively;

3b. Artificial Cycling, in which energy-matter is re-routed back to a defined compartment. However, the energy-matter is segregated and differentiated from energy-matter passing out into the cycle. This type of cycling could be shown to be non-cyclical with greater resolution of the compartment. The equations given by Higashi *et al.* (1993) do not apply, but those given in the previous section of this Chapter do.

In most systems if resolution of compartments were to be at the individual level, then only very rarely would true cycles (given as 3a above) occur. Higashi *et al.* (1993) stress that no distinction as to prior history (first passage versus subsequent passage) is carried to destination compartments. There is however a problem in that if their equations are to be applied to real systems, then such systems should preferably also be divided into compartments which function in this same way. However, given the resolution of the compartment in real studies first passage and subsequent passage energy-matter may be actively distinguished and the equations describing energy-matter flow in cycles as could include finite integers, and not as processes which run infinitely. Higashi *et al.* (1993) state that they 'expect that, with further detailed study, most if not all of the compiled food webs (Briand and Cohen, 1987; Sugihara *et al.*, 1989) would show significant energy-matter cycling'. They go further by defining 'significant' in that without the

cycling pathways, one or more of the participating organisms could not exist at the observed population abundances. If this is the case then it is possible, and highly probable, that the cycling of energy determines both quantitatively and qualitatively the structure and dynamics of ecosystems. In the present investigation it has been shown that the structuring of an ecosystem into compartment units may quantitatively and qualitatively affect the apparent importance of energy-matter recycling. As such their statement could be equivalent to the statement 'there are linear energy-matter pathways in food webs which are obviously significant and whose detail would be lost and become apparent cyclical pathways upon further study including 'traditional' compartmentalization would appear as cyclical, thus over-emphasizing the importance of energy-matter recycling. Furthermore, without these linear pathways one or more of the participating organisms could not exist at the observed population abundances'. The detail of linearity is lost is the result of the compartment boundaries established. In a simple system with autotrophs, herbivores and carnivores, if the herbivores and carnivore were aggregated into a single compartment then indeed apparently cyclical (although not necessarily infinitely cyclical) pathways would be 'significant' as defined by Higashi *et al.* (1993). It is important to note that if we wish to compare recycling in different ecosystems there must be some form of standardization of the compartments. Thus when we compare systems with recycling with those without recycling it must not be forgotten that those 'without' could be transposed into those 'with' by redefinition or enlargement of compartment boundaries, or vice-versa.

Ecologists study the relationships of organisms with one another and with their non-living environment (Ulanowicz, 1984). In the quantification of energy-matter flow however, it has often been the case that compartment definition has not been made to allow a thorough description of flow, rather ecologists may have failed by emphasizing taxa rather than interactions. This is contradictory to the suggestion of Ulanowicz (1984) that the network flow analysis approach is eminently ecological in nature, with the focus being on interaction rather than upon the taxa themselves. The lack of ability to address a problem does not cancel its existence; the problems highlighted in this paper must be considered. Although we may be unable to unravel all of the complexities of energy flow in real systems, this does not mean that they can be ignored.

Trophic networks are much more complex than traditionally recognized. Even so the contemporary work on energy-matter recycling still has many problems, which have yet to be fully appreciated and resolved. Detritus for example, should not be regarded as an homogenous unit, rather it may be divisible into components which are acted upon very differently. Ulanowicz (1983) states that 'Because of the high cost of gathering data on all the flows occurring in an ecosystem, extremely few networks with more than 10 nodes [compartments] have been fully

quantified'. Although this situation is improving there are still obviously many problems to overcome. These problems must be overcome. Production recycling is a particularly important topic with regard to marine copepods and the 'finite loop hypothesis' is much more applicable under circumstances of cannibalism. This work examined food webs under steady-state conditions however, most real systems are far from such. In real systems there may be strong shifts in food web structure with time, and periods of localized extinction of some components. Non steady-state conditions of these types may once result in the termination of cyclical pathways. Once again therefore 'Finite loops' detailed herein may be most applicable.

CHAPTER 8

TOWARDS A BIOLOGICAL MODEL OF ZOOPLANKTON PRODUCTION AND ENERGY FLOW IN SOUTHAMPTON WATER

8.1 INTRODUCTION

The metazoan mesozooplankton component of Southampton Water has been examined previously by several workers including Raymont and Carrie (1964), Zinger (1989) and Lucas (1993). Other important components of the plankton have also been examined in this area in previous years. Workers have focused on phytoplankton (Savage, 1965,1967; Bryan, 1979; Iriarte, 1991; Kifle, 1992; Iriarte and Purdie, 1994), cyanobacteria (Iriarte, 1991), bacteria (Diwan, 1977; Antai, 1989), heterotrophic nanoflagellates (Antai, 1989) and ciliates (Burkill, 1978; 1982; Leakey, 1989). The abundance and population dynamics of benthic sub-tidal and inter-tidal macrofauna have also been studied in some detail (Hibbert, 1975; Oyenekan, 1981). Although some of these studies include production estimates of particular components, many do not. Those with relevant information on carbon flow have been incorporated where possible into the present chapter to allow the construction of a compartment model of annual carbon flux through many of the dominant components. Some of the studies which do incorporate production or ingestion demands have had to be altered where the techniques and methodologies utilised were inappropriate. Some of these alterations have already been detailed (eg. as in Chapter 6), while the remainder are examined in this chapter before their inclusion into models of carbon flux for two sites Calshot and N.W.Netley. Calshot at the mouth of the estuary and N.W.Netley in the central main body of the estuary.

8.2 PRODUCTION BY AUTOTROPHIC ALGAE

In their construction of a carbon flow box model for Southampton Water, Leakey *et al.* (1992) divided the production of phytoplankton in Southampton Water into two fractions, the production by algae >10μm and the production by algae <10μm. Many of the ciliates encountered within Southampton Water are <30μm in diameter, the production of algal cells >10μm in diameter would therefore have been largely unavailable for direct grazing by the ciliate population (Leakey *et al.*, 1992). The algae >10μm will however be the fraction predominantly available through direct grazing to the dominant metazoans, in particular the copepods and

cirripede larvae. Copepodites are classically believed to have a feeding size threshold of 5-10μm, below which they may not efficiently utilise prey items (Berggreen *et al.*, 1988; Clarke and Roff, 1990). Harris *et al.* (1982) demonstrated that different copepod species and stages compete for the same 10 to 40μm particles, whereas smaller cells (<10μm) seemed relatively unimportant in copepod diets. Daan (1989) also found evidence of declining survival of nauplii to copepodite and adults when diatoms (>10μm in size) declined in number and flagellates (<10μm in size) increased. The lower limits of capture may be below 10μm, eg. *Acartia tonsa* nauplii and *Pseudodiaptomus marinus* nauplii and copepodites may capture particles of 2-4μm (Uye and Kasahara, 1983; Berggreen *et al.*, 1988). Similarly *Calanus pacificus* nauplii and copepodites capture particles down to 4-11μm (Fernandez, 1979), *A.tonsa* and *Paracalanus parvus* females capture particles as small as 1-4 (Bartram, 1981), and *Diaptomus sicilis* females capture particles down to 3-4μm (Vanderploeg *et al.*, 1984). However, the total copepod population demands met by particles <10μm will generally be small in comparison to those made on the fraction >10μm. Working with natural samples taken from Southampton Water, Barlow and Monteiro (1979) found that the dominant size fractions grazed by copepods and cirripede nauplii were between 6 to 31μm (median diameter). The separation into size fractions chosen in this study ie. >10μm grazed by mesozooplankton and <10μm grazed by ciliates, should be fairly representative of the actual situation. With respect to these upper sizes commonly grazed by metazoans, Leakey *et al.* (1992) found that 63-100% of the total chlorophyll was in the <50μm fraction, and in most cases there was no significant difference between the <50μm fraction and the total. The >10μm fraction should therefore be dominated by algae within the size ranges grazed by copepods and cirripedes within Southampton Water.

Estimates of primary production have been made most recently for 1990 by Iriarte and Purdie (1994) over an annual cycle at the two sites N.W.Netley and Calshot Spit Buoy. In this work *in situ* rates of primary production were estimated using the ^{14}C technique (Steemann-Nielsen, 1952) in conjunction with on-deck incubations of typically 4 hours duration. These results were converted to daily rates by measuring photosynthesis at various screened light levels and using estimates of the daily irradiance experienced.

Primary production rates were estimated directly from chlorophyll a concentrations by Leakey *et al.* (1992) using a conversion factor of 39.8 mgC mgChl a^{-1} d^{-1}, this factor was determined from data collected in Southampton Water between February 1974 and March 1975 by Bryan (1979). The <10μm phytoplankton fraction has been found to account for 61% of the total algal biomass in Southampton Water on average (Leakey *et al.*, 1992); indeed in the same work this percentage was used to divide primary production between these two size fractions.

The figure of 39% of primary production by the >10μm fraction differs from the partitioning of primary production rates reported by Kifle (1992), where 66-67% of the total annual primary production was in the >10μm fraction at both Calshot and N.W.Netley. Care should be taken in fractionating primary production through the utilisation of relative biomass proportions, as smaller plankton may typically have differing rates of growth. Primary production rates have therefore been re-estimated from the totals given by Leakey *et al.* (1992), by assuming the portion of primary production in the size fraction >10μm was 66.5% of the total (see Table 8.2.1). The total rates of primary production as given by Iriarte and Purdie (1994), and estimated from data collected during the 14 month abundance program (see Chapter 2), were also both divided using this ratios.

The estimates of primary production made by Iriarte and Purdie (1994) are only 21 and 11% of the values reported by Leakey *et al.* (1992) at the Calshot and N.W.Netley sites respectively. Inter-annual variation in chlorophyll a concentrations may certainly play a role in these differences, although the method used by Leakey *et al.* (1992) typically also gives greater rates of primary production for each unit of chlorophyll a. To give an example, a concentration of chlorophyll a of $5mgm^{-3}$ would give a primary production estimate of $1.08gCm^{-2}d^{-1}$ utilising the equation derived from the data of Iriarte and Purdie (1994) (see Chapter 2). This chlorophyll a concentration however, gives an estimated rate of primary production of $1.59gCm^{-2}d^{-1}$ utilising the method of Leakey *et al.* (1992). The chlorophyll a levels found during 1986-1987 by Leakey *et al.* (1992) reached 27 mgm^{-3} at Calshot and $74mgm^{-3}$ at N.W.Netley. The highest chlorophyll levels reported by Iriarte and Purdie (1994) however, were 9.9 and $9.7mgm^{-3}$ at Calshot and N.W.Netley respectively. No corrections have been made in th present study to the total annual estimates of Leakey *et al.* (1992), although fractionation of primary production has been altered utilising the ratio already described.

Estimates of primary production have been derived from the chlorophyll a concentrations collected during the 14 month abundance programme (see Chapter 2). This method gives annual primary production estimates of 50.38 and $40.29gCm^{-3}yr^{-1}$ at N.W.Netley and Calshot respectively. The values of Iriarte and Purdie (1994) are 32% and 44% of those for 1993 at Calshot and N.W.Netley respectively, but again, chlorophyll a is typically greater during this year (1993) than those reported in Iriarte and Purdie (1994). There are therefore three annual estimates available for primary production for Calshot and N.W.Netley, these have been combined into annual averages before inclusion into the compartment model in this chapter. The averages for Calshot are $25.35gCm^{-3}yr^{-1}$ and $12.77gCm^{-3}yr^{-1}$ in the >10μm and <10μm fractions respectively, while at N.W.Netley they are $61.95gCm^{-3}yr^{-1}$ and $31.21gCm^{-3}yr^{-1}$.

YEAR	FRACTION	CALSHOT $gCm^{-3}yr^{-1}$ (% OF TOTAL)	N.W.NETLEY $gCm^{-3}yr^{-1}$ (% OF TOTAL)	SOURCE
1990	TOTAL[a]	13.05 (100)	22.09 (100)	Iriarte and Purdie (1994)
	>3μm	10.81 (82.8)	17.83 (80.7)	
	1-3μm	1.42 (10.9)	2.89 (13.1)	
	<1μm	0.82 (6.3)	1.37 (6.2)	
	>10μm[b]	8.68 (66.5)	14.69 (66.5)	
	<10μm[b]	4.37 (33.5)	7.40 (33.5)	
1986-1987	TOTAL	61.00 (100)	207.00 (100)	Leakey *et al.* (1992)
	>10μm[b]	40.57 (66.5)	137.66 (66.5)	
	<10μm[b]	20.44 (33.5)	69.35 (33.5)	
1993	TOTAL	40.29 (100)	50.38 (100)	This study
	>10μm[b]	26.79 (66.5)	33.50 (66.5)	
	<10μm[b]	13.50 (33.5)	16.88 (33.5)	

TABLE 8.2.1 Fractionated and unfractionated annual primary production estimates at each of the permanent sites.

a Primary production measured for given size fractions, total estimated by simply summing size fractionated rates.

b Size fractionated primary production estimated applying percentage contributions given in Kifle (1991).

Table 8.2.1 details the estimates utilised to determine these annual averages.

8.3 THE TRANSFER OF ENERGY THROUGH THE PLANKTONIC MICROBIAL POPULATION

Planktonic ciliates dominate the microzooplankton in many different marine environments (Smetacek, 1981; Revelante and Gilmartin, 1983,1987). Furthermore, they are considered to be important consumers of nanoplanktonic algae (Fenchel, 1987), while the smaller aloricate forms are significant grazers of bacterial production. Recently they have been described as important food sources for large metazoan predators, including calanoid copepods. Indeed, selection of ciliates in preference to algae has been observed in the estuarine copepod *Acartia* sp. (Stoecker and Sanders, 1985; Stoecker and Egloff, 1987; Stoecker and Capuzzo, 1990). Small aloricate ciliates may also constitute a valuable, high quality food resource for juvenile macrozooplankton (Stoecker and Egloff, 1987). Ciliates may therefore be of some importance in the diet of larger zooplankters as a supplement to other food sources, and as a significant link to the highly productive microbial community. In this section the work of Leakey *et al.* (1992) is used to quantify the energy flux through this component of the plankton of Southampton Water. Where it is felt necessary, and when it is believed to increase the accuracy of a food-web model, re-analysis has been undertaken.

Leakey *et al.* (1992) made a total of 13 estimates of the daily potential ciliate production rate at the Calshot and N.W. Netley sites between June 1986 and June 1987. The ciliate component included in their estimates of production comprised the tintinnid and aloricate forms, *Mesodinium rubrum* was not included and is therefore not included in the re-analyzed data set presented here. In their study, ciliates were quantitatively enumerated and the lengths and diameters of cells measured. Cell volumes were then estimated through equating the shapes of each taxa to a geometric configuration. Carbon standing stock was estimated assuming 190fgC μm^{-3} (Putt and Stoecker, 1989). Production was estimated from the predictive equation for ciliate growth as derived by Montagnes *et al.* (1988). This equation gives upper limits of growth and production as it was determined from laboratory cultures. Estimates of the potential annual production of heterotrophic ciliates at Calshot and N.W.Netley given by Leakey *et al.* (1992) were 2.2 and 9.2$gCm^{-3}yr^{-1}$ respectively. Throughout their sampling programme estimates of daily ciliate production ranged from <1 to 18 $\mu gC\ l^{-1}\ d^{-1}$ at the Calshot site and <1 to 141 $\mu gC\ l^{-1}\ d^{-1}$ at the N.W. Netley site. The inner estuarine site at N.W. Netley appeared to have been the more productive of the two sites during most months of the year. Ingestion demands of ciliates were estimated using a gross growth efficiency of 40% (being the mid-value in a range of 30 to 50%

given in Fenchel (1987)). The first revision made to the results of Leakey *et al.* (1992) was that as the growth rate estimates represented near maximal food saturated rates, an attempt was made to scale these values to more representative *in situ* rates. Recent work in a shallow eutrophic inlet (Sutton Harbour, Plymouth Sound, U.K.) by Leakey *et al.* (1994) has shown measured growth rates of ciliates to be 44 to 68% of that predicted using the Montagnes *et al.* (1988) equation. Although these results were collected at a single site, and on only one occasion, the results do allow a comparison between predicted and natural *in situ* growth in a nutritionally favourable environment. The average rate of growth of the four dominant taxa in the study of Leakey *et al.* (1994) grew at a rate of 53.4% of the maximum food saturated rate. The production rates of Leakey *et al.* (1992) have therefore been multiplied by 0.534 in an attempt to correct for sub-optimal growth.

Other changes from the model presented in Leakey *et al.* (1992) include the addition of an organic carbon pool which drives bacterial production, and the inclusion of heterotrophic nanoflagellates, which are generally considered to be the major bacteriovores in pelagic waters (Fenchel, 1987). High abundances of these small protists have been recorded at Calshot and N.W. Netley during the summer months (Antai, 1989). Furthermore, ciliates have been included as grazers of these nanoflagellates. Leakey *et al.* (1992) indicated that this indirect food source could be of greater importance than that derived directly from bactivory in this area. Mixotrophy is generally regarded as being of importance to some algal species, but as its importance has not been determined in this area, then no trophic links have been included in the box models. Production recycling may also be an important carbon source to ciliates and bacteria. No attempt was made to enumerate this in the present study, although the loops are indicated in the box models for N.W.Netley and Calshot (see Figures 8.7.1 and 8.7.2). The ciliate compartments are likely to have non-cyclical production recycling as a result of compartmentalization, this group contains many species and a large size range, with ciliate-ciliate feeding being likely (Leakey *et al.*, 1992).

Bacterial production estimates have been taken from Antai (1989). Annual estimates at Calshot are 8,300mgC$m^{-3}yr^{-1}$, while at N.W.Netley they are an order of magnitude greater at 83,000mgC$m^{-3}yr^{-1}$. In the box model flow diagrams bacteria are assumed to obtain their carbon from an organic pool which is derived from algal exudation, sloppy feeding and dead organisms or organisms parts.

Table 8.3.1 summarizes the production rates of ciliates, bacteria, copepods and primary production estimated for Southampton Water, in addition to giving estimates for other areas where these measurements have been completed.

PRODUCTION RATES $mgCm^{-3}yr^{-1}$ (% OF TOTAL PRIMARY PRODUCTION)									
PRIMARY PRODUCTION			SECONDARY PRODUCTION						
FRACTIONATED			TOTAL	TOTAL CILIATE	TINTINNID	BACTERIA	COPEPODS	SITE	SOURCE
>10µm		<10µm							
9,798.7 (81.0)		2,298.5 (19.0)	12,097.2 (100)	132.7[A] (1.1)	-	2.419.4 (assumed 20)	176.4 (1.5)	Gulf of Maine, USA	Montagnes *et al.*, 1988[D]
>20µm	2-20µm	<2µm							
2,278.2 (28.5)	2,601.8 (32.5)	3,118.2 (39.0)	7,998.2 (100)	525.1 (6.6)	59.4 (0.7)	1,199.7 (assumed 15)	395.0 (4.9)	Lime Cay, Jamaica	Roff *et al.*, 1990[D]
>10µm		<10µm							
19,250 (50.0)		19,250 (50.0)	38,500 (100)	-	3,300 (8.6)	-	<4.745 (<12.3)	Narragansett Bay, USA	Verity, 1987
			10,357 (100)	2.036 (19.7)	-	-	429 (4.1)	Southern Kattegat	Kiørboe and Nielsen, 1994; Nielsen and Kiørboe, 1994
>10µm		<10µm							
25,345 (66.5)		12,768 (33.5)	38,113 (100)	1,175[B] (3.1)[E]-631 (1.7)[F]	333[B] (0.9)[E]-624 (1.6)[F]	8,300 (21.8)[C,G]	189 (0.5)	Calshot, Solent, U.K.	Present Study
61,949 (66.5)		31,207 (33.5)	93,156 (100)	4,913[B] (5.3)[E]	694[B] (0.7)[E]	83,000 (89.1)[C,G]	527 (0.6)	N.W.Netley	Present Study

TABLE 8.3.1 Comparisons of the relative production of the microbial populations and metazoans in different pelagic studies, including estimates for Southampton Water.

A Montagnes *et al.* (1988) equation used to estimate growth rates. B Montagnes *et al.*, (1988) equation used to estimate growth rates, but subsequently modified by multiplying by 0.534. C Production estimated by applying growth rates (estimated from function relating growth to temperature and bacterial abundance) to measured biomass. D Converted from units of $kJm^{-2}yr^{-1}$ to $mgCm^{-3}yr^{-1}$ using appropriate mean water column depths. Phytoplankton kJ converted to carbon assuming 1mgC=0.055kJ in Roff *et al.*, 1990; calculated from Richman 1958, and assuming 1g phytoplankton yields 15.8kcal (Platt, 1971) and 1 kcal=4.1855 kJ for Montagnes *et al.*, 1988. Ciliate and tintinnid values were converted from kJ to mgC by assuming that 20.15J per mgDW (Finlay, 1978), 0.17g DW ml^{-1} (Laybourn and Finlay, 1976), and 1ml protoplasm contains 0.071gC (Fenchel and Finlay, 1983). Copepod production converted from kJ assuming 1gDW=6kcal (Tremblay and Roff, 1983), 40% of DW is carbon (Omori and Ikeda, 1984; Båmstedt, 1986) and 1kcal=4.1855kJ. E from Leakey *et al.* (1992). F from Burkill (1982). G from Antai (1989).

Methods of production estimation do vary between studies for each of the groups. Errors associated with different methods vary, and the accuracy of the estimates will also vary between studies. Comparisons of ciliate and copepod production, in this handful of studies from estuarine/neritic areas, shows braodly similar ciliate annual rate of production. Ciliates have estimated annual production between 1.1 and 19.7% of total primary production, while copepods have annual production rates between 0.5 and <12.3% of primary production.

8.4 THE IMPORTANCE OF THE BENTHIC COMMUNITY

A major examination of the macro-benthic community within Southampton Water was undertaken by Oyenekan (1981), and estimates of production were reported. These estimates however are questionable since mistakes were made in the application of cohort production estimates, and in the identification of cohorts (*personal observations*). It was felt that for comparative purposes it would be of interest to include the production of the macro-benthic community. Estimates were therefore made using the annual average biomass data given in Oyenekan (1981) for the year 1979. The station chosen to represent Calshot was station 20, and to represent N.W.Netley was station 2. These stations are situated in or near the central channel of the estuary and are located less than 6 kilometres from the two sites to which they have been assigned. Both sites were dominated by polychaetes, making up over 88.8 and 99.4% of the total annual average ash-free dry weight at station 20 and 2 respectively. Since biomass was very variable between the Southampton Water sites studied by Oyenekan (1981), and as there have been some changes in the macro-benthic community, from the high *Mercenaria mercenaria* standing stock of that time to currently very low values (M.Sheader, *pers. comm.*), then the results should be viewed with some caution.

Annual average ash-free dry weight measurements for 1979 were converted to units of carbon assuming carbon weight is 40% of the ash-free dry weight (Steele, 1974). These mean annual macro-benthic standing stocks were then converted to estimates of annual production using an annual P/B ratio of 2.0. This value was chosen as being typical of polychaetes, in particular *Nereis diversicolor* and *Nephtys hombergii* (see Robertson, 1979). *Nereis diversicolor* accounted for 77% of the annual average biomass at station 2, while *Nephtys hombergi* accounted for 58% of the average annual biomass at station 20. The annual macro-benthic production for 1979 was therefore estimated as $0.74 gCm^{-2}yr^{-1}$ at Station 2 (assigned to N.W.Netley), and $1.71 gCm^{-2}yr^{-1}$ at Station 20 (assigned to Calshot). These values were converted for comparative purposes into units of production per m^3 by dividing by the average water column depth (8m at N.W.Netley and 10m at Calshot Spit). The importance of the benthic community as a source of

energy-matter has been highlighted in Chapters 6 and 7. Given the scarcity of information on benthic populations in Southampton Water, particularly with regard to their dietary demands and reproductive outputs, any attempt at fitting this group into the annual carbon flux box model comprehensively is problematic.

Unfortunately there are no estimates of meio- or micro-benthic abundance, biomass or production within Southampton Water. The meiobenthic group has already been highlight with regards to harpacticoid copepods in Chapter 2, and may be a particularly important component, needing further study.

8.5 MEROPLANKTONIC GROUPS

As a result of time constraints the production of the meroplanktonic groups were not assessed in this study. These organisms are likely to play an important role in the pelagic food web in this area. Cirripede, mollusc and polychaete larvae are particularly abundant at times (see Chapter 3), and it would be likely that these may be dominant in terms of pelagic production at times. The input of these groups may also be an important energy-matter source to higher predators, as examined in Chapter 6. The diets of many meroplanktonic organisms appears not to have been studied in detail. However, Lebour (1922) noted that the holoplanktonic polychaete *Tomopteris* and larval *Poecilochaetus* were seldom found with any discernible contents in their guts, but suggested that their food was 'of the most minute kind'. In a later paper Lebour (1923) described *Tomopteris helgolandica* as having a gut contents composed of microscopic unicellular food, however, in the same work it is reported how a *Tomopteris* under laboratory conditions was found to ingest *Sagitta*, and an individual taken from a plankton tow containing a larval herring. Larval annelids of different species were described as having variable diets, but most of them were principally diatom feeders, while larval molluscs and decapods appeared to feed upon diatoms (Lebour, 1922). Cirripedes are likely to feed upon algae, detritus and possibly micro-heterotrophs. Barlow and Monteiro (1979) found that *Eliminus modestus* larvae from Southampton Water fed upon the same size particles as *Acartia clausi*, when cultured in natural sea water. The particles that were predominantly grazed were ~10-30μm in diameter.

8.6 THE PRODUCTION AND INGESTION BY THE CALANOID COPEPOD POPULATION

Production estimates for the mesozooplankton component within Southampton Water have been estimated previously by two workers. An estimate was made by Leakey *et al.* (1992) in an attempt to demonstrate how the carbon fixed by autotrophic algae was partitioned between the mesozooplankton and ciliates. Leakey *et al.* (1992) used dry weight data for the mesozooplankton component (ie. net caught material >100μm) given in Zinger (1989), and dry weights of collected material were converted to carbon by assuming a carbon:dry weight ratio of 0.35 (Parsons *et al.*, 1984). Further, through the application of an annual community P:B ratio of 34, they estimated annual production for this component. Production estimates of the mesozooplankton component were also made by Lucas (1993), to allow comparisons between the mesozooplankton (predominately the copepods and cirripedes) and the estimates of gelatinous predator production. The ash-free dry weight of the >200μm fraction was measured, and subsequently the temperature to P/B relationship given in Uye (1982a) was applied. The methods used to estimate mesozooplankton production in these two studies were not designed to give estimates of great accuracy. Although applying annual P/B ratios and temperature dependent daily P/B ratios to biomass and temperature may give fairly accurate estimates of the production of copepods, applications of these techniques were inappropriate to the data in each of the studies mentioned above. In both, measurements of zooplankton weights were not measures of only the zooplankton weights, but included suspended sediment and detritus. Such particles can dominate samples taken with a 118μm mesh net (*personal observations*), and the methods used will have produced massive over estimation of the zooplankton weights, particularly in the results of Leakey *et al.* (1992) where dry weights rather than ash-free dry weights were utilised. For neritic environments, corrections for sediment or detritus have been previously made (eg. Baker, 1973). Within Southampton Water the quantities of detritus and SPM often have far greater displacement volumes than the zooplankton in samples taken with a 118μm mesh net, quantity were also apparently very variable between samples (*personal observations*). Without further study no simple correction procedure could be applied. In the present investigation, production of copepods has been estimated using abundance values together with an estimate of mean individual weight. Details of the methods used to determine copepod production are given in Chapter 5, and the results are summarised in Table 8.6.1.

SITE	GROUP	PERIOD	PRODUCTION ($mgCm^{-3}yr^{-1}$)	SOURCE OF ABUNDANCE DATA
Calshot	*Acartia* sp.	Dec. 92 - Dec. 93	20.5	This study
	Centropages hamatus		9.7	
	Temora longicornis		5.6	
	Para/Pseudocalanus		1.9	
	Total Calanoids		37.7	
Calshot	Total Calanoids	April 85- April 86	284.5	Zinger (1989)
Calshot	Total Calanoids	April 86- April 87	243.2	Zinger (1989)
Greenland (nr. Hamble)	Total Calanoids	April 90 - April 91	50.5	Lucas (1993)
Greenland (nr. Hamble)	Total Calanoids	Dec. 90 - Dec. 91	84.3	Lucas (1993)
Hamble	Total Calanoids	May 85 - May 86	238.2	Zinger (1989)
Hamble	Total Calanoids	April 86 - April 87	181.8	Zinger (1989)
N.W.Netley	Total Calanoids	April 85 - April 86	646.3	Zinger (1989)
N.W.Netley	Total Calanoids	May 86 - May 87	407.0	Zinger (1989)
Cracknore	Total Calanoids	May 85 - May 86	269.3	Zinger (1989)
Cracknore	Total Calanoids	May 86 - May 87	422.5	Zinger (1989)
Cracknore	Total Calanoids	March 90 - March 91	135.9	Lucas (1993)
Cracknore	Total Calanoids	Dec. 90 - Dec. 91	117.7	Lucas (1993)

TABLE 8.6.1 Annual estimates of calanoid copepod production through Southampton Water. All estimates derived using the MLR equation derived in Chapter 4, methods detailed in Chapter 5.

N.B. No estimates for N.W.Netley have been determined from the results of Lucas (1993) because of the short period for which data are available.

Given that the abundances determined by Lucas (1993) are likely to be underestimates as a result of the mesh size used (indeed the production values are generally lower than in other years of measurement, see Table 8.5.1), only the results determined from the abundance data of Zinger (1989), and the size-abundance data in the present study have been used to compile average annual production figures. The average calanoid copepod production value at Calshot is 188.5mgCm^{-3}yr^{-1} (with a range from 37.7 to 284.5mgCm^{-3}yr^{-1}), while at N.W.Netley the figure is 526.7mgCm^{-3}yr^{-1} (with a range from 407.0 to 646.3mgCm^{-3}yr^{-1}). Thus calanoid copepod production would appear to be greater at the inner estuarine site of N.W.Netley than at Calshot, although the percentages which average annual calanoid copepod production is of total primary production is very similar for both sites, 0.5% and 0.6% at Calshot and N.W.Netley respectively (see Table 8.3.1).

Estimates of annual ingestion demands of calanoid copepods may be included in the carbon flux box model. Kiørboe *et al.* (1985) found that *Acartia tonsa* maintained in the laboratory, under a range of algal concentrations, had gross growth efficiencies K_1 (in carbon terms) of between 39 and 49%. Abou Debs (1984) estimated that the K_1 (in carbon terms) of *Temora stylifera*, at a range of food culture concentration in the laboratory, ranged between 52 and 60%. Corner (1961) found that the K_1 of *Calanus helgolandicus* varied between 37.2 and 48.9%, while Mullin and Brooks (1970a) found that in the laboratory *Rhincalanus nasutus* had a K_1 (in carbon terms) ranging between 21 and 55%, and *Calanus helgolandicus* had a K_1 which varied between 18 and 72%. Escaravage and Soetaert (1995) calculated that *Eurytemora affinis* and *Acartia tonsa* had mean growth efficiencies of 38% and 35% (in carbon terms) respectively. As published values centre around 45%, this value has been adopted to estimate ingestion demands by calanoids. This efficiency may however give an underestimation of ingested carbon considering the feeding conditions within the estuary, the high suspended sediment and detritus, and the apparent reduced rates of growth by copepods in turbid regions (Burkill and Kendall, 1982; Irigoien and Castel, 1995; this study). The average annual ingestion demands are estimated as 419mgCm^{-3}yr^{-1} at Calshot, and 1,170mgCm^{-3}yr^{-1} at N.W.Netley.

Table 8.6.2 gives compiled results from studies of neritic and estuarine copepod production, measurements of production associated parameters are also included where possible. The column P2/P1x100 represents copepod production divided by total primary production expressed as a percentage, ie. the gross trophic level transfer efficiency. Values for calanoid copepods in Southampton Water were always less than 1% over an annual period. Production transfer efficiencies between primary production and calanoid copepods have also been shown to be similar in other areas (both in cases where single species have been examined, but also when

the entire community has been accounted for). Greater efficiencies of transfer have also been noted ie. greater than 20% in the Inland Sea of Japan (Uye *et al.*, 1987). Efficiencies as high as 20-50% have also been found, however, in these cases it was believed that the copepods were feeding on imported material also (Escaravage and Soetaert, 1995). Comparisons of production between different areas is often complicated by the great variety of methods which have been used to estimate the production of copepods and other groups. Although different methods will be needed in different environments, nonetheless some standardisation procedures should be made. To give an example, where possible, development rates should not be made under food saturated conditions and then extrapolated to the field. Instead they should be conducted as closely to those found in the environment as possible.

The annual average estimates for Southampton Water are within the total calanoid copepod annual estimates which have previously been reported. From the compiled annual estimates of calanoid copepod production (see Table 8.6.2) it would appear that for this group production is almost always less than 2,000mgCm^{-3}yr^{-1} in these neritic, most commonly temperate, studies. An estimate of 3,170mgCm^{-3}yr^{-1} has been recorded, in a lagoon with very minimal flushing (Landry, 1978a), but this was not a typical coastal location. The values of Uye and Liang (1996) for total pelagic copepods (including cyclopoids) in Fukuyama Harbour, Japan, do exceed 2,000mgCm^{-3}yr^{-1}. On a depth integrated basis the highest annual production rate recorded is 38,400mgCm^{-2}yr^{-1}, from Northumberland coastal waters, U.K. (Roff *et al.*, 1988). This value was the highest of estimates made from a 15 years data set, whereas most other studies are for a maximum of one to two years. The estimation technique in this study also assumed copepod growth rates were maximal. Highest depth integrated values for Southampton Water were estimated as 5,170mgCm^{-2}yr^{-1}, at the N.W.Netley site. The lowest value obtained in this study of Southampton Water was 377mgCm^{-2}yr^{-1}, during 1993 at the Calshot site. This value is very low in comparison to many other studies, and although similar values have been found, these are usually for the sites where only a single species has been examined (eg. 391.0mgCm^{-2}yr^{-1} for *Acartia bifilosa* in Gdańsk Bay, Poland, [Ciszewski & Witek, 1977], 145mgCm^{-2}yr^{-1} for *Pseudodiaptomus marinus* in Tomo, Inland Sea of Japan [Uye *et al.*, 1983]). Presumably if these species are dominant then these areas would also have similar total annual productions. Total annual estimates for Ogac Lake, Canada, were similar to the Southampton Water minimum value being 577-757mgCm^{-2}yr^{-1} (McLaren, 1969). Remarkably the annual value at Calshot during 1993 is very similar to the daily value of 40-120mgCm^{-2}yr^{-1} found during August in the Skagerrak (Peterson *et al.*, 1991). Presumably high flushing rates, a shallow euphotic zone, high turbidity and low growth in Southampton Water account for the low biomass and production by copepods.

SPECIES REGION	TEMPERATURE (°C)	ANNUAL PRODUCTION mgC m^{-3} yr^{-1} (mgC m^{-2} yr^{-1})	CHL a (µg l^{-1})	DAILY P/B (d^{-1})	ANNUAL P/B (yr^{-1})	(P2/P1)*100	SOURCE
Acartia bifilosa Gdańsk Bay, Poland	7-18	3.6[H] (391.0)	-	0.032-0.121	16.75	-	Ciszewski & Witek, 1977
Acartia bifilosa Gironde, France	-	- (-)	~2-20	0.03-0.14	28	-	Irigoien and Castel, 1995
Acartia clausi nearshore Black Sea	14.9	26.7[J] (-)	-	0.014-0.044	13.0	0.1[A][yr^{-1}]	Greze & Baldina, 1964
Acartia clausi nearshore Plymouth, U.K.	13.0	41.9[J] (-)	-	0.034	8.7	-	Greze & Baldina, 1964
Acartia clausi nearshore Black Sea	7.8-21.4[B]	- (-)	-	0.08(average) 0.04-0.175(range)	32	-	Greze *et al.*, 1968
Acartia clausi Azov Sea, U.S.S.R.	-	- (-)	-	0.04	14.4-17.0[C]	-	Zaika, 1968
Acartia clausi Mediterranean (Golfe de Marseille)	-	- (-)	-	0.05	-	-	Gaudy, 1970
Acartia clausi Azov Sea, U.S.S.R.	-	- (-)	-	0.063	-	-	Maloviskaya, 1973
Acartia clausi neritic Black Sea	-	- (-)	-	0.22	-	-	Greze, 1978
Acartia clausi (*A.hudsonica*?) Jakle's Lagoon, U.S.A.	8-20	2,670-3,170 (8,000-9,500)	4-68	0.12-0.23	57[D]	-	Landry, 1978a
Acartia clausi (*A.omorii*?) Inner Onagawa Bay, Japan	4.7-21.6	163 (2,450)	>0.1-25.6	0.053-0.34	-	1.225-2.45[E][yr^{-1}]	Uye, 1982a
Acartia tonsa[F] Patuxent River Estuary, U.S.A.	24-26.5	- (-)	-	0.360-0.523[D]	-	5[G][(part of yr)$^{-1}$]	Heinle, 1966
Acartia tonsa Rhode River Sub-Estuary, U.S.A.	-	- (-)	-	0.195(summer avr.) 0.652(max.)	-	-	Allan *et al.*, 1976
Acartia tranteri Westernport Bay, Australia	11-22	130 (1,300)	1.14	0.025-0.26	-	1.3[yr^{-1}] 0.1-1.3[d^{-1}]	Kimmerer & McKinnon, 1987
Centropages kroyeri nearshore Black Sea	14.9	5.5[J] (-)	-	0.077	11.5	-	Greze & Baldina, 1964
Paracalanus parvus nearshore Black Sea	7.8-21.4[B]	- (-)	-	0.06(avr) 0.038-0.089(range)	25	-	Greze *et al.*, 1968
Pseudocalanus elongatus nearshore Black Sea	7.8-21.4[B]	- (-)	-	0.16(avr) 0.104-0.203(range)	58	-	Greze *et al.*, 1968
Pseudocalanus elongatus Gdańsk Bay, Poland	3-7	72.2[I] (7,801.9)	-	0.010-0.049	12.42	-	Ciszewski & Witek, 1977
Eurytemora affinis Rhode River sub-Estuary, U.S.A.	-	- (-)	-	0.046(summer avr.) 0.8(max.)	-	-	Allan *et al.*, 1976
Eurytemora affinis Bristol Channel, U.K.	6-14	- (-)	0.3-5.8(range) 1.6(year avr.)	0.03-0.13	33	-	Burkill & Kendall, 1982

Eurytemora herdmani	8-18	- (-)	-	0.16-0.17[D]	-	-	McLaren & Corkett, 1981
Halifax Harbour, Canada							
Pseudodiaptomus hessei	13-26	120-1,720[J] (240-3,440)	-	0.11-0.38	78.5-100.2	-	Jerling & Wooldridge, 1981
Sunday River Estuary, S.Africa							
Pseudodiaptomus marinus	8-25	20.7 (145)	7	~0.005-0.27	-	-	Uye *et al.*, 1983
Tomo, Inland Sea of Japan							
Oithona minuta	7.8-21.4[B]	- (-)	-	0.08(avr.)	31	-	Greze *et al.*, 1968
nearshore Black Sea				0.050-0.144(range)			
Oithona similis	-	- (-)	-	0.04	16	-	Zaika, 1968
nearshore Black Sea							
SCOTAIN SHELF, N.AMERICA							
Calanus finmarchicus	3-17	48.8[J] (4357.8)	-	-	-	-	McLaren *et al.*, 1989
Metridia lucens		46.0[J] (4107.8)	-	-	-	-	
Centropages typicus		25.2[J] (2250.4)	-	-	-	-	
Pseudocalanus newmani		21.2[J] (1893.2)	-	-	-	-	
Paracalanus parvus		10.8[J] (964.4)	-	-	-	-	
Oithona similis		10.4[J] (928.7)	-	-	-	-	
Clausocalanus sp.		5.6[J] (500.1)	-	-	-	-	
Calanus hyperboreus		5.2[J] (464.4)	-	-	-	-	
Calanus gracialis		1.6[J] (142.9)	-	-	-	-	
Candacia armata		1.6[J] (142.9)	-	-	-	-	
TOTAL		176.4[J] (15,752.5)	-	-	-	-	
OGAC LAKE BAFFIN ISLAND, CANADA							
Pseudocalanus minutus	-	11.8-20.5 (354-511)	-	-	4.0-8.3	-	McLaren, 1969
Oithona similis		6.7-17.4 (202-347)	-	-	2.3-4.2	-	
TOTAL		19.2-25.2 (577-757)	-	-	-	-	
NORTHUMBERLAND COASTAL WATERS, U.K.							
Acartia clausi	5.8-14.4	10.7[J] (580.3)	-	-	-	-	Evans, 1977
Acartia longiremis		4.6[J] (244.1)	-	-	-	-	
Oithona sp.		5.4[J] (286.9)	-	-	-	-	
Temora sp.		17.6[J] (951.3)	-	-	-	-	
Pseudocalanus sp.		19.2[J] (1,033.8)	-	-	-	-	
TOTAL		57.5[J] (3,096.4)					
NORTHUMBERLAND COASTAL WATERS, U.K.							
TOTAL[L]	-	165.9-711.1[K] (8,960-38,400)	-	-	-	-	Roff *et al.*, 1988

KINGSTON COASTAL WATERS, JAMAICA							
Acartia sp.	27-29	5.5[K] (164.8)	0.15-1.38[M]	-	-	-	Chisholm and Roff, 1990b
Calanopia americana		3.7[K] (112.0)		-	-	-	
Centropages velificatus		34.7[K] (1041.6)		-	-	-	
Clausocalanus furcatus		13.5[K] (406.4)		-	-	-	
Corycaeus sp.		13.9[K] (416.0)		-	-	-	
Oithona sp.		66.7[K] (2,000.0)		-	-	-	
Paracalanus aculeatus		126.0[K] (3,780.8)		-	-	-	
Temora turbinata		21.4[K] (641.6)		-	-	-	
Undinula vulgaris		23.0[K] (689.6)		-	-	-	
TOTAL		321.6[K] (9,648.0)		-	-	-	
FUKUYAMA HARBOUR, INLAND SEA OF JAPAN							
Acartia omorii	8.9-26	749 (5,620)	~0.5-322	~0.05-0.6	-	-	Liang and Uye, 1996
Centropages abdominalis		355 (2,660)		0.18-0.37	-	-	Liang *et al.*, 1996
TOTAL (of reported 2)		1,104 (8,280)		-	-	-	Liang and Uye, 1996; Liang *et al.*, 1996
Copepod community	as above?	2,500 (18,400)	-	as above?	64	-	Uye and Liang, 1996
WESTERSCHELDS ESTUARY, NETHERLANDS							
Acartia tonsa	6-22	695.5 (4,868.5)	1-18	-	-	~22[yr^{-1}][I]	Escaravage and Soetaert, 1995
Eurytemora affinis		905 (6,335)		-	-	~28[yr^{-1}][I]	
TOTAL (of reported 2)		1,600.5 (11,203.5)		-	-	~50[yr^{-1}][I]	
SOUTHERN KATTEGAT							
TOTAL	4-19	~429 (~12,000)	~0.1->10.7	-	-	4.1[yr^{-1}]	Kiørboe and Nielsen, 1994
Copepod spp. Kungsbacka Fjord, Sweden	0-20	112.5 (1,800)	-	0.02-0.06	15	1.8[yr^{-1}]	Olsson & Ölundh, 1974
Copepod spp. Kaneohe Bay, U.S.A.	27-29	- (-)	-	0.78	285[D]	-	Newbury & Bartholomew, 1976
Herbivorous Copepod spp. Inland Sea of Japan	10.9-22.1	708 (26,400)	~1-12	0.09-0.36 (multiple site mean)	-	21.7[yr^{-1}] 0.8-106[mth^{-1}]	Uye *et al.*, 1987
Copepod spp. Skagerrak	16-17	- (-)	1.03-6.00	0.182	-	-	Peterson *et al.*, 1991
SOUTHAMPTON WATER, U.K.							
CALSHOT							
Acartia sp. (93)	6.0-18.4	20.5 (205.1)	0.66-11.9	0.07-0.23	41	0.05[yr^{-1}]	Present Investigation
Centropages hamatus (93)		9.7 (96.6)	0.66-11.9	0.05-0.20	58	0.02[yr^{-1}]	
Temora longicornis (93)		5.6 (56.1)	0.66-11.9	0.03-0.15	42	0.01[yr^{-1}]	
Pseudo / Paracalanus (93)		1.9 (19.3)	0.66-11.9	0.06-0.19	52	0.005[yr^{-1}]	
TOTAL CALANOIDS (93)		37.7 (377.1)	0.66-11.9	-	45	0.09[yr^{-1}]	
TOTAL CALANOIDS (85-86)	6.0-18.3	284.5 (2,845)	-	-	-	0.75[N][yr^{-1}]	estimated from results of Zinger (1989)
TOTAL CALANOIDS (86-87)	4.8-18.2	243.2 (2,432)	-	-	-	0.64[N][yr^{-1}]	estimated from results of Zinger (1989)

N.W. NETLEY, U.K.							
TOTAL CALANOIDS (85-86)	2.2-18.7	646.3 (5,170)	-	-	-	$0.69^{N}[yr^{-1}]$	estimated from results of Zinger (1989)
TOTAL CALANOIDS (86-87)	4.8-19.5	407.0 (3,256)	-	-	-	$0.45^{N}[yr^{-1}]$	estimated from results of Zinger (1989)

TABLE 8.6.2 Production estimates and associated parameters for neritic and estuarine copepod populations from other studies, and as estimated for Southampton Water.

A As given in Uye (1982a). B Range given are those of the seasonal averages. C Range for the years 1963-1965. D Daily P:B range calculated for copepodite and adult not nauplii as incorrect individual weights were applied to these stages. E Estimated by author form primary production data for coastal regions of Japan from the International Biological Programme (primary production≈100-200$gCm^{-2}yr^{-1}$; Hogetsu *et al.*, 1977). F Data only produced for 2 month period (July 16 - September 17, 1964). G Calculated from primary production data for the same period and region, as produced by Stross and Stottlemyer (1965). H Wet Weight values given converted to Carbon units by assuming a carbon:wet weight ratio of 0.056 (Parsons *et al.*, 1984). I Estimated from mean annual primary production of 22.5$gCm^{-2}yr^{-1}$, average of range given in paper J Converted to carbon from dry weight assuming carbon to be 40% of dry weight (Omori and Ikeda, 1984; Båmstedt, 1986). K Copepod production values converted from kJ to carbon by assuming 25$kJ.gDW^{-1}$ (mid-range value of Tremblay and Roff, 1983), and 40% of DW is carbon. L Species included in production estimate being *Acartia clausii*, *A.longiremis*, *Pseudocalanus* sp., *Oithona similis* and *Temora longicornis*, M Total chlorophyll including chlorophyll a and phaeo-pigments. N Average primary production rate used in estimate.

Although no annual production figure was given by Burkill and Kendall (1982) for *Eurytemora affinis* in the Bristol Channel, they found the total daily production of the copepodites (although in some instances not all stages were examined) of this species to range between $0.03\mu gCm^{-3}d^{-1}$ in November to $0.68\mu gCm^{-3}d^{-1}$ in May (after carbon adjustment ie. carbon is 40% of dry weight, and assuming CIV's grow at the same rate as CV's). *Acartia* spp. at Calshot had a production range of between 0 and $240\mu gCm^{-3}d^{-1}$. Unfortunately the relative importance of *Eurytemora affinis* at the sites studied by Burkill and Kendall (1982) within the Bristol Channel was not detailed.

Within Southampton Water calanoid copepod production makes up less than 1% of the total annual primary production. Similar values have been found in other areas (see Table 8.6.2), although greater transfer efficiencies have also been reported. Uye *et al.* (1987) estimated that total herbivorous copepod production was 21.7% of total primary production in the Inland Sea of Japan. While Escaravage and Soetaert (1995) estimated that *Acartia tonsa* and *Eurytemora affinis* production combined was ~50% of the total primary production in the Westerschelds estuary, Netherlands. In this work the authors were led to conclude that copepods were reliant upon imported food to meet their total food demand during large portions of the year. It is possible that suppression of growth as a result of high SPM concentrations in their area of study, could have led to an overestimation of growth and therefore production (see discussion in Chapter 3).

Although total copepod nauplii were counted in the present study, this group will have been massively under sampled by the 118μm mesh net (see Raymond and Carrie, 1964), then the abundance changes can only be used as a guide to the relative changes in the copepod nauplii. Production by nauplii has not therefore been included in the figures derived. There would appear to have been less than ten estimates of nauplii production in natural populations, almost all of which are for temperate regions. Most of the currently available estimates have been compiled by Mullin (1988), who concluded that '25% is the likely upper limit to the fraction of total secondary production in a natural, marine population of copepods which is attributable to naupliar somatic growth [as a % of the total]'. Values are typically a minor component of the total, indeed the average production by nauplii as a percentage of copepod production is ~10% (average derived from: 15% for *Acartia clausi* (*A.hudsonica*?) in Jakle's Lagoon, USA [Landry, 1978a]; 24% for *Acartia clausi* (*A.omorii*?) in Onagowa Bay, Japan [Uye, 1982a: see Mullin, 1988]; 2% for *Pseudodiaptomus marinus* in the Inland Sea of Japan [Uye *et al.*, 1983: see Mullin, 1988] 1-4% for *Calanus pacificus* (*helgolandicus*) in the Southern Californian Bight, USA [Mullin and Brooks, 1970b]; <10% for *Calanus finmarchicus* in the Fladen Ground, North Sea [Fransz and Diel, 1985], and 9% and 5.7% for *Centropages abdominalis* and *Acartia omorii* respectively in a

eutrophic inlet, Inland Sea of Japan [Liang *et al.*, 1996; Liang and Uye, 1996]).

8.7 DISCUSSION

Figures 8.7.1 and 8.7.2 demonstrate the model of carbon flow through the biological components of the plankton at the N.W.Netley and Calshot sites. At Calshot average annual primary production exceeded $38gCm^{-3}yr^{-1}$, while bacterial production (in a single year) was estimated at $8.3gCm^{-3}yr^{-1}$ ie. around 22% of the primary production. Such a ratio however, does not infer a trophic level transfer efficiency of 22% as production recycling processes and horizontal import of material are likely to be significant for this compartment. At N.W.Netley primary production is greater than at Calshot, being $93gCm^{-3}yr^{-1}$, while bacterial production is estimated to also be greater than at Calshot, being $83gCm^{-3}yr^{-1}$. Once again production recycling may account to some extent for the similar values for production by algae and bacteria. Inter-annual variability must also not be discounted, especially as the bacterial production value is from a single year. Organic inputs of material from upstream areas into this area may drive bacterial and other heterotrophic production. Inputs may be less significant at the Calshot site as a result of dilution processes with offshore waters.

Carbon flow at both sites appears to be dominated by microbial groups. The ciliates may have a production some 6.3 to 9.3 times greater than the calanoid copepods at the Calshot and N.W.Netley sites respectively. When including other meroplanktonic groups, the ciliates are still likely to have production rates several times greater than rates for mesozooplankton. Quantitative studies of pelagic ciliates and other microzooplankton were pioneered over eighty years ago (Lohmann, 1908), although it was only recently that a renewed interest has been taken in this group as a dynamic component of planktonic food webs (Beers, 1978). Many recent investigations have pointed to the importance of the microzooplankton, in particular the ciliates, in the energy fluxes. Given the apparently low production of the copepods in comparison to the micro-heterotrophic ciliates, it would appear likely that although the calanoids may be dependent upon the micro-heterotrophs as a food source, most of the carbon flowing into the micro-heterotrophs does not become mero- or macro-planktonic production at these sites. At Calshot the microbial community may be regarded predominantly as a sink rather than a source of fixed carbon, in that at least $8.30gCm^{-3}yr^{-1}$ flows into the microbial group (bacterial production) annually, yet it is unlikely that more than a small fraction of the $0.42gCm^{-3}yr^{-1}$ ingested demand of copepods is met by microbial feeding. Even if it were met entirely by the microbial components, the respiration within the microbial community would exceed this output.

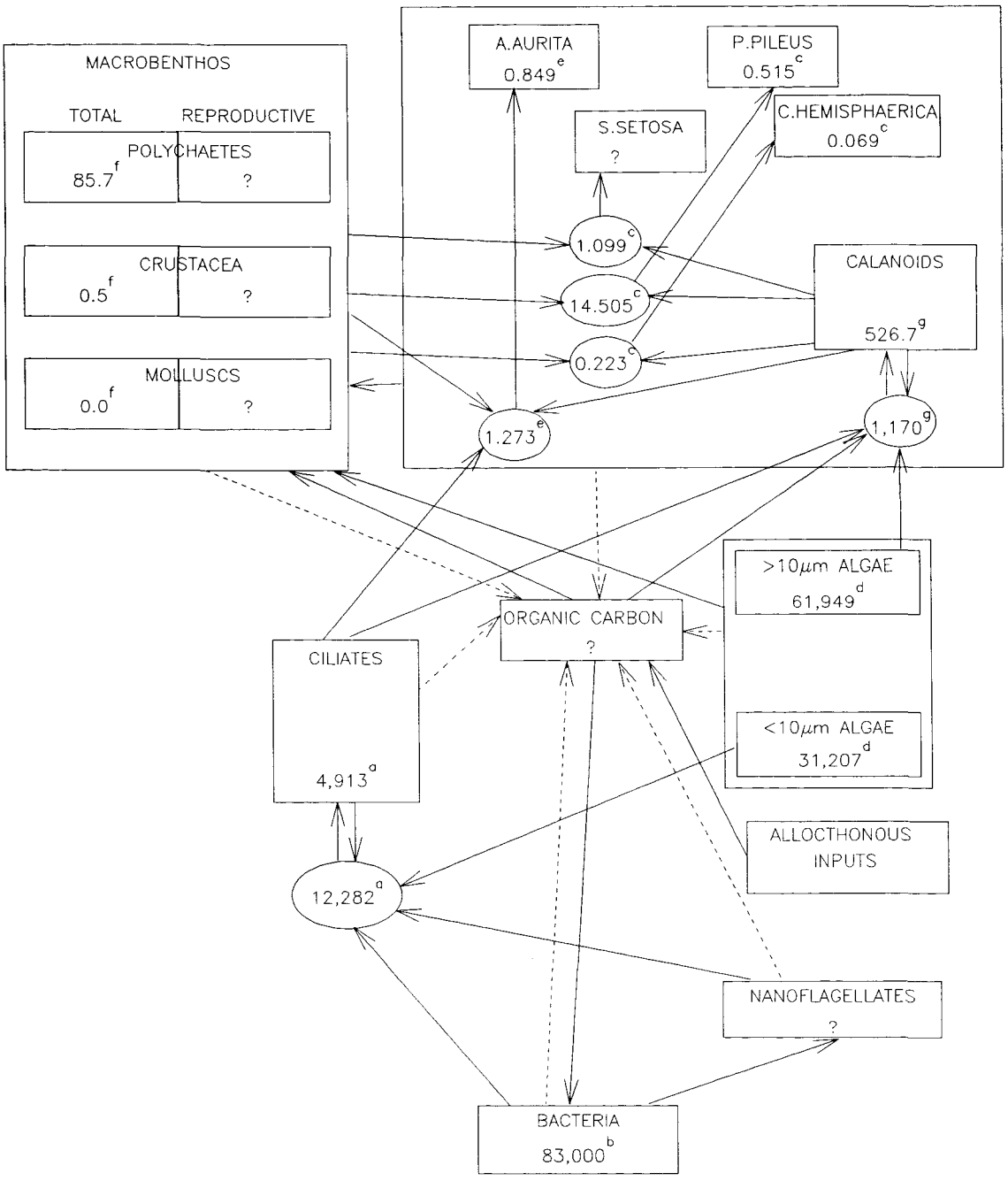


FIGURE 8.7.1 Estimated annual carbon flow (mgC m^{-3} yr^{-1}) through components of the planktonic and benthic community at N.W.Netley. Values in boxes are production estimates, those in circles are estimated annual carbon requirements (ingestion demand) of the components above them.

a. Values adapted from Leakey et al., (1992) for the period June 1986 to June 1987. Maximum estimates multiplied by 0.534 to correct for over estimation see text.
b. Values given by Antai (1989) for the period January 1987 to January 1988.
c. Values calculated from the data given by Lucas (1993), see text.
d. Values estimated from all annual primary production estimates, see text.
e. Values produced in this study for the period January 1993 to January 1994.
f. Values calculated from biomass data given by Oyenekan (1991) for the year 1979.
g. Values annual averages derived from abundance data, see text.

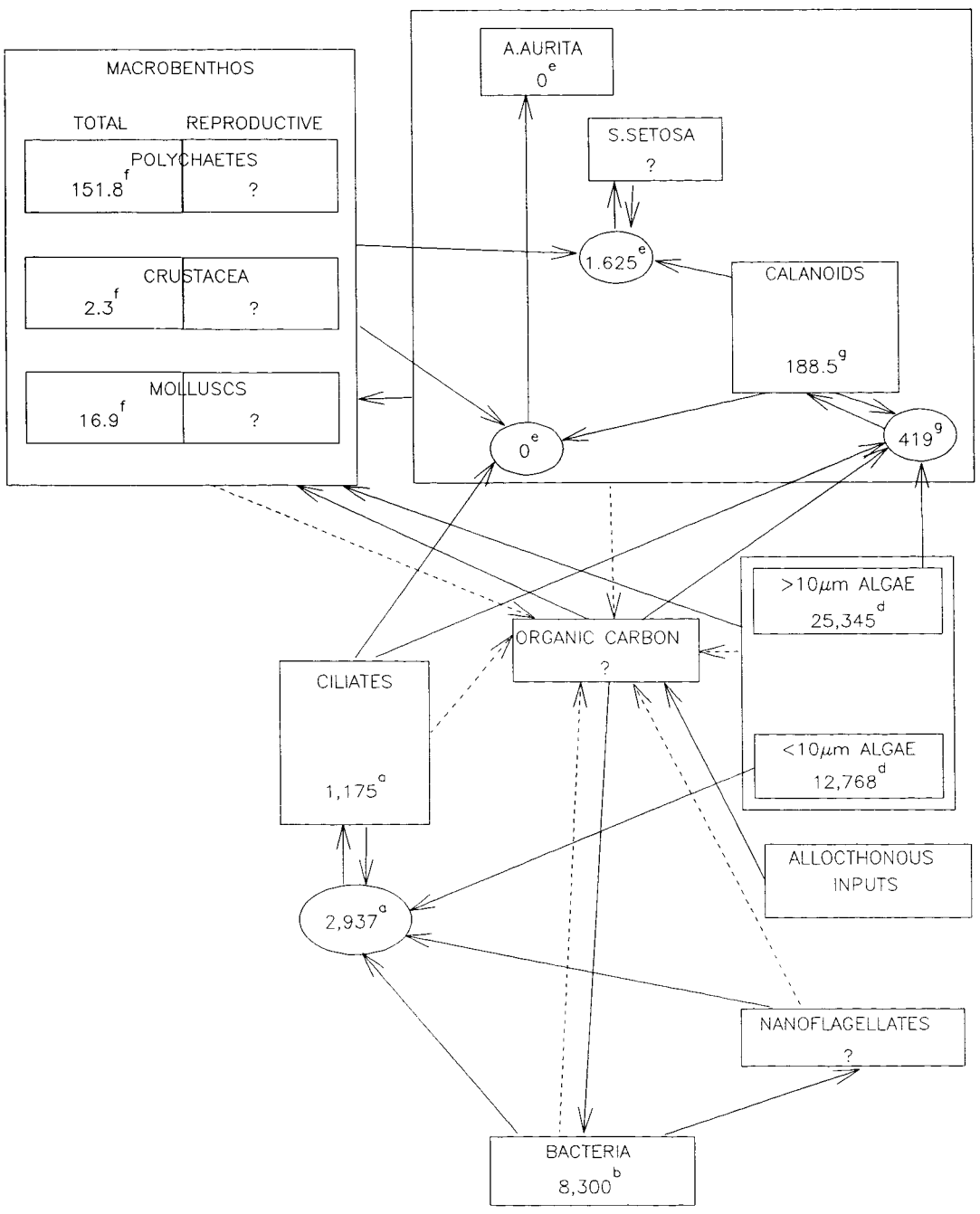


FIGURE 8.7.2 Estimated annual carbon flow (mgC m^{-3} yr^{-1}) through components of the planktonic and benthic community at Calshot. Values in boxes are production estimates, those in circles are estimated annual carbon requirements (ingestion demand) of the components above them.

a. Values adapted from Leakey et al., (1992) for the period June 1986 to June 1987 Maximum estimates multiplied by 0.534 to correct for over estimation, see text
b. Values given by Antai (1989) for the period January 1987 to January 1988
c. Values calculated from the data given by Lucas (1993), see text
d. Values estimated from all annual primary production estimates, see text
e. Values produced in this study for the period December 1992 to December 1993
f. Values calculated from biomass data given by Oyenekan (1991) for the year 1979
g. Annual average estimate, see text

At N.W.Netley the situation is even more pronounced, annual bacterial production has been estimated as $83.00gCm^{-3}yr^{-1}$, while annual ingestion demand of calanoid copepods may be estimated at $1.17gCm^{-3}yr^{-1}$, a mere 1.4% of bacterial production.

Macrobenthic production would appear to be very similar to the production (on a per m^3 basis) to calanoid copepod production at Calshot, while at N.W.Netley the production of macrobenthos is almost an order of magnitude less than the production by calanoid copepods (on a per m^3 basis). Domination by benthic organisms in terms of production and ingestion, and as a proportion of total primary production, in comparison to pelagic mero- and macro-plankton have been found in other coastal areas. Kimmerer and McKinnon (1987) noted that in Westernport Bay, Australia, the macro-benthic annual production was around $10gCm^{-2}$, annual primary production was given as $100gCm^{-2}$, while total *Acartia tranteri* production (the dominant copepod) had an annual production rate of $1.3gCm^{-2}$. Benthic macro-faunal production was therefore almost 8 times greater than mesozooplankton production.

This study has attempted to quantify the production of zooplankton, and combine this with the production of other components previously examined. Any study of a food web will simplify processes which occur. Only through continued effort will the fine structure of food webs be resolved (Pimm *et al.*, 1991). It should be highlighted that the food web models derived are effort limited, however, a combined effort from many studies has been possible, and the results are more comprehensive than in many other contemporary models.

FUTURE IMPROVEMENTS

The results presented within this body of work are the first steps to gaining an insight into some of the important flow pathways and the order of ingestion and production rates. No gut content analysis or clearance rate of copepods and meroplanktonic larvae have yet to be completed; these must be included in further investigations. Such work would aid in the determination of their impacts upon prey. Given the apparent complexity of such a system, in common with most other studies, broad assumptions have had to be made regarding the production, ingestion and flow of energy-matter. The accuracy of these assumptions should be tested in further work. Annual estimates of different compartments have been made in different years, while the production by such groups may be very variable inter-annually.

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APPENDIX 1

ABUNDANCE / BIOMASS PROGRAMME SAMPLING DETAILS

SAMPLING DATE:	10/12/92
WEATHER CONDITIONS:	Fine, cold.
SAMPLING DATE:	11/01/93
WEATHER CONDITIONS:	Windy, overcast, (previously stormy and rainy within the last 24 hours).
COMMENTS:	Too rough to take any samples at Calshot, and water samples at Hamble.
SAMPLING DATE:	26/01/93
WEATHER CONDITIONS:	Cold, breezy, water turbulent and mixed. At 13.30 began to rain.
SAMPLING DATE:	25/02/93
WEATHER CONDITIONS:	Overcast, strong S.W. winds at seaward most sites, calmer within the estuary. Water turbulent and mixed.
SAMPLING DATE:	12/03/93
WEATHER CONDITIONS:	Very calm, warm, hazy sunshine. At 13.00 began to rain (shower lasted for 15 minutes).
COMMENTS:	200µm mesh net used in taking all zooplankton samples.
SAMPLING DATE:	26/03/93
WEATHER CONDITIONS:	Warm, clear sky, light breeze, water very calm.
COMMENTS:	200µm mesh net used in taking all zooplankton samples.
SAMPLING DATE:	23/04/93
WEATHER CONDITIONS:	Rainy, overcast, water rough and stirred. Rain stopped and wind decreased at 13.15
SAMPLING DATE:	06/05/93
WEATHER CONDITIONS:	Very good, warm, clear sky, calm water, breezy towards more exposed seaward sites (ie. Calshot and Hamble).
SAMPLING DATE:	21/05/93
WEATHER CONDITIONS:	Good-sunny, breezy.
COMMENTS:	Appears to be a *Phaeocystis* bloom in the estuary particularly at the more seaward sites, nets clogged after short period in water.
SAMPLING DATE:	22/06/93
WEATHER CONDITIONS:	Fine, warm, sunny.
COMMENTS:	Appears to be a *Phaeocystis* bloom in the estuary, particularly in the upstream areas.
SAMPLING DATE:	21/07/93
WEATHER CONDITIONS:	Overcast, became more cloudy and dull as day progressed, water calm.
COMMENTS:	Red-tide (*Mesodinium rubrum*?) bloom at Cracknore and Bury Buoy region.
SAMPLING DATE:	19/08/93

WEATHER CONDITIONS:	Warm, clear sky, hazy sunshine.
SAMPLING DATE:	01/09/93
WEATHER CONDITIONS:	Warm, very calm, small amount of cloud cover.
SAMPLING DATE:	15/10/93
WEATHER CONDITIONS:	Very cold, clear sky, water calm.
SAMPLING DATE:	01/11/93
WEATHER CONDITIONS:	Overcast, cold, foggy, water rough towards the Calshot site.
SAMPLING DATE:	15/11/93
WEATHER CONDITIONS:	Clear sky, cold, breeze at more seaward sites.
SAMPLING DATE:	01/12/93
WEATHER CONDITIONS:	Cold, water calm, slight cloud cover at beginning of sampling, increasing as time went on, complete cover when sampling completed. Heavy rain in previous 24 hours.
SAMPLING DATE:	28/01/94
WEATHER CONDITIONS:	Clear sky, windy and water rough, very cold, stormy in the previous 24 hours.
SAMPLING DATE:	11/02/94
WEATHER CONDITIONS:	Raining heavily before and at beginning of sampling period. Sky overcast, conditions windy and strong waves. Water turbid.
COMMENTS:	Water too rough to sample at Calshot.

APPENDIX 2

DATE	SITE	DEPTH (m)	SAMPLING TIME	FLOW METER REVOLUTIONS	VOLUME FILTERED (m-3)	TEMPERATURE (oC)	SALINITY (‰)	OXYGEN CONC. (ml O2.l-1)	SATURATION CONC. (ml O2.l-1)	OXYGEN SAT. (%)	CHLOROPHYLL a (mg.m-3)	PHAEO-PIGMENTS (mg.m-3)	SECCHI DISK DEPTH (m)	PRIMARY PRODUCTION ESTIMATE (gCm-2d-1)
10/12/92	CALSHOT	5	10.30	420	11.4	9.2	33.0	6.800	6.514	104.389	0.62	1.17	-----	
	CALSHOT	10		570	15.4	9.2	33.2	6.700	6.506	102.985	0.74	1.74		0.253
	HAMBLE	5	11.30	570	15.4	8.9	32.5	5.915	6.579	89.905	1.44	0.88	-----	
	HAMBLE	10		640	17.3	8.9	32.8	4.794	6.567	73.007	0.78	1.17		0.335
	N.W.NETLEY	5	12.00	880	23.8	9.0	31.6	6.835	6.602	103.525	0.82	0.55	-----	
	N.W.NETLEY	10		1000	27.0	9.0	32.9	6.659	6.548	101.702	0.70	0.72		0.268
	CRACKNORE	5	12.50	520	14.1	9.5	31.0	6.789	6.554	103.591	0.90	1.85	-----	
	CRACKNORE	10		820	22.2	9.6	31.6	6.667	6.514	102.348	0.98	1.56		0.302
	BURY BUOY	5	13.15	400	10.8	9.7	31.1	6.460	6.520	99.075	0.51	0.97	-----	
	BURY BUOY	10		730	19.7	9.8	31.8	5.576	6.477	86.091	0.74	1.32		0.242
11/01/93	CALSHOT	5	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	
	CALSHOT	10		-----	-----	-----	-----	-----	-----	-----	-----	-----		-----
	HAMBLE	5	11.15	330	8.9	-----	-----	-----	-----	-----	-----	-----	-----	
	HAMBLE	10		900	24.3	-----	-----	-----	-----	-----	-----	-----		-----
	N.W.NETLEY	5	11.45	245	6.6	7.9	32.3	6.604	6.739	97.994	0.86	1.31	-----	
	N.W.NETLEY	10		130	3.5	7.9	32.8	6.806	6.717	101.318	0.98	2.56		0.299
	CRACKNORE	5	12.25	120	3.2	7.8	29.9	6.881	6.860	100.304	1.09	2.18	-----	
	CRACKNORE	10		130	3.5	7.7	31.3	6.702	6.814	98.354	0.62	0.91		0.286
	BURY BUOY	5	13.05	355	9.6	7.2	30.1	6.562	6.947	94.452	1.25	1.65	-----	
	BURY BUOY	10		355	9.6	7.1	30.5	6.112	6.946	87.997	1.13	2.09		0.350
26/01/93	CALSHOT	5	11.20	660	17.8	8.2	32.8	6.990	6.672	104.773	0.62	1.33	-----	
	CALSHOT	10		630	17.0	8.2	33.0	6.992	6.663	104.938	0.70	1.20		0.249
	HAMBLE	5	12.00	675	18.3	7.9	31.5	7.018	6.774	103.601	1.05	1.48	-----	
	HAMBLE	10		480	13.0	8.0	32.4	6.816	6.719	101.437	3.51	11.27		0.560
	N.W.NETLEY	5	12.35	495	13.4	8.0	30.8	6.671	6.789	98.261	1.85	3.16	-----	
	N.W.NETLEY	10		540	14.6	8.0	31.4	6.961	6.763	102.930	2.44	4.69		0.534
	CRACKNORE	5	13.15	560	15.1	8.3	30.9	7.048	6.738	104.598	0.86	1.31	-----	
	CRACKNORE	10		590	16.0	8.4	31.4	6.760	6.701	100.877	1.95	2.80		0.392
	BURY BUOY	5	13.45	805	21.8	8.6	30.8	6.903	6.697	103.083	2.50	2.04	-----	
	BURY BUOY	10		400	10.8	8.6	31.1	6.699	6.684	100.229	2.07	4.11		0.561
25/02/93	CALSHOT	5	12.00	925	25.0	7.3	33.5	6.111	6.780	90.129	4.29	3.63	-----	
	CALSHOT	10		770	20.8	7.4	33.6	5.917	6.760	87.526	3.51	2.82		0.871
	HAMBLE	5	12.45	700	18.9	7.3	33.0	7.144	6.802	105.023	5.27	4.76	-----	
	HAMBLE	10		910	24.6	7.3	33.4	7.058	6.785	104.028	4.49	7.39		1.059
	N.W.NETLEY	5	13.20	710	19.2	7.4	31.8	7.000	6.839	102.347	4.10	3.29	-----	
	N.W.NETLEY	10		1080	29.2	7.4	32.4	6.853	6.813	100.588	4.49	3.69		0.947
	CRACKNORE	5	13.55	690	18.7	7.4	30.8	6.998	6.884	101.658	3.90	2.17	-----	
	CRACKNORE	10		1150	31.1	7.3	31.5	6.943	6.869	101.082	3.51	2.82		0.833
	BURY BUOY	5	14.15	900	24.3	7.6	30.9	6.911	6.848	100.926	3.28	1.37	-----	
	BURY BUOY	10		740	20.0	7.5	31.3	6.823	6.846	99.668	3.16	2.12		0.740
12/03/93	CALSHOT	5	12.20	765	20.7	6.8	34.1	7.417	6.833	108.548	9.75	11.36	-----	
	CALSHOT	10		800	21.6	6.8	33.8	6.681	6.846	97.586	5.46	5.62		1.582
	HAMBLE	5	13.00	970	26.2	7.1	33.6	6.914	6.807	101.566	2.77	1.66	-----	
	HAMBLE	10		620	16.8	6.8	33.9	6.635	6.842	96.977	7.41	10.00		1.099
	N.W.NETLEY	5	13.25	770	20.8	7.1	32.4	7.043	6.861	102.658	5.07	4.43	-----	
	N.W.NETLEY	10		1000	27.0	6.9	32.7	5.895	6.879	85.692	5.07	8.12		1.095
	CRACKNORE	5	14.00	960	26.0	7.1	30.7	7.107	6.937	102.455	4.29	2.57	-----	
	CRACKNORE	10		955	25.8	7.0	31.7	6.475	6.908	93.732	3.90	2.17		0.908
	BURY BUOY	5	14.25	750	20.3	7.1	30.9	6.930	6.928	100.033	3.51	2.29	-----	
	BURY BUOY	10		1265	34.2	6.9	31.1	6.886	6.951	99.062	4.29	2.31		0.871

DATE	SITE	DEPTH (m)	SAMPLING TIME	FLOW METER REVOLUTIONS	VOLUME FILTERED (m-3)	TEMPERATURE (oC)	SALINITY (‰)	OXYGEN CONC. (ml O2.l-1)	SATURATION CONC. (ml O2.l-1)	OXYGEN SAT. (%)	CHLOROPHYLL a (mg.m-3)	PHAEO-PIGMENTS (mg.m-3)	SECCHI DISK (m)	PRIMARY PRODUCTION ESTIMATE (gCm-2d-1)
26/03/93	CALSHOT	5	12.05	610	16.5	8.2	32.8	6.851	6.672	102.690	2.34	1.88	1.2	
	CALSHOT	10		820	22.2	8.3	32.7	5.614	6.661	84.286	1.37	1.01		0.478
	HAMBLE	5	12.40	1390	37.6	8.3	32.3	6.839	6.678	102.414	2.54	1.42	1.4	
	HAMBLE	10		890	24.1	8.2	32.5	6.592	6.684	98.617	1.76	1.41		0.535
	N.W.NETLEY	5	13.15	1060	28.7	8.6	31.4	6.102	6.671	91.473	1.09	0.70	1.4	
	N.W.NETLEY	10		1060	28.7	8.4	32.0	5.402	6.675	80.923	1.48	1.05		0.369
	CRACKNORE	5	13.45	990	26.8	8.6	30.9	7.078	6.692	105.764	1.37	1.27	1.8	
	CRACKNORE	10		1250	33.8	8.5	31.2	6.908	6.695	103.188	1.56	0.81		0.403
	BURY BUOY	5	14.15	1190	32.2	8.7	30.9	6.464	6.677	96.809	1.13	1.09	1.7	
	BURY BUOY	10		830	22.4	8.6	31.1	6.556	6.684	98.090	1.25	0.76		0.350
23/04/93	CALSHOT	5	11.30	570	15.4	10.9	32.5	7.718	6.294	122.619	2.54	2.48	1.0	
	CALSHOT	10		1510	40.8	10.9	32.6	7.832	6.290	124.509	2.15	2.08		0.572
	HAMBLE	5	12.00	1370	37.0	11.2	32.0	7.917	6.273	126.203	2.15	1.81	1.2	
	HAMBLE	10		1170	31.6	11.2	31.9	7.927	6.277	126.283	1.95	1.48		0.516
	N.W.NETLEY	5	12.40	1650	44.6	11.6	30.7	7.818	6.270	124.683	1.76	1.94	1.0	
	N.W.NETLEY	10		940	25.4	11.5	30.7	7.967	6.284	126.786	1.56	1.34		0.441
	CRACKNORE	5	13.15	700	18.9	11.4	29.3	7.056	6.353	111.064	1.37	1.54	1.4	
	CRACKNORE	10		1340	36.2	11.2	30.1	6.894	6.349	108.589	0.94	1.12		0.344
	BURY BUOY	5	13.45	1120	30.3	11.2	28.1	7.279	6.429	113.219	0.55	0.77	1.2	
	BURY BUOY	10		1050	28.4	10.7	29.9	6.494	6.426	101.051	0.62	0.80		0.234
06/05/93	CALSHOT	5	10.30	715	19.3	12.8	32.8	7.316	6.033	121.275	3.51	2.29	1.0	
	CALSHOT	10		1260	34.1	12.6	32.9	7.227	6.054	119.371	4.68	3.76		0.908
	HAMBLE	5	11.15	1040	28.1	12.6	32.7	6.990	6.062	115.312	4.49	2.90	1.4	
	HAMBLE	10		590	16.0	12.7	32.7	6.906	6.049	114.167	6.63	4.45		1.190
	N.W.NETLEY	5	11.45	710	19.2	13.1	31.6	6.861	6.040	113.599	3.51	2.29	0.9	
	N.W.NETLEY	10		850	23.0	13.0	31.6	6.017	6.052	99.416	3.51	2.82		0.796
	CRACKNORE	5	12.20	910	24.6	12.9	30.1	4.923	6.122	80.417	1.95	2.01	0.8	
	CRACKNORE	10		920	24.9	13.0	30.8	4.868	6.082	80.033	1.95	2.01		0.496
	BURY BUOY	5	12.45	735	19.9	13.0	30.2	5.356	6.105	87.729	1.76	1.15	1.4	
	BURY BUOY	10		920	24.9	12.9	30.7	5.573	6.099	91.375	1.25	1.18		0.411
21/05/93	CALSHOT	5	10.15	570	15.4	13.0	33.1	7.579	5.996	126.397	10.14	2.52	4.3	
	CALSHOT	10		550	14.9	13.0	33.1	7.534	5.996	125.647	13.65	3.76		2.406
	HAMBLE	5	11.05	530	14.3	13.2	32.4	7.238	5.997	120.690	8.24	2.73	3.5	
	HAMBLE	10		400	10.8	13.2	32.5	6.726	5.993	112.222	8.97	3.69		1.582
	N.W.NETLEY	5	11.45	520	14.1	13.4	31.5	6.515	6.006	108.481	1.33	1.09	3.5	
	N.W.NETLEY	10		430	11.6	13.3	32.0	6.117	6.000	101.958	7.41	1.56		0.961
	CRACKNORE	5	12.30	580	15.7	13.6	31.4	5.695	5.984	95.164	0.70	1.25	2.1	
	CRACKNORE	10		315	8.5	13.4	31.7	6.090	5.998	101.530	1.95	0.95		0.376
	BURY BUOY	5	13.15	530	14.3	13.6	31.6	5.649	5.977	94.512	0.39	0.56	1.7	
	BURY BUOY	10		335	9.1	13.6	31.6	5.439	5.977	90.999	0.39	0.56		0.197
22/06/93	CALSHOT	5	12.10	810	21.9	17.0	33.5	5.814	5.517	105.375	7.02	3.01	2.6	
	CALSHOT	10		930	25.1	16.8	33.8	5.969	5.529	107.958	6.63	2.87		1.432
	HAMBLE	5	13.10	750	20.3	17.4	32.2	5.540	5.518	100.403	10.14	1.47	2.4	
	HAMBLE	10		900	24.3	17.3	33.1	5.432	5.499	98.789	7.80	2.23		1.844
	N.W.NETLEY	5	13.40	560	15.1	17.4	31.8	6.492	5.531	117.374	7.02	1.95	2.4	
	N.W.NETLEY	10		620	16.8	17.6	32.1	5.912	5.500	107.497	7.41	2.62		1.507
	CRACKNORE	5	14.15	220	5.9	17.4	31.1	5.950	5.554	107.122	8.19	2.36	2.8	
	CRACKNORE	10		580	15.7	17.5	31.4	5.510	5.534	99.573	5.46	1.93		1.432
	BURY BUOY	5	15.00	515	13.9	17.3	31.0	4.623	5.569	83.019	5.07	1.26	2.1	
	BURY BUOY	10		420	11.4	17.5	31.4	4.262	5.534	77.020	5.46	1.40		1.133

DATE	SITE	DEPTH (m)	SAMPLING TIME	FLOW METER REVOLUTIONS	VOLUME FILTERED (m-3)	TEMPERATURE (oC)	SALINITY (‰)	OXYGEN CONC. (ml O2.l-1)	SATURATION CONC. (ml O2.l-1)	OXYGEN SAT. (%)	CHLOROPHYLL a (mg.m-3)	PHAEO-PIGMENTS (mg.m-3)	SECCHI DISK (m)	PRIMARY PRODUCTION ESTIMATE (gCm-2d-1)
21/07/93	CALSHOT	5	12.00	940	25.4	17.2	34.5	5.479	5.463	100.293	5.46	8.26	1.4	
	CALSHOT	10		825	22.3	17.6	34.1	5.415	5.434	99.650	3.59	4.22		0.991
	HAMBLE	5	12.30	1430	38.7	17.7	33.5	5.677	5.443	104.297	10.14	6.22	1.6	
	HAMBLE	10		1240	33.5	17.8	33.4	5.127	5.436	94.317	10.92	6.23		2.144
	N.W.NETLEY	5	13.00	860	23.3	17.6	33.4	4.664	5.457	85.470	7.22	5.45	1.2	
	N.W.NETLEY	10		945	25.6	17.8	33.0	4.740	5.449	86.989	13.26	12.07		2.088
	CRACKNORE	5	13.40	820	22.2	17.5	32.7	5.666	5.491	103.196	33.93	10.39	1.6	
	CRACKNORE	10		750	20.3	17.9	32.7	5.327	5.448	97.774	11.31	5.05		4.465
	BURY BUOY	5	14.20	985	26.6	17.9	32.5	5.005	5.455	91.754	33.54	10.78	1.2	
	BURY BUOY	10		465	12.6	17.8	32.9	4.895	5.452	89.780	58.90	12.87		8.996
19/08/93	CALSHOT	5	11.15	750	20.3	18.3	33.4	5.867	5.384	108.969	8.58	9.89	1.4	
	CALSHOT	10		855	23.1	18.4	33.6	5.359	5.367	99.843	7.61	7.96		1.676
	HAMBLE	5	11.55	550	14.9	18.7	33.1	5.584	5.353	104.318	5.85	4.70	1.6	
	HAMBLE	10		710	19.2	18.7	33.4	5.239	5.343	98.048	7.02	6.70		1.358
	N.W.NETLEY	5	12.25	740	20.0	18.6	32.5	5.336	5.382	99.141	8.19	10.28	1.2	
	N.W.NETLEY	10		850	23.0	18.6	32.7	4.143	5.376	77.067	12.09	16.93		2.069
	CRACKNORE	5	13.00	940	25.4	18.7	31.5	5.151	5.404	95.315	9.36	5.94	1.6	
	CRACKNORE	10		665	18.0	18.7	32.0	4.915	5.388	91.220	5.27	4.76		1.526
	BURY BUOY	5	13.25	560	15.1	18.6	31.5	4.718	5.414	87.137	17.16	5.79	1.6	
	BURY BUOY	10		700	18.9	18.6	31.9	4.327	5.402	80.106	5.07	4.69		2.256
01/09/93	CALSHOT	5	10.50	1140	30.8	17.4	34.0	5.264	5.458	96.440	4.88	5.94	1.6	
	CALSHOT	10		1320	35.7	17.4	34.0	5.214	5.458	95.524	5.85	8.93		1.152
	HAMBLE	5	11.25	970	26.2	17.4	33.8	5.399	5.465	98.795	5.46	3.51	2.0	
	HAMBLE	10		1010	27.3	17.4	33.9	4.502	5.462	82.430	5.66	4.90		1.190
	N.W.NETLEY	5	12.00	1120	30.3	17.7	33.1	4.356	5.456	79.836	4.68	4.29	1.6	
	N.W.NETLEY	10		1245	33.7	17.7	33.1	4.805	5.456	88.065	5.27	6.08		1.077
	CRACKNORE	5	12.35	1055	28.5	17.7	32.2	4.637	5.486	84.528	6.44	3.85	1.6	
	CRACKNORE	10		1510	40.8	17.8	32.6	4.629	5.462	84.748	3.12	6.11		1.040
	BURY BUOY	5	13.10	890	24.1	17.9	32.4	4.700	5.458	86.111	10.92	4.91	1.6	
	BURY BUOY	10		960	26.0	17.8	32.8	4.356	5.456	79.846	4.49	5.54		1.601
15/10/93	CALSHOT	5	11.00	760	20.6	14.7	29.5	5.512	5.919	93.121	3.94	5.24	1.2	
	CALSHOT	10		900	24.3	14.9	29.5	5.540	5.895	93.977	4.25	4.51		0.908
	HAMBLE	5	11.35	605	16.4	14.5	28.9	4.570	5.965	76.608	5.54	5.54	1.4	
	HAMBLE	10		800	21.6	14.5	29.3	5.451	5.951	91.601	3.04	3.29		0.946
	N.W.NETLEY	5	12.05	675	18.3	14.7	28.3	5.281	5.963	88.564	3.90	2.70	1.2	
	N.W.NETLEY	10		580	15.7	14.6	28.6	5.476	5.964	91.815	4.41	4.30		0.920
	CRACKNORE	5	12.45	655	17.7	14.8	27.3	5.187	5.987	86.633	2.89	2.18	1.6	
	CRACKNORE	10		850	23.0	14.8	27.9	4.696	5.965	78.722	3.32	3.54		0.718
	BURY BUOY	5	13.20	1080	29.2	15.2	27.3	5.003	5.939	84.246	2.18	2.04	1.6	
	BURY BUOY	10		955	25.8	15.3	27.4	5.435	5.923	91.763	1.01	1.99		0.428
01/11/93	CALSHOT	5	11.00	870	23.5	10.7	32.7	6.835	6.314	108.255	3.28	3.37	1.2	
	CALSHOT	10		620	16.8	10.7	32.6	6.328	6.318	100.162	4.06	4.02		0.827
	HAMBLE	5	11.35	880	23.8	10.6	32.1	5.435	6.352	85.569	2.34	3.04	1.6	
	HAMBLE	10		890	24.1	10.6	32.3	6.359	6.344	100.243	2.85	3.17		0.620
	N.W.NETLEY	5	12.10	1030	27.9	10.6	30.7	6.422	6.408	100.217	3.04	3.13	1.6	
	N.W.NETLEY	10		1300	35.2	10.7	31.3	6.358	6.370	99.814	3.35	3.56		0.735
	CRACKNORE	5	12.45	1035	28.0	10.8	29.9	5.923	6.412	92.368	2.38	2.90	2.0	
	CRACKNORE	10		1230	33.3	10.8	30.6	5.746	6.384	90.004	3.74	5.44		0.710
	BURY BUOY	5	13.15	925	25.0	11.2	29.8	5.055	6.361	79.472	1.87	3.09	1.6	
	BURY BUOY	10		645	17.4	11.2	30.0	5.616	6.353	88.403	0.86	2.10		0.384

DATE	SITE	DEPTH (m)	SAMPLING TIME	FLOW METER REVOLUTIONS	VOLUME FILTERED (m-3)	TEMPERATURE (oC)	SALINITY (‰)	OXYGEN CONC. (ml O2.l-1)	SATURATION CONC. (ml O2.l-1)	OXYGEN SAT. (%)	CHLOROPHYLL a (mg.m-3)	PHAEO-PIGMENTS (mg.m-3)	SECCHI DISK (m)	PRIMARY PRODUCTION ESTIMATE (gCm-2d-1)
15/11/93	CALSHOT	5	10.35	540	14.6	9.7	32.5	7.507	6.462	116.163	4.10	5.67	1.0	
	CALSHOT	10		910	24.6	9.8	32.6	6.816	6.444	105.772	3.98	8.11		0.898
	HAMBLE	5	11.10	790	21.4	9.3	31.6	6.999	6.558	106.726	2.93	2.67	1.2	
	HAMBLE	10		655	17.7	9.4	32.2	6.370	6.518	97.726	3.39	5.37		0.729
	N.W.NETLEY	5	11.40	675	18.3	9.2	30.6	6.081	6.615	91.931	3.08	3.30	1.4	
	N.W.NETLEY	10		1120	30.3	9.6	31.5	6.256	6.518	95.977	3.94	4.72		0.796
	CRACKNORE	5	12.25	555	15.0	9.6	29.4	6.204	6.606	93.915	2.89	3.66	0.5	
	CRACKNORE	10		735	19.9	9.6	30.4	5.664	6.564	86.288	3.63	6.24		0.748
	BURY BUOY	5	12.55	1360	36.8	9.8	29.9	6.297	6.556	96.055	3.35	3.72	1.0	
	BURY BUOY	10		780	21.1	9.8	29.7	5.946	6.564	90.585	2.50	3.57		0.684
01/12/93	CALSHOT	5	10.55	910	24.6	6.2	33.5	7.035	6.957	101.120	3.28	5.75	1.0	
	CALSHOT	10		1260	34.1	5.7	33.8	6.931	7.026	98.643	2.46	2.82		0.673
	HAMBLE	5	11.40	965	26.1	6.2	33.7	6.674	6.948	96.056	2.57	3.34	1.2	
	HAMBLE	10		1090	29.5	6.2	34.0	6.240	6.934	89.986	3.82	8.68		0.735
	N.W.NETLEY	5	12.10	1345	36.4	6.1	32.9	5.848	7.001	83.531	3.55	5.79	1.0	
	N.W.NETLEY	10		765	20.7	6.2	33.3	5.178	6.966	74.330	3.04	5.82		0.755
	CRACKNORE	5	12.40	1125	30.4	5.9	31.8	6.557	7.085	92.546	1.83	3.07	0.8	
	CRACKNORE	10		830	22.4	5.9	32.8	5.956	7.039	84.615	3.00	4.91		0.586
	BURY BUOY	5	13.10	1000	27.0	5.9	31.4	6.378	7.104	89.784	2.54	3.38	0.4	
	BURY BUOY	10		780	21.1	5.9	32.0	6.049	7.076	85.488	2.46	3.88		0.602
28/01/94	CALSHOT	5	10.25	770	20.8	7.0	32.5	7.118	6.872	103.577	2.69	4.06	0.5	
	CALSHOT	10		700	18.9	7.2	32.7	6.940	6.831	101.590	3.90	7.18		0.755
	HAMBLE	5	11.00	910	24.6	6.8	32.1	6.915	6.922	99.894	3.24	4.89	0.5	
	HAMBLE	10		780	21.1	6.8	32.3	6.896	6.913	99.749	3.98	8.16		0.815
	N.W.NETLEY	5	11.40	695	18.8	6.8	30.9	6.959	6.977	99.748	2.18	3.62	0.5	
	N.W.NETLEY	10		960	26.0	6.9	31.6	7.117	6.929	102.719	4.60	7.64		0.773
	CRACKNORE	5	12.15	685	18.5	6.7	29.4	6.990	7.062	98.986	1.29	2.62	1.0	
	CRACKNORE	10		500	13.5	7.0	31.2	6.962	6.930	100.456	3.51	5.46		0.583
	BURY BUOY	5	13.00	620	16.8	6.7	30.1	6.911	7.030	98.314	3.04	3.29	1.0	
	BURY BUOY	10		480	13.0	6.8	30.5	6.736	6.995	96.301	4.13	5.73		0.810
11/02/94	CALSHOT	5	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	
	CALSHOT	10		-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
	HAMBLE	5	10.25	1010	27.3	6.3	31.4	6.592	7.036	93.684	5.77	6.95	0.5	
	HAMBLE	10		705	19.1	6.3	31.6	6.623	7.027	94.247	4.25	5.72		1.084
	N.W.NETLEY	5	11.00	1010	27.3	6.3	29.8	6.471	7.110	91.009	4.56	4.57	0.5	
	N.W.NETLEY	10		2720	73.6	6.5	29.9	6.695	7.072	94.669	4.21	2.91		0.964
	CRACKNORE	5	11.45	1365	36.9	6.5	28.2	6.718	7.151	93.948	3.20	1.23	1.0	
	CRACKNORE	10		1670	45.2	6.5	28.6	6.690	7.132	93.800	1.87	3.25		0.609
	BURY BUOY	5	12.10	845	22.9	6.5	26.5	7.008	7.230	96.924	2.46	2.13	0.5	
	BURY BUOY	10		1025	27.7	6.7	28.3	6.531	7.112	91.827	2.81	3.10		0.628

GROUP	No. m-3															
	10/12/92	26/01/93	25/02/93	12/03/93	26/03/93	23/04/93	06/05/93	21/05/93	22/06/93	21/07/93	19/08/93	01/09/93	15/10/93	15/11/93	01/12/93	28/01/94
ACARTIA COPEPODITE I	0.00	5.62	18.00	35.43	66.67	42.21	49.22	19.48	39.57	104.33	362.07	303.57	29.13	30.82	18.29	2.40
ACARTIA COPEPODITE II	0.00	8.43	8.00	28.99	93.94	64.94	33.68	19.48	27.40	100.39	428.57	237.01	24.27	27.40	26.42	4.81
ACARTIA COPEPODITE III	0.00	2.81	6.00	16.10	100.00	12.99	46.63	6.49	12.18	110.24	298.03	120.13	26.70	30.82	34.55	2.40
ACARTIA COPEPODITES IV FEM	0.00	0.00	0.00	6.44	48.48	9.74	28.50	0.00	6.09	57.09	93.60	42.21	29.13	13.70	36.59	4.81
ACARTIA COPEPODITES IV MAL	0.00	0.00	6.00	12.88	75.76	25.97	31.09	12.99	6.09	47.24	137.93	40.58	19.42	10.27	28.46	0.00
ACARTIA COPEPODITES V FEM	0.00	2.81	4.00	25.76	48.48	9.74	46.63	3.25	0.00	43.31	96.06	21.10	33.98	6.85	26.42	0.00
ACARTIA COPEPODITES V MAL	0.00	2.81	8.00	3.22	33.33	22.73	54.40	12.99	0.00	33.46	86.21	17.86	16.99	10.27	20.33	2.40
ACARTIA BIFILOSA VI FEM	0.00	2.81	14.00	51.53	75.76	292.21	401.55	29.22	0.00	5.91	0.00	0.00	0.00	3.42	2.03	0.00
ACARTIA BIFILOSA VI MAL	0.00	8.43	2.00	19.32	63.64	123.38	173.58	16.23	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ACARTIA DISCAUDATA VI FEM	0.00	0.00	0.00	0.00	6.06	0.00	0.00	0.00	0.00	15.75	81.28	25.97	2.43	6.85	32.52	0.00
ACARTIA DISCAUDATA VI MAL	0.00	0.00	0.00	0.00	0.00	9.74	5.18	6.49	0.00	7.87	34.48	12.99	2.43	0.00	10.16	0.00
ACARTIA CLAUSII VI FEM	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.25	0.00	49.21	12.32	8.12	38.83	23.97	2.03	0.00
ACARTIA CLAUSII VI MAL	0.00	0.00	0.00	0.00	0.00	3.25	0.00	0.00	0.00	90.55	17.24	4.87	19.42	20.55	0.00	0.00
ACARTIA MARGALEFI VI FEM	0.00	0.00	0.00	0.00	0.00	0.00	2.59	0.00	0.00	0.00	0.00	9.74	0.00	0.00	0.00	0.00
ACARTIA MARGALEFI VI MAL	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	17.24	1.62	0.00	0.00	0.00	0.00
TOTAL ACARTIA SP.	0.00	33.71	66.00	199.68	612.12	616.88	873.06	129.87	91.32	665.35	1665.02	845.78	242.72	184.93	237.80	16.83
TEMORA LONGICORNIS COPEPODITE I	0.00	0.00	0.00	3.22	3.03	19.48	49.22	168.83	30.44	23.62	9.85	4.87	0.00	0.00	0.00	0.00
TEMORA LONGICORNIS COPEPODITE II	0.00	0.00	0.00	0.00	3.03	16.23	15.54	113.64	15.22	31.50	7.39	6.49	0.00	3.42	0.00	0.00
TEMORA LONGICORNIS COPEPODITE III	0.00	0.00	0.00	0.00	0.00	9.74	5.18	155.84	15.22	19.69	2.46	3.25	0.00	0.00	0.00	0.00
TEMORA LONGICORNIS COPEPODITE IV	0.00	0.00	0.00	0.00	0.00	16.23	12.95	74.68	6.09	39.37	7.39	1.62	0.00	0.00	0.00	0.00
TEMORA LONGICORNIS COPEPODITE V FEM	0.00	0.00	0.00	0.00	0.00	3.25	5.18	12.99	15.22	29.53	0.00	0.00	2.43	0.00	0.00	0.00
TEMORA LONGICORNIS COPEPODITE V MAL	0.00	0.00	0.00	0.00	0.00	0.00	0.00	12.99	3.04	7.87	4.93	0.00	0.00	0.00	0.00	0.00
TEMORA LONGICORNIS VI FEM	0.00	0.00	0.00	0.00	0.00	9.74	0.00	19.48	6.09	21.65	0.00	1.62	0.00	0.00	0.00	0.00
TEMORA LONGICORNIS VI MAL	0.00	0.00	0.00	0.00	3.03	16.23	0.00	3.25	9.13	17.72	4.93	1.62	0.00	0.00	0.00	0.00
TOTAL TEMORA LONGICORNIS	0.00	0.00	0.00	3.22	9.09	90.91	88.08	561.69	100.46	190.94	36.95	19.48	2.43	3.42	0.00	0.00
CENTROPAGE HAMATUS COPEPODITE I	0.00	0.00	0.00	0.00	0.00	3.25	12.95	97.40	91.32	120.08	78.82	110.39	14.56	0.00	0.00	0.00
CENTROPAGE HAMATUS COPEPODITE II	0.00	0.00	0.00	0.00	6.06	12.99	10.36	48.70	94.37	78.74	98.52	97.40	12.14	0.00	0.00	0.00
CENTROPAGE HAMATUS COPEPODITE III	0.00	0.00	0.00	0.00	3.03	0.00	36.27	35.71	76.10	64.96	100.99	64.94	4.85	17.12	0.00	0.00
CENTROPAGE HAMATUS COPEPODITE IV	4.39	0.00	0.00	3.22	0.00	3.25	5.18	12.99	45.66	55.12	96.06	38.96	12.14	34.25	14.23	0.00
CENTROPAGE HAMATUS COPEPODITE V FEM	0.00	0.00	0.00	0.00	0.00	0.00	0.00	16.23	6.09	25.59	19.70	6.49	0.00	10.27	0.00	0.00
CENTROPAGE HAMATUS COPEPODITE V MAL	0.00	0.00	0.00	0.00	3.03	0.00	12.95	6.49	24.35	17.72	32.02	4.87	4.85	3.42	2.03	0.00
CENTROPAGE HAMATUS VI FEM	0.00	0.00	0.00	0.00	3.03	6.49	2.59	0.00	9.13	29.53	22.17	11.36	2.43	0.00	2.03	0.00
CENTROPAGE HAMATUS VI MAL	0.00	0.00	0.00	0.00	0.00	6.49	0.00	0.00	12.18	23.62	4.93	0.00	0.00	0.00	6.10	0.00
TOTAL CENTROPAGES HAMATUS	4.39	0.00	0.00	3.22	15.15	32.47	80.31	217.53	359.21	415.35	453.20	334.42	50.97	65.07	24.39	0.00
PARACALANUS/PSEUDOCALANUS COPEPODITE I	0.00	0.00	0.00	3.22	0.00	16.23	12.95	6.49	0.00	0.00	0.00	0.00	36.41	37.67	4.07	0.00
PARACALANUS/PSEUDOCALANUS COPEPODITE II	0.00	0.00	0.00	0.00	6.06	9.74	2.59	0.00	0.00	0.00	0.00	1.62	41.26	6.85	8.13	0.00
PARACALANUS/PSEUDOCALANUS COPEPODITE III	0.00	0.00	0.00	0.00	0.00	0.00	7.77	9.74	0.00	0.00	0.00	0.00	21.84	3.42	2.03	0.00
PARACALANUS/PSEUDOCALANUS COPEPODITE IV FEM	0.00	0.00	0.00	6.44	0.00	3.25	0.00	3.25	0.00	0.00	0.00	1.62	14.56	17.12	6.10	0.00
PARACALANUS/PSEUDOCALANUS COPEPODITE IV MAL	4.39	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	19.42	0.00	0.00	0.00
PARACALANUS/PSEUDOCALANUS COPEPODITE V FEM	0.00	0.00	0.00	3.22	0.00	3.25	0.00	0.00	0.00	0.00	0.00	0.00	16.99	0.00	8.13	0.00
PARACALANUS/PSEUDOCALANUS COPEPODITE V MAL	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.85	6.85	2.03	0.00
PARACALANUS PARVUS VI FEM	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.62	21.84	27.40	6.10	0.00
PARACALANUS PARVUS VI MAL	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.85	3.42	4.07	2.40
PSEUDOCALANUS ELONGATUS VI FEM	0.00	0.00	0.00	0.00	0.00	3.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	7.21
PSEUDOCALANUS ELONGATUS VI MAL	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.07	0.00
TOTAL PARACALANUS/PSEUDOCALANUS	4.39	0.00	0.00	12.88	6.06	35.71	23.32	19.48	0.00	0.00	0.00	4.87	182.04	102.74	44.72	9.62
TOTAL CALANOID COPEPODS	8.77	33.71	66.00	219.00	642.42	775.97	1064.77	928.57	550.99	1271.65	2155.17	1204.55	478.16	356.16	306.91	26.44
CALANOIDS+NAUPLII	109.65	171.35	114.00	238.33	648.48	1240.26	1670.98	1668.83	550.99	1271.65	3435.96	1980.52	992.72	530.82	605.69	120.19

GROUP	No. m-3															
	10/12/92	26/01/93	25/02/93	12/03/93	26/03/93	23/04/93	06/05/93	21/05/93	22/06/93	21/07/93	19/08/93	01/09/93	15/10/93	15/11/93	01/12/93	28/01/94
COPEPOD NAUPLII	100.88	137.64	48.00	19.32	6.06	464.29	606.22	740.26	0.00	0.00	1280.79	775.97	514.56	174.66	298.78	93.75
BARNACLE NAUPLII	52.63	103.93	94.00	383.25	639.39	246.75	753.89	107.14	1092.85	1242.13	820.20	560.06	490.29	222.60	134.15	96.15
BARNACLE CIRRIPEDES	0.00	0.00	0.00	0.00	6.06	0.00	0.00	3.25	3.04	0.00	9.85	0.00	0.00	0.00	0.00	0.00
BARANACLE PARASITIC	0.00	0.00	0.00	0.00	6.06	0.00	0.00	0.00	6.09	0.00	2.46	3.25	0.00	0.00	0.00	0.00
TOTAL BARNACLE	52.63	103.93	94.00	383.25	651.52	246.75	753.89	110.39	1101.98	1242.13	832.51	563.31	490.29	222.60	134.15	96.15
POLYCHAETE LARVAE	4.39	36.52	52.00	12.88	45.45	19.48	67.36	22.73	188.74	61.02	34.48	12.99	43.69	6.85	8.13	14.42
BIVALVE LARVAE	4.39	2.81	0.00	0.00	0.00	9.74	2.59	214.29	200.91	312.99	270.94	51.95	12.14	30.82	4.07	4.81
BRYOZOAN LARVAE	70.18	81.46	24.00	35.43	9.09	35.71	25.91	16.23	91.32	90.55	0.00	76.30	43.69	65.07	48.78	175.48
ASCIDIAN LARVAE	0.00	2.81	0.00	0.00	0.00	0.00	0.00	3.25	30.44	9.84	4.93	1.62	7.28	0.00	2.03	0.00
VELIGER LARVAE	4.39	2.81	6.00	0.00	3.03	90.91	380.83	81.17	213.09	411.42	421.18	112.01	291.26	58.22	16.26	12.02
BRACHYURANS	0.00	0.00	0.00	19.32	6.06	16.23	15.54	12.99	21.31	15.75	4.93	0.00	0.00	0.00	0.00	0.00
FORAMANIFERA	8.77	294.94	196.00	0.00	39.39	204.55	341.97	0.00	0.00	265.75	463.05	66.56	121.36	890.41	634.15	533.65
EUTERPINA ACUTIFRONS	30.70	8.43	0.00	0.00	6.06	3.25	0.00	9.74	210.05	1120.08	2490.15	2071.43	2524.27	732.88	170.73	0.00
OTHER HARPACTICOIDS	4.39	19.66	10.00	9.66	6.06	19.48	49.22	6.49	70.02	466.54	61.58	51.95	19.42	41.10	40.65	14.42
TOTAL HARPACTICOIDS	35.09	28.09	10.00	9.66	12.12	22.73	49.22	16.23	280.06	1586.61	2551.72	2123.38	2543.69	773.97	211.38	14.42
CYCLOPOIDS	0.00	11.24	0.00	0.00	0.00	3.25	0.00	0.00	0.00	0.00	7.39	1.62	0.00	0.00	0.00	19.23
LITTORINA EGG CAPSULES	0.00	14.04	32.00	45.09	60.61	84.42	28.50	9.74	0.00	1.97	0.00	0.00	0.00	0.00	0.00	14.42
MITES	4.39	8.43	0.00	3.22	6.06	12.99	12.95	0.00	0.00	15.75	22.17	21.10	0.00	20.55	10.16	0.00
EGGS	4.39	95.51	8.00	0.00	51.52	35.71	7.77	22.73	103.50	5.91	0.00	4.87	24.27	17.12	6.10	33.65
OIKOPLEURA SP.	0.00	0.00	0.00	0.00	0.00	3.25	72.54	1172.08	3.04	133.86	93.60	95.78	111.65	113.01	34.55	0.00
OSTRACODS	0.00	0.00	0.00	0.00	0.00	3.25	2.59	6.49	0.00	0.00	0.00	3.25	2.43	0.00	2.03	0.00
FISH LARVAE	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00

APPENDIX 3

DEVELOPMENT RATE STUDY 1

TIME 0

SAMPLING DATE:		22/08/94
WEATHER CONDITIONS:		Warm, clear sky, water calm.
SAMPLING TIME:		
CALSHOT PIER	54μm sample	11.55
	Start Incubation	12.15

TIME t

SAMPLING DATE:		24/08/94
WEATHER CONDITIONS:		
SAMPLING TIME:		Water calm, sunny with occasional cloud cover.
CALSHOT PIER	54μm sample	11.00
	End Incubation	11.55

DEVELOPMENT RATE STUDY 2

TIME 0

SAMPLING DATE:		21/09/94
WEATHER CONDITIONS:		Overcast with occasional bright spells towards the end of sampling, cool.
SAMPLING TIME:		
CALSHOT PIER	54μm sample	12.00
	Start Incubation	12.20

TIME t

SAMPLING DATE:		23/09/94
WEATHER CONDITIONS:		Overcast with bright patches, water calm.
SAMPLING TIME:		
CALSHOT PIER	54μm sample	11.30
	End Incubation	12.25

DEVELOPMENT RATE STUDY 3

TIME 0

SAMPLING DATE:		19/10/94
WEATHER CONDITIONS:		Overcast grey sky, heavy rain and fog.
SAMPLING TIME:		
CALSHOT PIER	54μm sample	11.15
	Start Incubation	11.55

TIME t

SAMPLING DATE:		21/10/94
WEATHER CONDITIONS:		Overcast with sunny patches, water calmer than at previous

sampling.

SAMPLING TIME:

CALSHOT PIER	54μm sample	10.10
	End Incubation	11.35

DEVELOPMENT RATE STUDY 4

TIME 0

SAMPLING DATE: 19/12/94

WEATHER CONDITIONS: Clear sky with slight cloud cover, water fairly calm, cold.

SAMPLING TIME:

CALSHOT PIER	54μm sample	11.05
	Start Incubation	11.45

TIME t

SAMPLING DATE: 21/12/94

WEATHER CONDITIONS: Overcast although clearing through day, hazy, very cold, water very calm.

SAMPLING TIME:

CALSHOT PIER	54μm sample	11.10
	End Incubation	12.30

DEVELOPMENT RATE STUDY 5

TIME 0

SAMPLING DATE: 07/02/95

WEATHER CONDITIONS: Completely overcast and dull, water calm.

SAMPLING TIME:

CALSHOT PIER	54μm sample	11.05
	Start Incubation	12.30

TIME t

SAMPLING DATE: 09/02/95

WEATHER CONDITIONS: Overcast and dull, water rougher than previous sampling event.

SAMPLING TIME:

CALSHOT PIER	54μm sample	11.25
	End Incubation	12.40

DEVELOPMENT RATE STUDY 6

TIME 0

SAMPLING DATE: 21/02/95

WEATHER CONDITIONS: Cold, Clear sky with broken cloud, windy and choppy sea.

COMMENTS: 160μm mesh net used for sample collection for first time.

SAMPLING TIME:

CALSHOT PIER	54μm sample	11.30
	Start Incubation	12.15

TIME t

SAMPLING DATE: 23/02/95

WEATHER CONDITIONS: Fine, Sunny with broken cloud.

SAMPLING TIME:

CALSHOT PIER	54μm sample	10.30
	End Incubation	11.50

DEVELOPMENT RATE STUDY 7

TIME 0

SAMPLING DATE: 09/03/95

WEATHER CONDITIONS: Overcast, rained for short period during sampling, water fairly calm.

COMMENTS:

SAMPLING TIME:

CALSHOT PIER	54μm sample	11.00
	Start Incubation	11.50

TIME t

SAMPLING DATE: 10/03/95

WEATHER CONDITIONS: Warm, very sunny, slightly breezy.

COMMENTS: Samples collected by road as boat not available, surface salinity, temperature and water samples collected from the pier rather than the usual collection point.

SAMPLING TIME:

CALSHOT PIER	54μm sample	NA
	End Incubation	12.55

DEVELOPMENT RATE STUDY 8

TIME 0

SAMPLING DATE: 29/03/95

WEATHER CONDITIONS: Clear sky, very bright and sunny. Strong wind with severe chill.

SAMPLING TIME:

CALSHOT PIER	54μm sample	11.15
	Start Incubation	12.05

TIME t

SAMPLING DATE: 31/03/95

WEATHER CONDITIONS: Overcast, slight breeze.

SAMPLING TIME:

CALSHOT PIER	54μm sample	11.15
	End Incubation	12.25

DEVELOPMENT RATE STUDY 9

TIME 0

SAMPLING DATE: 19/04/95

WEATHER CONDITIONS: Warm and sunny. Water very calm. Clear sky, becoming cloudier as day progressed.

SAMPLING TIME:

CALSHOT PIER	54μm sample	11.15
	Start Incubation	12.15

TIME t

SAMPLING DATE: 21/04/95

WEATHER CONDITIONS: Calm, sunny, slight cloud cover.

SAMPLING TIME:

CALSHOT PIER	54μm sample	10.30
	End Incubation	11.45

DEVELOPMENT RATE STUDY 10

TIME 0

SAMPLING DATE: 18/05/95

WEATHER CONDITIONS: Overcast with clear spells. Slight wind and cold.

SAMPLING TIME:

CALSHOT PIER	54μm sample	10.55
	Start Incubation	12.05

TIME t

SAMPLING DATE: 19/05/95

WEATHER CONDITIONS: Changeable, overcast with sunny patches. Water calm with light breeze.

SAMPLING TIME:

CALSHOT PIER	54μm sample	11.45
	End Incubation	13.05

APPENDIX 4

Species	Temperature (°C)	Measured g (d^{-1})	Body Weight ($\mu gC.Individual^{-1}$)	Predicted g (d^{-1}) Huntley-Lopez	Ikeda-Motoda	Multiple Linear Regression (This Study)	Reference
Natural feeding conditions (including *in situ* incubation techniques):							
Acartiidae:							
Acartia longiremis	16.5	0.22	0.48	0.278	0.262	0.234	9
A.longiremis	16.5	0.11	0.8	0.278	0.227	0.201	9
A.longiremis	16.5	0.07	4.4	0.278	0.139	0.121	9
Acrocalanidae:							
Acrocalanus inermis	24.5	0.36	0.018	0.675	2.577	0.981	8
A.inermis	24.5	0.78	0.024	0.675	2.314	0.900	8
A.inermis	24.5	1.18	0.032	0.675	2.077	0.827	8
A.inermis	24.5	1.22	0.044	0.675	1.843	0.752	8
A.inermis	24.5	0.56	0.0525	0.675	1.725	0.719	8
A.inermis	24.5	0.28	0.07	0.675	1.549	0.655	8
A.inermis	24.5	0.24	0.0795	0.675	1.477	0.630	8
A.inermis	24.5	0.52	0.0935	0.675	1.390	0.601	8
A.inermis	24.5	0.82	0.163	0.675	1.128	0.509	8
A.inermis	24.5	0.86	0.3095	0.675	0.887	0.421	8
A.inermis	24.5	0.76	0.595	0.675	0.694	0.346	8
A.inermis	24.5	0.31	0.825	0.675	0.614	0.314	8
A.inermis	24.5	0.14	0.9	0.675	0.594	0.306	8
Calanidae:							
Calanus finmarchicus	16.5	0.11	50	0.278	0.069	0.059	9
Calanus propinquus	0	0.0274	230	0.045	0.015	0.015	5
C. propinquus	0	0.0555	209	0.045	0.015	0.015	5
C. propinquus	0	0.0136	220	0.045	0.015	0.015	5
Calanoides acutus	0	0.0038	133	0.045	0.016	0.017	5
C. acutus	0	0.0418	141	0.045	0.016	0.017	5
C. acutus	0	0.0037	135	0.045	0.016	0.017	5
Undinula vulgaris	29.85	0.048	88.4	1.223	0.159	0.106	6
Centropagidae:							
Centropages typicus	16.5	0.28	0.52	0.278	0.256	0.228	9
C.typicus	16.5	0.34	1.04	0.278	0.210	0.186	9
C.typicus	16.5	0.28	2	0.278	0.174	0.153	9

C.typicus	16.5	0.25	12.3	0.278	0.103	0.089	9
Centropages verificatus	28	0.62	0.442	0.996	1.234	0.462	10
C.verificatus	28	0.50	1.012	0.996	0.877	0.361	10
C.verificatus	28	0.44	2.150	0.996	0.642	0.289	10
C.verificatus	28	0.38	3.901	0.996	0.502	0.242	10
Eucalanidae:							
Rhincalanus gigas	0	0.001	503	0.045	0.014	0.012	5
R. gigas	0	0.0084	511	0.045	0.014	0.011	5
R. gigas	0	0.0006	492	0.045	0.014	0.012	5
Metridiidae:							
Metridia gerlachei	0	0.0568	162	0.045	0.016	0.016	5
M. gerlachei	0	0.0901	161	0.045	0.016	0.016	5
M. gerlachei	0	0.0195	159	0.045	0.016	0.016	5
Paracalanidae:							
Paracalanus parvus	16.5	0.25	0.24	0.278	0.320	0.287	9
P.parvus	16.5	0.35	0.44	0.278	0.269	0.240	9
P.parvus	16.5	0.23	0.8	0.278	0.227	0.201	9
P.parvus	16.5	0.38	1.52	0.278	0.188	0.166	9
P.parvus	16.5	0.1	2.68	0.278	0.160	0.140	9
P.parvus	16.5	0.11	3.3	0.278	0.151	0.132	9
Paracalanus sp.	28	4.133	0.0024	0.996	10.647	2.182	3
Paracalanus sp.	28	2.632	0.008	0.996	6.474	1.525	3
Paracalanus sp.	28	0.699	0.02	0.996	4.434	1.161	3
Paracalanus sp.	28	0.494	0.028	0.996	3.859	1.050	3
Paracalanus sp.	28	0.773	0.036	0.996	3.478	0.975	3
Paracalanus sp.	28	1.073	0.052	0.996	2.988	0.874	3
Paracalanus sp.	28	1.541	0.108	0.996	2.209	0.703	3
Paracalanus sp.	28	0.552	0.276	0.996	1.499	0.532	3
Paracalanus sp.	28	0.854	0.4	0.996	1.286	0.476	3
Paracalanus sp.	28	0.464	0.728	0.996	1.004	0.398	3
Paracalanus sp.	28	0.701	1.032	0.996	0.870	0.359	3
Paracalanus aculeatus	28	0.58	0.146	0.996	1.950	0.643	10
P.aculeatus	28	0.65	0.355	0.996	1.351	0.493	10
P.aculeatus	28	0.38	0.742	0.996	0.996	0.396	10
P.aculeatus	28	0.29	1.212	0.996	0.814	0.342	10

Pseudocalanidae:							
Pseudocalanus sp.	16.5	0.23	0.12	0.278	0.391	0.353	9
Pseudocalanus sp.	16.5	0.27	0.2	0.278	0.338	0.303	9
Pseudocalanus sp.	16.5	0.23	0.32	0.278	0.295	0.264	9
Pseudocalanus sp.	16.5	0.35	0.48	0.278	0.262	0.234	9
Pseudocalanus sp.	16.5	0.26	0.72	0.278	0.233	0.207	9
Pseudocalanus sp.	16.5	0.20	1.24	0.278	0.200	0.176	9
Pseudocalanus sp.	16.5	0.15	2.0	0.278	0.174	0.153	9
Temoridae:							
Eurytemora affinis	9.9	0.198	0.612	0.134	0.104	0.149	2
E.affinis	9.9	0.107	1.04	0.134	0.093	0.127	2
E.affinis	9.9	0.073	1.528	0.134	0.086	0.114	2
E.affinis	9.9	0.198	0.612	0.134	0.104	0.149	2
E.affinis	9.9	0.108	1.04	0.134	0.093	0.127	2
E.affinis	9.9	0.073	1.528	0.134	0.086	0.114	2
E.affinis	14.4	0.18	0.9	0.220	0.168	0.172	2
E.affinis	14.4	0.079	1.38	0.220	0.150	0.151	2
E.affinis	14.4	0.18	0.9	0.220	0.168	0.172	2
E.affinis	14.4	0.082	1.388	0.220	0.150	0.151	2
E.affinis	6.5	0.1	0.144	0.092	0.087	0.189	2
E.affinis	6.5	0.064	0.204	0.092	0.082	0.170	2
E.affinis	6.5	0.044	0.312	0.092	0.076	0.150	2
E.affinis	6.5	0.144	0.416	0.092	0.072	0.138	2
E.affinis	6.5	0.024	0.9	0.092	0.063	0.110	2
E.affinis	6.5	0.012	1.26	0.092	0.059	0.099	2
Temora longicornis	16.5	0.39	0.12	0.278	0.391	0.353	9
T.longicornis	16.5	0.35	0.2	0.278	0.338	0.303	9
T.longicornis	16.5	0.20	0.28	0.278	0.306	0.274	9
T.longicornis	16.5	0.37	0.56	0.278	0.251	0.223	9
T.longicornis	16.5	0.03	9.4	0.278	0.111	0.096	9
Temora turbinata	28	0.40	0.352	0.996	1.356	0.494	10
T.turbinata	28	0.44	0.637	0.996	1.061	0.414	10
T.turbinata	28	0.45	1.181	0.996	0.822	0.345	10
T.turbinata	28	0.27	1.987	0.996	0.663	0.295	10
T.turbinata	28	0.40	2.941	0.996	0.564	0.263	10
Mixed small copepods	29.85	0.086	9.3	1.223	0.421	0.207	6
Small copepods	0	0.5000	7	0.045	0.022	0.041	5

Small copepods	0	1.0833	6	0.045	0.023	0.043	5
Small copepods	0	0.1875	8	0.045	0.022	0.039	5
Copepodids	0	0.0341	82	0.045	0.017	0.020	5
Copepodids	0	0.0778	99	0.045	0.017	0.019	5
Copepodids	0	0.0058	69	0.045	0.017	0.021	5

Laboratory 'food saturated' and *in situ* maximum conditions:

Calanidae:							
Undinula darwini	27.5	0.281	16.733	-	-	-	7
Calanus agulhensis	15.5	0.46	1.88	-	-	-	11
C.agulhensis	15.5	0.44	3.72	-	-	-	11
C.agulhensis	15.5	0.41	8.88	-	-	-	11
C.agulhensis	15.5	0.33	17.68	-	-	-	11
C.agulhensis	15.5	0.27	35.52	-	-	-	11
C.agulhensis	15.5	0.18	80.80	-	-	-	11
Calanus pacificus	15.5	0.45	2.00	-	-	-	11
C.pacificus	15.5	0.41	3.60	-	-	-	11
C.pacificus	15.5	0.36	10.00	-	-	-	11
C.pacificus	15.5	0.28	23.20	-	-	-	11
C.pacificus	15.5	0.15	56.00	-	-	-	11
Candaciidae:							
Candacia aethiopica	27.5	0.025	27.533	-	-	-	7
Centropagidae:							
Sinocalanus tenellus	20.3	0.879	0.039	-	-	-	1
S.tenellus	20.3	0.601	0.070	-	-	-	1
S.tenellus	20.3	0.645	0.108	-	-	-	1
S.tenellus	20.3	0.518	0.171	-	-	-	1
S.tenellus	20.3	1.058	0.251	-	-	-	1
S.tenellus	20.3	0.777	0.491	-	-	-	1
S.tenellus	20.3	0.914	0.836	-	-	-	1
S.tenellus	20.3	0.36	1.527	-	-	-	1
S.tenellus	20.3	0.46	2.154	-	-	-	1
S.tenellus	20.3	0.547	1.527	-	-	-	1
S.tenellus	20.3	0.53	2.654	-	-	-	1

Eucalanidae:							
Rhincalanus sp.	27.5	0.038	43.067	-	-	-	7
Euchaetidae:							
Euchaeta marina	27.5	0.115	38.133	-	-	-	7
Metridiidae:							
Pleuromamma abdominalis	27.5	0.022	94.467	-	-	-	7
Oncaeidae:							
Oncaea sp.	27.5	0.099	4.333	-	-	-	7
Pseudiaptomidae:							
Pseudodiaptomus marinus	20	0.283	0.075	-	-	-	4
P.marinus	20	0.309	0.103	-	-	-	4
P.marinus	20	0.246	0.145	-	-	-	4
P.marinus	20	0.213	0.192	-	-	-	4
P.marinus	20	0.105	0.246	-	-	-	4
P.marinus	20	0.568	0.280	-	-	-	4
P.marinus	20	0.567	0.490	-	-	-	4
P.marinus	20	0.219	0.857	-	-	-	4
P.marinus	20	0.203	1.295	-	-	-	4
P.marinus	20	0.309	1.909	-	-	-	4
P.marinus	20	0.277	1.295	-	-	-	4
P.marinus	20	0.342	2.729	-	-	-	4
P.marinus	20	0.183	6.466	-	-	-	4

References: 1,†Kimoto *et al.*, (1986). 2,*Burkill and Kendall (1982). 3,*Newbury and Bartholomew (1976). 4,†Uye *et al.*, (1983). *5,Schnack *et al.* (1985). 6,*Gerber and Gerber (1979). 7,†Petipa *et al.*, (1975b) 8,*Kimmerer (1980) - taken from table 9 page 78. 9,*Peterson *et al.*, (1991) - including *pers. comm.* of data from original paper. 10, *Chisholm and Roff (1990b). 11, †Data as derived in Peterson and Hutchings, 1995.

† Food saturated conditions

*Natural feeding conditions/*in situ* incubation

APPENDIX 5

CALSHOT

DATE	DAY NUMBER	NUMBER OF DAYS BETWEEN SAMPLES	NUMBER OF INDIVIDUALS (m-3)	MEAN DIAMETER (mm)	MEAN DRY WEIGHT (mg)	MEAN CARBON WEIGHT (ugC)	INCREMENT SUMMATION		INSTANTANEOUS GROWTH		I.S.G.R.
							PRODUCTION (ugCm-3)	ugCm-3d-1	PRODUCTION (ugCm-3)	ugCm-3d-1	(d-1)
10/12/92	344		0.000	---	---	---					
		32					0.000	0.0000	0.000	0.0000	*
11/01/93	376		0.000	---	---	---					
		15					0.000	0.0000	0.000	0.0000	*
26/01/93	391		0.000	---	---	---					
		30					0.000	0.0000	0.000	0.0000	*
25/02/93	421		0.000	---	---	---					
		15					0.000	0.0000	0.000	0.0000	*
12/03/93	436		0.000	---	---	---					
		14					0.000	0.0000	0.000	0.0000	*
26/03/93	450		0.000	---	---	---					
		28					0.000	0.0000	0.000	0.0000	*
23/04/93	478		0.000	---	---	---					
		13					0.000	0.0000	0.000	0.0000	*
06/05/93	491		0.000	---	---	---					
		15					0.000	0.0000	0.000	0.0000	*
21/05/93	506		0.000	---	---	---					
		32					0.000	0.0000	0.000	0.0000	*
22/06/93	538		0.000	---	---	---					
		29					0.000	0.0000	0.000	0.0000	*
21/07/93	567		0.000	---	---	---					
		29					0.000	0.0000	0.000	0.0000	*
19/08/93	596		0.000	---	---	---					
		13					0.000	0.0000	0.000	0.0000	*
01/09/93	609		0.000	---	---	---					
		44					0.000	0.0000	0.000	0.0000	*
15/10/93	653		0.000	---	---	---					
		17					0.000	0.0000	0.000	0.0000	*
01/11/93	670		0.000	---	---	---					
		14					0.000	0.0000	0.000	0.0000	*
15/11/93	684		0.000	---	---	---					
		16					0.000	0.0000	0.000	0.0000	*
01/12/93	700		0.000	---	---	---					
		59					0.000	0.0000	0.000	0.0000	*
28/01/94	759		0.000	---	---	---					
		14					0.000	0.0000	0.000	0.0000	*
11/02/94	773		---	---	---	---					
							0.000		0.000		0.0000

HAMBLE

DATE	DAY NO.	NUMBER OF DAYS BETWEEN SAMPLES	NO. OF INDIVIDUALS (m-3)	MEAN DIAMETER (mm)	MEAN DRY WEIGHT (mg)	MEAN CARBON WEIGHT (ugC)	INCREMENT SUMMATION PRODUCTION (ugCm-3)	INCREMENT SUMMATION ugCm-3d-1	INSTANTANEOUS GROWTH PRODUCTION (ugCm-3)	INSTANTANEOUS GROWTH ugCm-3d-1	I.S.G.R. (d-1)
10/12/92	344		0.000	---------	---------	---------					
		32					0.000	0.0000	0.000		*
11/01/93	376		0.000	---------	---------	---------					
		15					0.000	0.0000	0.000		*
26/01/93	391		0.000	---------	---------	---------					
		30					RECRUITMENT:	0.0176	RECRUITMENT:	0.0176	*
25/02/93	421		0.273	1.76	0.029	1.933	0.528		0.528		
		15					RECRUITMENT:	0.1231	RECRUITMENT:	0.1231	*
12/03/93	436		0.305	2.75	0.112	7.783	1.846		1.846		
		14					0.061	0.0043	0.060	0.0043	0.002
26/03/93	450		0.094	3.00	0.115	8.088					
		28					0.000	0.0000	0.000	0.0000	*
23/04/93	478		0.000	---------	---------	---------					
		13					0.000	0.0000	0.000	0.0000	*
06/05/93	491		0.000	---------	---------	---------					
		15					0.000	0.0000	0.000	0.0000	*
21/05/93	506		0.000	---------	---------	---------					
		32					0.000	0.0000	0.000	0.0000	*
22/06/93	538		0.000	---------	---------	---------					
		29					0.000	0.0000	0.000	0.0000	*
21/07/93	567		0.000	---------	---------	---------					
		29					0.000	0.0000	0.000	0.0000	*
19/08/93	596		0.000	---------	---------	---------					
		13					0.000	0.0000	0.000	0.0000	*
01/09/93	609		0.000	---------	---------	---------					
		44					0.000	0.0000	0.000	0.0000	*
15/10/93	653		0.000	---------	---------	---------					
		17					0.000	0.0000	0.000	0.0000	*
01/11/93	670		0.000	---------	---------	---------					
		14					0.000	0.0000	0.000	0.0000	*
15/11/93	684		0.000	---------	---------	---------					
		16					0.000	0.0000	0.000	0.0000	*
01/12/93	700		0.000	---------	---------	---------					
		59					0.000	0.0000	0.000	0.0000	*
28/01/94	759		0.000	---------	---------	---------					
		14					0.000	0.0000	0.000	0.0000	*
11/02/94	773		0.000	---------	---------	---------					
							2.435		2.434		

N.W.NETLEY

DATE	DAY NO.	NUMBER OF DAYS BETWEEN SAMPLES	NO. OF INDIVIDUALS (m-3)	MEAN DIAMETER (mm)	MEAN DRY WEIGHT (mg)	MEAN CARBON WEIGHT (ugC)	INCREMENT SUMMATION PRODUCTION (ugCm-3)	INCREMENT SUMMATION ugCm-3d-1	INSTANTANEOUS GROWTH PRODUCTION (ugCm-3)	INSTANTANEOUS GROWTH ugCm-3d-1	I.S.G.R. (d-1)
10/12/92	344		0.000	---------	---------	---------					
		32					0.000	0.0000	0.000	0.0000	*
11/01/93	376		0.000	---------	---------	---------					
		15					0.000	0.0000	0.000	0.0000	*
26/01/93	391		0.000	---------	---------	---------					
		30					RECRUITMENT:	0.0181	RECRUITMENT:	0.0181	*
25/02/93	421		0.250	1.85	0.032	2.167	0.542		0.542		
		15					RECRUITMENT:	0.1235	RECRUITMENT:	0.1235	*
12/03/93	436		0.847	1.96	0.041	2.827	1.853		1.853		
		14					RECRUITMENT:	1.5862	RECRUITMENT:	1.5862	*
26/03/93	450		2.421	2.91	0.142	9.938	22.207		22.207		
		28					153.502	5.4822	81.942	2.9265	0.089
23/04/93	478		0.343	5.78	1.726	121.010					
		13					670.785	51.5988	456.958	35.1506	0.280
06/05/93	491		0.069	19.32	65.578	3377.247					
		15					0.000	0.0000	0.000	0.0000	*
21/05/93	506		0.000	---------	---------	---------					
		32					0.000	0.0000	0.000	0.0000	*
22/06/93	538		0.000	---------	---------	---------					
		29					0.000	0.0000	0.000	0.0000	*
21/07/93	567		0.000	---------	---------	---------					
		29					0.000	0.0000	0.000	0.0000	*
19/08/93	596		0.000	---------	---------	---------					
		13					0.000	0.0000	0.000	0.0000	*
01/09/93	609		0.000	---------	---------	---------					
		44					0.000	0.0000	0.000	0.0000	*
15/10/93	653		0.000	---------	---------	---------					
		17					0.000	0.0000	0.000	0.0000	*
01/11/93	670		0.000	---------	---------	---------					
		14					0.000	0.0000	0.000	0.0000	*
15/11/93	684		0.000	---------	---------	---------					
		16					0.000	0.0000	0.000	0.0000	*
01/12/93	700		0.000	---------	---------	---------					
		59					0.000	0.0000	0.000	0.0000	*
28/01/94	759		0.000	---------	---------	---------					
		14					0.000	0.0000	0.000	0.0000	*
11/02/94	773		0.000	---------	---------	---------					
							848.888		563.502		

CRACKNORE

DATE	DAY NO.	NUMBER OF DAYS BETWEEN SAMPLES	NO. OF INDIVIDUALS (m-3)	MEAN DIAMETER (mm)	MEAN DRY WEIGHT (mg)	MEAN CARBON WEIGHT (ugC)	INCREMENT SUMMATION		INSTANTANEOUS GROWTH		I.S.G.R.
							PRODUCTION (ugCm-3)	ugCm-3d-1	PRODUCTION (ugCm-3)	ugCm-3d-1	(d-1)
10/12/92	344		0.000	---------	---------	---------					
		32					0.000	0.0000	0.000	0.0000	*
11/01/93	376		0.000	---------	---------	---------					
		15					0.000	0.0000	0.000	0.0000	*
26/01/93	391		0.000	---------	---------	---------					
		30					RECRUITMENT: 4.446	0.1482	RECRUITMENT: 4.446	0.1482	*
25/02/93	421		1.332	2.07	0.048	3.338					
		15					RECRUITMENT: 15.356	1.0237	RECRUITMENT: 15.356	1.0237	*
12/03/93	436		3.605	2.48	0.078	5.493					
		14					57.984	4.1417	62.093	4.4352	0.105
26/03/93	450		2.722	4.00	0.340	23.822					
		28					130.331	4.6547	67.363	2.4058	0.056
23/04/93	478		0.190	5.91	1.617	113.335					
		13	*				4954.323	381.1017	9427.688	725.2068	0.314
06/05/93	491		1.009	29.67	95.337	4931.473					
		15					7206.783	480.4522	5961.385	397.4256	0.077
21/05/93	506		0.347	41.21	301.928	15560.947					
		32					14123.263	441.3520	10125.080	316.4088	0.052
22/06/93	538		0.085	94.00	1574.833	80946.425					
		29					0.000	0.0000	0.000	0.0000	*
21/07/93	567		0.000	---------	---------	---------					
		29					0.000	0.0000	0.000	0.0000	*
19/08/93	596		0.000	---------	---------	---------					
		13					0.000	0.0000	0.000	0.0000	*
01/09/93	609		0.000	---------	---------	---------					
		44					0.000	0.0000	0.000	0.0000	*
15/10/93	653		0.000	---------	---------	---------					
		17					0.000	0.0000	0.000	0.0000	*
01/11/93	670		0.000	---------	---------	---------					
		14					0.000	0.0000	0.000	0.0000	*
15/11/93	684		0.000	---------	---------	---------					
		16					0.000	0.0000	0.000	0.0000	*
01/12/93	700		0.000	---------	---------	---------					
		59					0.000	0.0000	0.000	0.0000	*
28/01/94	759		0.000	---------	---------	---------					
		14					0.000	0.0000	0.000	0.0000	*
11/02/94	773		0.000	---------	---------	---------					
							26492.486		25663.412		

BURY

DATE	DAY NO.	NUMBER OF DAYS BETWEEN SAMPLES	NO. OF INDIVIDUALS (m-3)	MEAN DIAMETER (mm)	MEAN DRY WEIGHT (mg)	MEAN CARBON WEIGHT (ugC)	INCREMENT SUMMATION		INSTANTANEOUS GROWTH		I.S.G.R.
							PRODUCTION (ugCm-3)	ugCm-3d-1	PRODUCTION (ugCm-3)	ugCm-3d-1	(d-1)
10/12/92	344		0.000	---------	---------	---------					
		32					0.000	0.0000	0.000	0.0000	*
11/01/93	376		0.000	---------	---------	---------					
		15					0.000	0.0000	0.000	0.0000	*
26/01/93	391		0.000	---------	---------	---------					
		30					RECRUITMENT: 2.038	0.0679	RECRUITMENT: 2.038	0.0679	*
25/02/93	421		0.371	2.31	0.078	5.494					
		15					RECRUITMENT: 1.802	0.1202	RECRUITMENT: 1.802	0.1202	*
12/03/93	436		0.887	2.12	0.062	4.330					
		14					RECRUITMENT: 16.637	1.1884	RECRUITMENT: 16.637	1.1884	*
26/03/93	450		1.599	2.95	0.165	11.532					
		28					26.879	0.9600	19.696	0.7034	0.043
23/04/93	478		0.355	4.21	0.557	39.044					
		13					195.597	15.0459	186.065	14.3127	0.260
06/05/93	491		0.125	10.32	16.315	854.031					
		15					488.564	32.5709	498.361	33.2241	0.130
21/05/93	506		0.070	37.00	114.104	5864.941					
		32					3726.586	116.4558	4042.206	126.3189	0.080
22/06/93	538		0.036	92.00	1482.060	76177.885					
		29					0.000	0.0000	0.000	0.0000	*
21/07/93	567		0.000	---------	---------	---------					
		29					0.000	0.0000	0.000	0.0000	*
19/08/93	596		0.000	---------	---------	---------					
		13					0.000	0.0000	0.000	0.0000	*
01/09/93	609		0.000	---------	---------	---------					
		44					0.000	0.0000	0.000	0.0000	*
15/10/93	653		0.000	---------	---------	---------					
		17					0.000	0.0000	0.000	0.0000	*
01/11/93	670		0.000	---------	---------	---------					
		14					0.000	0.0000	0.000	0.0000	*
15/11/93	684		0.000	---------	---------	---------					
		16					0.000	0.0000	0.000	0.0000	*
01/12/93	700		0.000	---------	---------	---------					
		59					0.000	0.0000	0.000	0.0000	*
28/01/94	759		0.000	---------	---------	---------					
		14					0.000	0.0000	0.000	0.0000	*
11/02/94	773		0.000	---------	---------	---------					
							4458.104		4766.806		

CRACKNORE 1990

DATE	DAY NO.	NO. DAYS BETWEEN BETWEEN SAMPLES	NO. OF INDIVIDUALS (m-3)	MEAN DRY WEIGHT (mg)	MEAN CARBON WEIGHT (ugC)	INCREMENT SUMMATION		INSTANTANEOUS GROWTH		I.S.G.R.
						PRODUCTION (ugCm-3)	ugCm-3d-1	PRODUCTION (ugCm-3)	ugCm-3d-1	(d-1)
12/02/90	408		0.000	----------	----------					
		18				RECRUITMENT:	0.005	RECRUITMENT:	0.005	*
02/03/90	426		0.090	0.013	0.932	0.084		0.084		
		10				RECRUITMENT:	0.812	RECRUITMENT:	0.812	*
12/03/90	436		5.380	0.022	1.525	8.121		8.121		
		16				242.451	15.153	287.880	17.993	0.235
28/03/90	452		2.220	0.932	65.328					
		28				2211.243	78.973	1369.011	48.893	0.118
25/04/90	480		0.390	32.822	1759.767					
		22	*			19084.192	867.463	33615.756	1527.989	0.149
17/05/90	502		0.420	915.810	47072.621					
		8				8017.176	1002.147	6270.318	783.790	0.070
25/05/90	510		0.030	1879.469	82704.515					
		14				1729.687	123.549	1602.034	114.431	0.047
08/06/90	524		0.015	3104.660	159579.499					
						31292.954		43153.205		

CRACKNORE 1991

DATE	DAY NO.	NO. DAYS BETWEEN BETWEEN SAMPLES	NO. OF INDIVIDUALS (m-3)	MEAN DRY WEIGHT (mg)	MEAN CARBON WEIGHT (ugC)	INCREMENT SUMMATION		INSTANTANEOUS GROWTH		I.S.G.R.
						PRODUCTION (ugCm-3)	ugCm-3d-1	PRODUCTION (ugCm-3)	ugCm-3d-1	(d-1)
01/03/91	790		0.000	----------	----------					
		17				RECRUITMENT:	3.489	RECRUITMENT:	3.489	*
18/03/91	807		7.390	0.115	8.027	59.320		59.320		
		9				RECRUITMENT:	26.290	RECRUITMENT:	26.290	*
27/03/91	816		8.710	0.485	33.976	236.611		236.611		
		19				296.358	15.598	247.869	13.046	0.048
15/04/91	835		2.850	1.216	85.249					
		14				1875.942	133.996	933.498	66.678	0.192
29/04/91	849		0.360	22.935	1254.060					
		13	*			23011.571	1770.121	24756.024	1904.310	0.159
13/05/91	862		2.360	192.819	9941.963					
		12				7117.236	593.103	6580.328	548.361	0.031
24/05/91	874		0.850	279.568	14376.378					
		24				36309.399	1512.892	29889.090	1245.379	0.070
17/06/91	898		0.300	1508.233	77523.159					
		11				-6367.558	-578.869	-8915.307	-810.482	-0.069
28/06/91	909		0.010	708.991	36442.138					
						62538.879		53787.433		

CRACKNORE 1994

DATE	DAY NO.	NO. DAYS BETWEEN BETWEEN SAMPLES	NO. OF INDIVIDUALS (m-3)	MEAN DRY WEIGHT (mg)	MEAN CARBON WEIGHT (ugC)	INCREMENT SUMMATION		INSTANTANEOUS GROWTH		I.S.G.R.
						PRODUCTION (ugCm-3)	ugCm-3d-1	PRODUCTION (ugCm-3)	ugCm-3d-1	(d-1)
28/01/94	759		0.000	----------	----------					
		14				RECRUITMENT:	0.059	RECRUITMENT:	0.059	*
11/02/94	773		0.220	0.053	3.737	0.822		0.822		
		11				RECRUITMENT:	0.402	RECRUITMENT:	0.402	*
22/02/94	784		0.890	0.084	5.895	4.424		4.424		
		7				RECRUITMENT:	0.461	RECRUITMENT:	0.461	*
01/03/94	791		1.750	0.062	4.373	3.228		3.228		
		7				9.314	1.331	9.738	1.391	0.115
08/03/94	798		1.680	0.140	9.804					
		15				17.512	1.167	17.901	1.193	0.051
23/03/94	813		1.470	0.298	20.923					
		16				237.217	14.826	307.929	19.246	0.139
08/04/94	829		1.260	3.066	194.708					
		13				153.286	11.791	130.791	10.061	0.052
21/04/94	842		0.370	6.351	382.789					
		5				251.434	50.287	268.447	53.689	0.209
26/04/94	847		0.340	19.649	1091.053					
		14				2893.573	206.684	3841.935	274.424	0.158
10/05/94	861		0.31	193.793	9994.356					
		14	*			34050.879	2432.206	36700.487	2621.463	0.130
24/05/94	875		0.6	1248.831	61915.215					
		10				2348.725	234.872	2230.436	223.044	0.011
03/06/94	885		0.03	1349.64	69371.484					
		5				-286.468	-57.294	-304.306	-60.861	-0.046
08/06/94	890		0.01	1070.975	55048.107					
		5	*			14364.667	2872.933	5105.844	1021.169	0.132
13/06/94	895		0.14	2072.7	106536.771					
		10				-2121.676	-212.168	-2363.906	-236.391	-0.029
23/06/94	905		0.020	1556.728	80015.827					
						51926.938		45953.770		

GREENLAND 1990

DATE	DAY NO.	NO. DAYS BETWEEN BETWEEN SAMPLES	NO. OF INDIVIDUALS (m-3)	MEAN DRY WEIGHT (mg)	MEAN CARBON WEIGHT (ugC)	INCREMENT SUMMATION PRODUCTION (ugCm-3)	ugCm-3d-1	INSTANTANEOUS GROWTH PRODUCTION (ugCm-3)	ugCm-3d-1	I.S.G.R. (d-1)
12/02/90	408		0.000	---	---					
		18				RECRUITMENT:	0.005	RECRUITMENT:	0.005	*
02/03/90	426		0.160	0.009	0.615	0.098		0.098		
		10				RECRUITMENT:	0.040	RECRUITMENT:	0.040	*
12/03/90	436		0.280	0.025	1.772	0.398		0.398		
		44				823.992	18.727	678.332	15.417	0.182
25/04/90	480		0.032	102.797	5283.775					
		22				1086.321	49.378	1214.151	55.189	0.099
17/05/90	502		0.020	915.668	47065.339					
						1910.809		1892.979		

GREENLAND 1991

DATE	DAY NO.	NO. DAYS BETWEEN BETWEEN SAMPLES	NO. OF INDIVIDUALS (m-3)	MEAN DRY WEIGHT (mg)	MEAN CARBON WEIGHT (ugC)	INCREMENT SUMMATION PRODUCTION (ugCm-3)	ugCm-3d-1	INSTANTANEOUS GROWTH PRODUCTION (ugCm-3)	ugCm-3d-1	I.S.G.R. (d-1)
01/03/91	790		0.000	---	---					
		17				RECRUITMENT:	0.526	RECRUITMENT:	0.526	*
18/03/91	807		1.750	0.073	5.107	8.937		8.937		
		9				15.180	1.687	10.600	1.178	0.149
27/03/91	816		0.350	0.279	19.564					
		19				38.723	2.038	31.129	1.638	0.119
15/04/91	835		0.110	2.681	187.926					
		14	*			431.608	30.829	565.740	40.410	0.171
29/04/91	849		0.220	38.100	2055.817					
						494.448		616.407		

N.W.NETLEY 1991

DATE	DAY NO.	NO. DAYS BETWEEN BETWEEN SAMPLES	NO. OF INDIVIDUALS (m-3)	MEAN DRY WEIGHT (mg)	MEAN CARBON WEIGHT (ugC)	INCREMENT SUMMATION PRODUCTION (ugCm-3)	ugCm-3d-1	INSTANTANEOUS GROWTH PRODUCTION (ugCm-3)	ugCm-3d-1	I.S.G.R. (d-1)
#01/03/91	790		0.000	---	---					
		12				RECRUITMENT:	1.226	RECRUITMENT:	1.226	*
13/03/91	802		1.920	0.109	7.662	14.711		14.711		
		5				RECRUITMENT:	7.647	RECRUITMENT:	7.647	*
18/03/91	807		5.420	0.139	9.769	38.237		38.237		
		9				55.456	6.162	44.893	4.988	0.107
27/03/91	816		1.560	0.366	25.659					
		19				275.168	14.483	255.154	13.429	0.125
15/04/91	835		0.630	3.951	276.954					
		14	*			610.917	43.637	308.872	22.062	0.046
29/04/91	849		1.490	9.585	527.113					
		13				2626.838	202.064	1092.244	84.019	0.153
13/05/91	862		0.080	75.358	3873.403					
		12				-17.048	-1.421	-17.531	-1.461	-0.008
24/05/91	874		0.02	68.725	3532.445					
						3604.279		1736.579		

#NO SAMPLE