UNIVERSITY OF SOUTHAMPTON

REPRODUCTIVE PROCESSES IN THE EUROPEAN LOBSTER, *Homarus gammarus*

VOLUME 1 OF 2

Emma Free, B.Sc.

Thesis submitted for the Degree of Doctor of Philosophy

Department of Oceanography, Faculty of Science

May 1994

UNIVERSITY OF SOUTHAMPTON

ABSTRACT

FACULTY OF SCIENCE

OCEANOGRAPHY

Doctor of Philosophy

REPRODUCTIVE PROCESSES IN THE EUROPEAN LOBSTER *HOMARUS GAMMARUS*

by Emma Free

The population biology, size at onset of maturity and individual fecundity of the European lobster, *Homarus gammarus*, have been studied in three fisheries on the English and Welsh coast. Differences were observed between the fisheries and temperature regimes of the three sample areas, and these were reflected by variations in size distributions, catch per unit effort and landings statistics. Current national fisheries management legislation consists solely of a minimum legal landing size legislation of 85 mm carapace length.

Estimates of the sizes of both male and female maturity varied considerably between the three study sites. The smallest ovigerous female was 81 mm carapace length at Bridlington, 95 mm carapace length at Dale and 76 mm carapace length at Selsey. The sizes at male maturity showed both spatial and temporal variation, and ranged between 73 mm and 87 mm carapace length. Regional variations in size at onset of maturity have important implications for fisheries management strategy, and may indicate the requirement for local minimum legal landing size legislation.

This study confirmed previous work suggesting a linear relationship between clutch size and female carapace length. This relationship exhibits regional and temporal variation, which requires further research for the determination of potential causes.

Local temperature effects are suggested to influence the duration of the reproductive cycle of the lobster and therefore individual fecundity. The spawning frequency of the lobster has been suggested to increase with increasing female size, and may show regional variation.

ACKNOWLEDGEMENTS

I would like to thank Dr. J. Addison, M.A.F.F., Lowestoft and Dr. P.A.Tyler of Southampton University for their help and supervision during the course of this work. I am also very grateful for the assistance given to me by Dr R.C.A. Bannister, Dr D.B. Bennett, Dr K.C. Collins, Dr M.Greer-Walker, Dr L. Hawkins, Dr S. Hutchinson, Dr A.C. Jensen, Dr S.R.J. Lovewell, Miss J. Mallinson and Dr P. Whitthames. I also owe many thanks to the crews of the "Debbie C", "Castle Bay of Dale" and "Romulus" for their patience and help on each of my field sampling trips, and to the Sea Fisheries Committees of the areas I have studied.

I would also like to thank many other people for their kindness and tolerence during the course of my work, including P. Bluett, S. Bronsdon, G. Burrows, C. Chapman, G. Lawson, C. Lucas and I. Osment. I am very grateful to my Parents for their support during my studies.

This work has been made possible by a N.E.R.C. C.A.S.E. grant awarded with M.A.F.F..

CONTENTS

LIST OF FIGURES

LIST OF TABLES

Tables Page number

CHAPTER 1 INTRODUCTION

1.1 Introduction to the fisheries ecology of *Homarus gammarus*

The European lobster, *Homarus gammarus* (Linnaeus, 1758), is a member of the decapod crustacean family Nephropidae, which also includes the commercially important species *Homarus americanus* (the American lobster) and *Nephrops norvegicus* (the Dublin Bay prawn, or Norwegian lobster). The European lobster has a widespread distribution, covering most of the continental European coastline (but not the Baltic Sea), the Mediterranean Sea, the United Kingdom, Ireland and the Azores (Phillips, Cobb and George, 1980; Holthuis, 1991).

The most common habitat of *Homarus spp.*, especially in inshore areas, consists of a sand substrate with overlying rocks and boulders (Cooper and Uzmann, 1980). Juveniles and adults may excavate tunnels under boulders and stones on mud, sand, or gravel (Dybern, 1973; Berrill, 1974; Howard, 1977; 1980). Man-made structures, such as shipwrecks, pipelines and artificial reefs may also provide suitable shelters for *Homarus spp.*. Lobster population size may be limited by habitat availability in areas with strong near-bed water currents (Howard and Nunny, 1983; Howard, 1988) because of their individual requirement for a degree of protection from fast flowing water. Suitable lobster habitat is usually reflected by the location of commercial lobster fishing grounds.

The *H. gammarus* fishery is based in at least thirteen European countries (Bennett, 1980), being of most commercial importance in France, England and Wales, and Scotland (Dow, 1980). In 1989, 587 tonnes of lobsters were landed in England and Wales, with a value of £4,569,000 (765 tonnes were landed in Scotland; value £6,790,000). In 1970, a comparable catch of 508 tonnes in England and Wales was valued at only £609,000 (MAFF official landing statistics). Compared with the United States of America which landed 27501 tonnes, and Canada 47983 tonnes, of *H. americanus* in 1990 respectively, the *H. gammarus* fishery is small but remains of considerable social and economic importance to many European coastal areas.

Landing statistics from the European lobster fisheries have showed a significant decrease in their catch over the forty years to the end of the 1970's (Bennett, 1980) (concurrent with an increase in total catch value). This reduction in lobster landings was most probably a result of a decrease in lobster abundance. Lobster landings from England and Wales remained fairly stable during the 1980's, at a higher level than the 1970's. However, landing statistics may also reflect short term and long term changes in fishing effort and efficiency, changes in catchability or the discovery of previously unexploited stock (e.g. offshore English Channel and the West Coast of Scotland) (Bennett, 1980). The development of offshore *H. americanus* fisheries effectively masked the decline of inshore stocks by maintaining relatively high landing figures (Cooper and Uzmann, 1977).

Variation in the abundance of commercially exploited stocks may be caused by the act of fishing and by environmental and biotic factors within the marine ecosystem (Jamieson, 1986).

The size compositions of *H. americanus* fisheries have been shown to vary considerably between regions, and from inshore to offshore populations (Cooper and Uzmann, 1980). Differences in size frequency distributions of *H. gammarus* have been reported between areas off the Irish coast (Gibson, 1967), off the east coast of England (Howard, 1980) and other areas in England and Wales (Bannister, 1986). The size composition of the edible crab *Cancer pagurus* in the English Channel has also been shown to vary both spatially (increasing in mean carapace width from East to West in the Channel, and from inshore to offshore) and temporally (Brown and Bennett, 1982).

Differences in the mean carapace length (CL) of lobster stocks have been attributed to a number of factors and are probably a function of varying degrees of trap selectivity, different levels of fishing pressure and habitat availability (Cooper and Uzmann, 1980; Addison and Lovewell, 1991). Physical habitat characteristics may affect lobster population size composition, because of the requirement for adequate shelter size (Howard, 1977; 1980). Trap type and resultant size selectivity effects may also bias the observed size composition of lobsters in any given fishery. The mean size of *H. americanus* was shown to decline succeeding the onset of intensive fishing in offshore sites (Skud and Perkins, 1969; Uzmann *et al*, 1977; Fogarty *et al*, 1982). Addison (1986) suggested that the level of fishing effort within a fishery is not necessarily the sole factor in determining the size frequency distribution of lobsters.

The size distribution of captured lobsters in a fishery may change temporally as a result of behavioural changes in catchability caused by both moulting and reproductive cycles (Thomas, 1951), or as a result of variation in recruitment to the fishery (Gibson, 1967). The reduced catchability of berried females over winter months may result in the appearance of larger females in summer size compositions, when the mature animals are not ovigerous and therefore more likely to be caught (Thomas, 1954). Weather may also have an effect on fishing mortality levels and therefore the observed lobster fishery size composition, with more exposed offshore grounds (with generally larger animals) only being fished during suitable conditions (Thomas, 1958).

The abundance and availability of lobsters may be affected by fluctuations in sea temperature (McLeese and Wilder, 1958; Paloheimo, 1963; Dow, 1977; 1980; Fogarty, 1988; Campbell *et al*, 1991). Moult frequency dependence on temperature, as well as temperature effects on larval survival, will influence recruitment into the fishery (Templeman, 1936; Saila and Flowers, 1972; Dow, 1977). Additionally, the reduced feeding levels of *Homarus spp.* during winter and in cold water temperatures will affect lobster catchability (Cooper and Uzmann, 1980).

Most studies investigating the sex ratios of *H. americanus*, both by diving and commercial trapping, have suggested an equal proportion of males and females, at least to the size at onset of maturity (Scarratt, 1973; Cooper, 1970; Ennis, 1971; Krouse, 1973; Cooper *et al*, 1975). Skud and Perkins (1969) observed an increase, and then decline, in female to male sex ratio between 80 and 130 mm CL, probably as a result of the reduced moult frequency of sexually mature females. Dybern *et al* (1967) observed an equal sex ratio of *H. gammarus* caught by diving in Swedish waters. Sex ratio estimates using trap-caught animals may be seasonally biased as a result of behavioural effects on feeding caused by moult and reproductive cycles (Ennis, 1973). Thomas (1954) showed variation in sex ratio (later attributed to moult frequency, (Thomas, 1955)) according to lobster size, with 52 %, 60 % and 39 % of the catch being female at 80 to 89 mm CL, 90 to 109 mm CL and 140 to 149 mm CL respectively. Thomas (1954) also noted a seasonality in *H. gammarus* sex ratio, with 60 to 64 % of the catch being female between April and June, but only 46 to 50 % in September and October. Watson (1974), working off Ireland, found between 51 and 61 % of the catch to be female. The reduction in the catchability of berried females as a result of their reduced feeding levels (Branford, 1977 c.f. Hallback and Warren, 1972), may help to conserve the number of females in a heavily exploited catch, thereby producing a fisheries-induced, low proportion of males within the fishery.

The natural mortality rate of *Homarus spp.* and other fishery species is difficult to estimate, causing difficulties in stock assessment and effective management (Campbell, 1980; Pauly, 1980). The instantaneous natural mortality coefficient (M) may be defined as the rate of death caused by all possible methods, except fishing, and comprises physiological mortality (disease, old age or both, with no intervention by predators), selective mortality (disease or old age facilitating predation), and chance (unrelated to physiological mechanisms and purely proportional to the number of possible encounters with potential predators) (Pauly, 1980). Suggested estimates of M for *H. americanus* range between 0.04 and 0.08 (Thomas, 1973), 0.02 (Ennis, 1979) and 0.02 to 0.35 (averaging 0.15) (Anthony, 1980). For fisheries modelling, Z (instantaneous total mortality coefficient) is usually calculated as M+F (instantaneous natural mortality coefficient plus the instantaneous fishing mortality coefficient).

Fishing mortality may differ considerably between fisheries and is reflected by size composition data (Bannister, 1986). *H. gammarus* fishing mortality coefficients (F), calculated by tagging, were suggested to be 0.5 off Berwickshire, 1938 to 1939 (Thomas, 1951), 1.17 in Yorkshire and 0.35 in Cornwall (Hepper, 1978). Bannister (1986) reported F values of males and females to be between 0.7 to 0.81 and 0.5 to 0.66 for Yorkshire, 0.53 to 0.87 and 0.45 to 0.69 for the South Coast, and 0.31 to 0.36 and 0.1 to 0.19 for South Wales (figures vary according to method of estimation). Gibson (1967) estimated total mortality for male *H. gammarus* for a fishery off the Irish coast to be between 46 and 58 %, similar to Simpson's (1958) estimate of 58 % for the north Welsh coast. F, and therefore Z, varies between males and females (Bannister, 1986), so that yield per recruit estimates requiring mortality estimates for their calculation (e.g. Beverton and Holt, 1957) must be derived for each sex, and consider seasonal behaviour effects before implementation into effort-based management strategies (Saila and Marchessault, 1980). Estimates of F along the US coastline are quite high, averaging 1.79 (Anthony, 1980) and 0.86 off Newfoundland (Ennis, 1979). Campbell (1980) reported that inshore *H. americanus* fisheries may suffer between 60 and 95 % exploitation rates (calculated as F/F+M), and that consequently most of the legal-sized animals are removed each year; annual landing statistics therefore being reasonable indicators of recruitment into the fishery.

Sub-legal-sized lobsters are frequently caught in pots and have to be discarded after the catch has been hauled and sorted (although escape gaps may be fitted to pots to reduce the number of smaller animals retained). This may lead to fishing mortality in lobsters below MLS (minimum legal landing size) as claw loss or predation may be suffered by sub-legal-sized *Homarus* returned after capture: therefore resulting in some economic loss to the fishery.

Reductions in the stock sizes of *Homarus* fisheries caused by high fishing intensity have led to concern over the potential for recruitment failure (Anon, 1979; Harding *et al*, 1983). Simpson (1975) stated that in most countries the measurement of fishing effort using landing statistics is problematical because of the nature of lobster fisheries, with small boats landing catches each day, at a large number of small ports which are often in isolated locations. The poor reliability of landing statistics as direct indicators of stock condition has led to the use of catch per unit effort (CPUE) as an index of lobster abundance. CPUE enables landing figures to be standardised according to the efficiency and effort with which the catch was made. CPUE may be calculated as the weight of lobsters caught per 100 traps hauled. However, the CPUE of trap fisheries is difficult to standardise because of the variability of pot type and pot immersion (or soak) time, and a satisfactory index of fishing effort has yet to be devised for these fisheries (Munro, 1974; Bennett and Brown, 1979; Skud, 1979; Miller, 1990). Bennett and Brown (1979) noted the importance of understanding the relationship between pot immersion time and catch size for use in checking the validity of CPUE as an estimate of abundance and for estimating mortality parameters for stock-production modelling of crustacean trap fisheries. Although catch per trap usually increases with pot immersion time, the increase may not be directly proportional (Thomas, 1973;

Caddy, 1977; Skud, 1979; Miller, 1990). Entry into baited traps will decrease when the bait is exhausted, at which point the catch will either stabilise or decline until the rate of escapement equals ingress (Munro, 1974). Skud (1979) observed that *H. americanus* catch per pot haul increased for the first six days of immersion, although the catch per pot per days soak declined after the first day. Bennett and Lovewell (1977) studied CPUE for Welsh *H. gammarus* fisheries and observed constant catch per trap haul for pot immersion times of up to five days. As only 2 % of hauls were made after five day soak periods (Simpson, 1975), Bennett and Brown (1979) stated that catch per trap haul, disregarding soak time, would be an adequate index of lobster abundance. However, Skud (1979) suggested that catch per haul is not a reliable measurement of abundance unless it is standardised for length of soak, or includes estimates of ingress and escape. Standardisation of catch per haul, based on constant soak time provides estimates of effective effort that suggest seasonal differences in availability and rate of escapement (Munro, 1974; Skud, 1979). Soak time may affect fishery cost-effectiveness: Skud (1979) suggested that catch and effort data showed that two or three day pot soaks would be more profitable than one day soak times, although the advantages of the length of soak varied with season and vessel operation. Miller (1983) evaluated the economic optimum number of traps that should be fished for *Chionoecetes opilio*, considering the cost of traps, the timing and frequency of fishing days and the relationship between soak time and catch. Miller (1983) suggested that the timing and frequency of fishing was important in determining the economic optimum number of traps, and that many fishermen exceeded this optimum number.

The catch of a baited trap is the result of a series of interactions between the animals attracted to it, the environment and the trap (Bennett, 1974; Simpson, 1975; Bennett and Brown, 1979). The availability of the target species is affected by physical environment, water temperature, salinity, tidal rhythms, water movements and sea bed topography (Bennett and Brown, 1979; Krouse, 1989). In addition animal abundance, population structure, activity and behaviour, moult and reproductive conditions are also important (Bennett and Brown, 1979; Robinson, 1979; Harding *et al*, 1983; Miller, 1990). The efficiency of the bait is affected by its condition, quantity, the species being targeted and natural food availability.

Entry into the trap is then governed by intraspecific factors such as territoriality, cannibalism, competition for food and attraction, as well as interspecific interactions (predation and competition for food). Trap ingress and escape will be affected by the trap design, selectivity, escape gaps, and gear saturation levels (Bennett and Brown, 1979). The effective fishing area of a trap depends on the effects of water currents, soak duration, the proportion of the lobster population that responds to the bait, and its response time to the olfactory response caused by the bait (Elner, 1980).

Comparisons of fishing effort both within and between fisheries are complicated by variations in expertise and skill in relation to fishing experience (Squires *et al*, 1974). The number of traps set in a fishery is poor evidence of fishing effort over a long period of time because of technological advances in boats, engines, hauling equipment and navigational equipment, all of which affect the relative efficiency of each trap hauled (Rutherford *et al*, 1967). If the fishing power of the gear remains the same, fishing time is kept constant, with the relative distribution of animals not changing, then changes in CPUE may be assumed to be caused by changes in stock density or vulnerability to capture (Morgan, 1979). Fishing effort is subject to market demands and lobster availability which determine fishing costs and potential profitability (Rutherford *et al*, 1967).

In areas where CPUE is low, lobsters are relatively small and fishing mortality rates highest, it may be assumed that fishing effort (or intensity) is high (Skud and Perkins, 1969, Cooper and Uzmann, 1980). Offshore *H. americanus* populations, which support the largest lobsters have higher CPUE than inshore fisheries. CPUE is significantly influenced by changes in catchability during a year as well as changes in abundance.

Fishing levels may be determined from the proportion of first year recruits apparent in size frequency distributions of the commercial catch of uninjured male lobsters (Squires, 1965; Squires *et al*, 1971). Squires *et al* (1974) suggested that the proportion of first year recruits in an exploited population is a less biased and more reliable comparison between fishing rates of different areas than an estimate based on fishing effort measured as number of traps hauled or pots per days soak.

The growth rate of *Homarus gammarus* is a function of both the increment at moult and moult frequency. Growth data have been obtained from captive animals or from tagging studies which have taken place in commercial fisheries. These studies have often given conflicting information on lobster growth rate (Aiken, 1980). Tagging data may contain an observational or tagging bias and will be influenced by the local environmental and geographic conditions as well as those of the study population (Aiken, 1980). An adequate comprehension of lobster growth rate is critical to fisheries management, especially for the effective use of MLS (minimum legal landing size) as a management tool (Hunt and Lyons, 1986).

Homarid lobster growth may also be effected by the onset of maturity, as mature female lobsters almost certainly have a lower growth rate (moult frequency and/or increment) than males (Simpson, 1961; Gibson, 1963; Wilder, 1963; Hepper, 1967; 1970; Ennis, 1972; Cooper and Uzmann, 1977). The growth of palinurid lobsters has been related to the onset of maturity (Hancock, 1977; Hunt and Lyons, 1986), water temperature (Chittleborough, 1975), injuries and fisheries handling, and exposure (Brown and Caputi, 1985; 1986).

Apparent geographical variation in growth rate may be caused by food availability, genetics, habitat, temperature and fishing intensity (Cooper and Uzmann, 1971; 1980; Pollock, 1973; Mauchline, 1977; Conan, 1978). The moult frequency and increment of *H. gammarus* may vary regionally (Bennett *et al*, 1978)(c.f. Hepper (1978), who found no indication of growth increment differences between Cornish and Yorkshire lobsters). Hewett (1974) suggested a linear relationship between log-intermoult period and log-body length in *Homarus gammarus*, although Mauchline (1977) observed a linear relationship between the log of environmental temperature and the log of intermoult duration for animals of an equal body size. Hepper (1978) suggested that *H. gammarus* off the English and Welsh coast of between 80 and 90 mm CL moult about once a year (between 0 and 3 times). Very young *H. gammarus* moult several times per year, and exhibit a decrease in moult frequency with age: the majority of commercially-caught male lobsters moult once a year, with the largest individuals indicating no external signs of having moulted for a number of years (Hepper, 1965).

The moult increment has been shown to be relatively greater in smaller individuals of *Homarus spp.* (Templeman, 1940; Mauchline, 1976), and Hepper

(1967) suggested a constant moult increment over a wide size range of individuals. Mauchline suggested that percent increase in length at ecdysis decreases logarithmically against body length. Sexual differences between moult increment have been observed for *Homarus gammarus* (Simpson, 1961; Hepper, 1967; 1972; Gibson, 1967); although Thomas (1973) and Wilder (1953) found no appreciable differences in growth at moult between males and females of *H. americanus*. The growth of mature male *H. americanus* is more rapid, and reaches a higher asymptote than that of mature females, presumably because of increased energy allocation by females towards egg production, rather than somatic growth (Campbell, 1983).

1.2 Fisheries management

The conservation of lobster stocks may be defined as comprising the protection of reproductive potential by a reduction in fishing mortality on adults, the control of fishing effort on the exploited portion of the population, and the improvement of juvenile survival and recruitment (Jamieson and Caddy, 1986).

Current European lobster fisheries management is based upon minimum landing size legislation (MLS). The 85 mm CL MLS has been enforced in England and Wales since May 1984, when it was raised from 83 mm CL as part of a two stage increase in MLS from 80 to 85 mm CL, commencing in May 1981.

Theoretically, minimum landing size should be linked to estimates of optimum yield assessments and knowledge of the size at maturity (SOM) of the managed stock, although this is not always the case (Bennett, 1980). An increase in MLS is intended to increase sustained yields by allowing more lobsters to mature (thereby improving stock reproductive potential), and by enhancing the potential yield with the later recruitment of small animals with faster growth rates. Estimates of the size at maturity of *H. gammarus* are scarce, and potential geographical variation in SOM increases the difficulty of selecting an appropriate MLS for successful stock management. Bennett (1980) suggested that most minimum landing size limits are set with little relevance to protection of brood stock and without surety of their potential for optimizing yield per recruit. However, many MLS were initially based on market demands, and have now been refined in order to optimize yield and broodstock levels. MLS is relatively easy to enforce, and may be based on economic factors as well as the protection of stock reproductive capacity (Jamieson and Caddy, 1986).

Protection of berried females currently exists in Spain and Limfjord in Denmark, and has existed in the American lobster fishery since the nineteenth century. In England and Wales in 1951, local Sea Fisheries Committee Bye-Laws regarding the protection of berried females were transformed into national legislation. The berried hen law was repealed in 1966 as it was difficult to enforce, as a result of widespread "scrubbing" (egg removal) of berried females, and could not be justified by the limited knowledge regarding the stock-recruitment relationship (Thomas, 1965). The ban on the landing of berried lobsters was regarded by many as an unwarranted loss of income, although it has been maintained as a Bye-Law in the Norfolk lobster fishery. Recent work (Bennett and Edwards, 1981), and that of Saila and Flowers (1965), suggested that although a ban on the landing of berried hens would result in an increase in spawning stock size, it may result in small losses in yield per recruit. Additionally, protection of the spawning stock will increase egg production but will not necessarily result in an increase in recruitment (Bannister, 1986). Bannister and Addison (1986) suggested that the results of such yield estimates are dependent on biological assumptions regarding the stock-recruitment relationship, and further emphasised the requirement for investigation into the true nature of the biological parameters concerned. Bennett (1981) suggested that in areas with no protection for berried females and sustaining high levels of exploitation, the importance of MLS to be above SOM was crucial.

V-notching of berried lobsters takes place along coastal Maine, both as a voluntary scheme and by the Department of Marine Resources (Daniel *et al*, 1989). Lobsters with a V-notch may not be landed. This scheme aims to protect the lobsters with proven reproductive capability thus enhancing egg production and ultimately recruitment. V-notched animals comprise a large proportion of mature female lobsters in traps, resulting in an alteration in the sex ratio of populations, and significantly increasing the number of sexually mature females within the fishery.

Closed fishing seasons exist in Portugal, Germany, Spain, Sweden and Norway, although these would be complicated to enforce in mixed fisheries, such as the *H. gammarus* and *C. pagurus* fisheries of the English Channel (Bennett, 1981). Other methods of lobster stock management in Europe include a ban on collection by diving in Sweden and Ireland and effort limitation by restricting trap numbers in Sweden. The United Kingdom does not currently have any restriction on fishing effort by trap numbers, limited entry nor by the use of closed seasons.

CHAPTER 2 POPULATION AND FISHERIES BIOLOGY.

Three main study sites were chosen in England and Wales to allow replication of the work and to enable comparisons of the fisheries, population structures and life history strategies at each location. The acquired results were then used in the study of the reproductive biology of *Homarus gammarus* and estimations of both fecundity and size at onset of maturity estimates.

Previous studies of collected data from lobster catches in England and Wales have shown potentially large differences in the population structure between different areas (Graham, 1949; Howard 1988; Addison and Lovewell, 1991) (Chapter 1). Variations in environmental factors are generally considered to have an important influence upon the population structure and reproductive behaviour of decapod crustacea (Sastry, 1983). Geographical variation in the size at sexual maturity of both *Homarus americanus* (Aiken and Waddy, 1976; 1980), and *Homarus gammarus* (Bennett and Howard, 1987) may be attributed to environmental differences, as may variations in growth rates (Aiken and Waddy, 1976; Aiken 1980) and therefore consideration of more than one site was thought necessary within this research programme.

The three sample sites, Bridlington, East Yorkshire; Selsey, West Sussex and Dale, Pembrokeshire, were selected because of their dispersed locations on the English and Welsh coasts (Figure 2.1), their accessibility, and because population size frequency data, sexual maturity assessments and fecundity samples have been collected during previous studies at the above sites. These historical data have also been presented and analyzed in this study.

2.1 Introduction to the study sites

2.1.1 Bridlington

The traditional lobster fishery based at Bridlington, Yorkshire, is maintained by approximately 14 coble boats of between 25 and 30 foot length. The fishing season is heavily restricted by low catchability and weather conditions during the winter months (October to March), and in this time offshore trawlers land the majority of any lobster catch in the region (despite a recent increase in potting activity during these months).

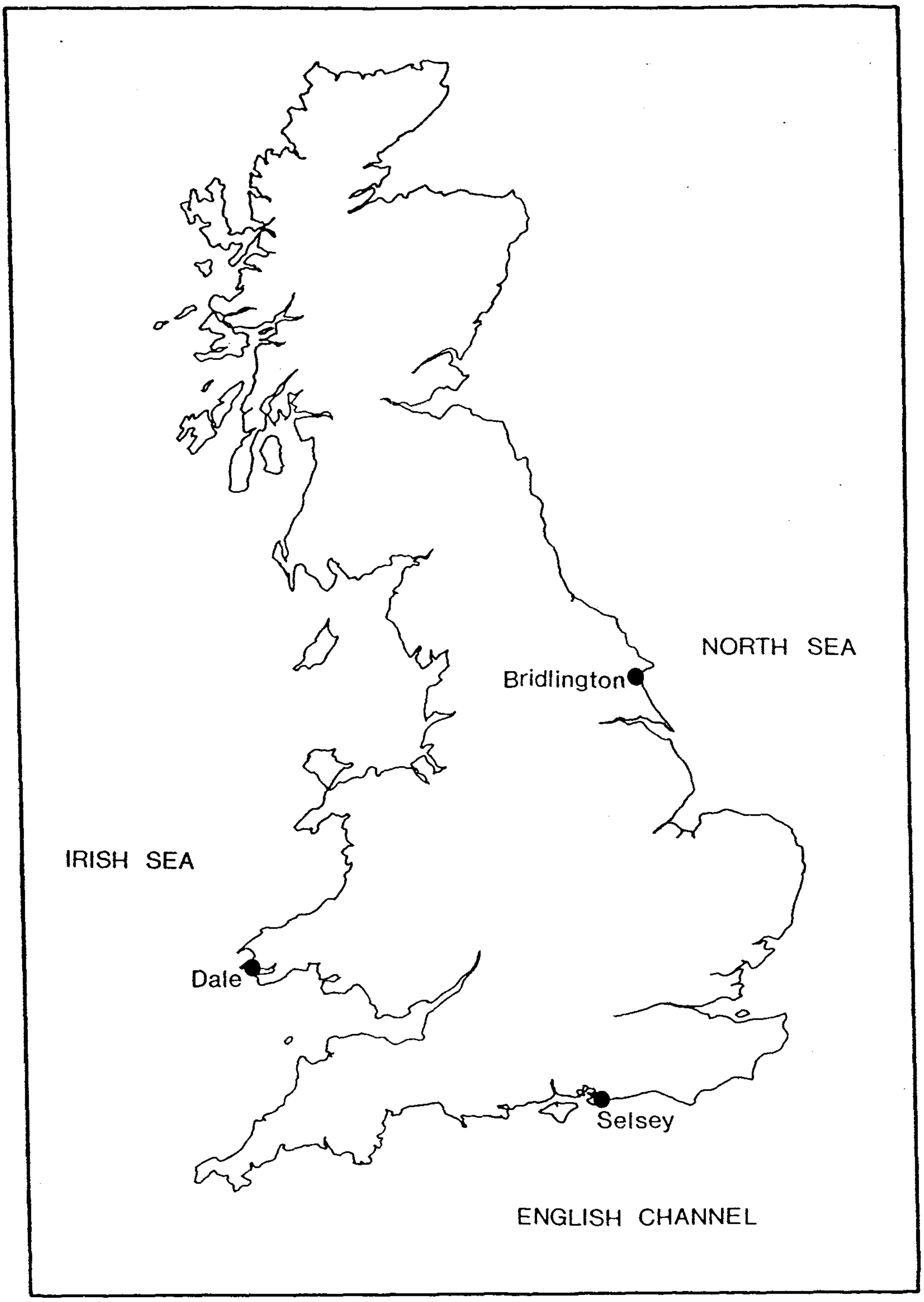


Figure 2.1 The position of the sampling sites used in this study.

In 1990, 50.81 tonnes of lobsters were landed in Bridlington; 40% of the total Yorkshire catch (M.A.F.F. official landing statistics).

Landings in Yorkshire represent 16% of the total of English and Welsh lobster landings between 1986 and 1990, compared with 20% between 1967 and 1970 (Edwards 1973). Catch records from the region show fairly stable landings between 1960 and 1986, with peaks in 1972 and 1986, followed by the figures rising to a peak in 1990 (Figure 2.2). Total English and Welsh officially recorded landing statistics between 1960 and 1990 are presented in Figure 2.3.

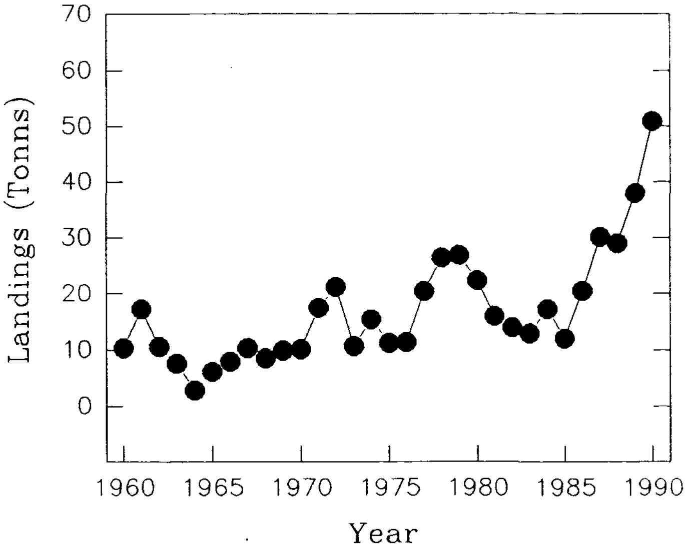


Figure 2.2 Officially recorded lobster landings, Bridlington, 1960 to 1990.

Sampling trips from Bridlington Harbour were made on board the commercial vessel F.V. "Debbie C". In addition, samples for fecundity and morphometry studies were collected from the port's lobster storage tanks. A list of sample dates and type is given in Appendix Table 2.1.

F.V. "Debbie C" is a 8 metre coble, crewed by 2 or 3 men who set strings of between 25 and 30 pots, in the area to the south of Bridlington and north of Withernsea as indicated in Figure 2.4. This area is between 1 and 5 km offshore,with depths ranging from 12 to 20 metres. Admiralty charts indicate a sea bed dominated by coarse and fine shingle, pebbles, gravel, broken shells and stones. A diving survey in the area by Howard (1986), revealed habitats suitable for large lobsters in 22 out of 30 of the dives made ("suitable" habitats were

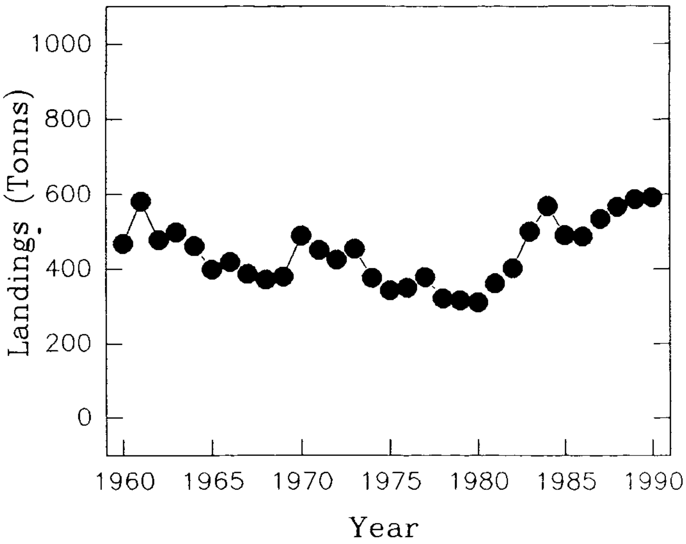


Figure 2.3 Officially recorded lobster landings in England and Wales, 1960 to 1990.

defined as large outcrops of rock or hollows greater than 50 cm).

Parlour traps (creels with a second inner chamber to prevent escape) are fished and are usually left for 2 days soak (weather permitting). Although the potting season usually extends from March through to October, edible crab *Cancer pagurus* is the main catch until May and after September. Prior to Sea Fisheries Committee Bye-Laws banning their use, lobsters were targeted by baiting with "soft" crabs (i.e. recently moulted crabs with soft exoskeletons) which appear to attract lobsters, and inhibit other crabs from entering. Rotten bait, especially mackerel, is now used instead, although variations in bait availability have sometimes affected fishing activity in the region. During the crab season pots are baited with relatively fresh fish, apparently preferred by crabs, although some lobsters are still caught.

The mean monthly sea surface temperatures for 1988 to 1991 inclusive and mean annual sea surface temperatures between 1982 and 1991 taken at Spurn Point, (approximately 31 km to the south of Bridlington), are shown in Figures 2.5 to 2.10 (M.A.F.F. data, Jones and Jeffs, 1991).

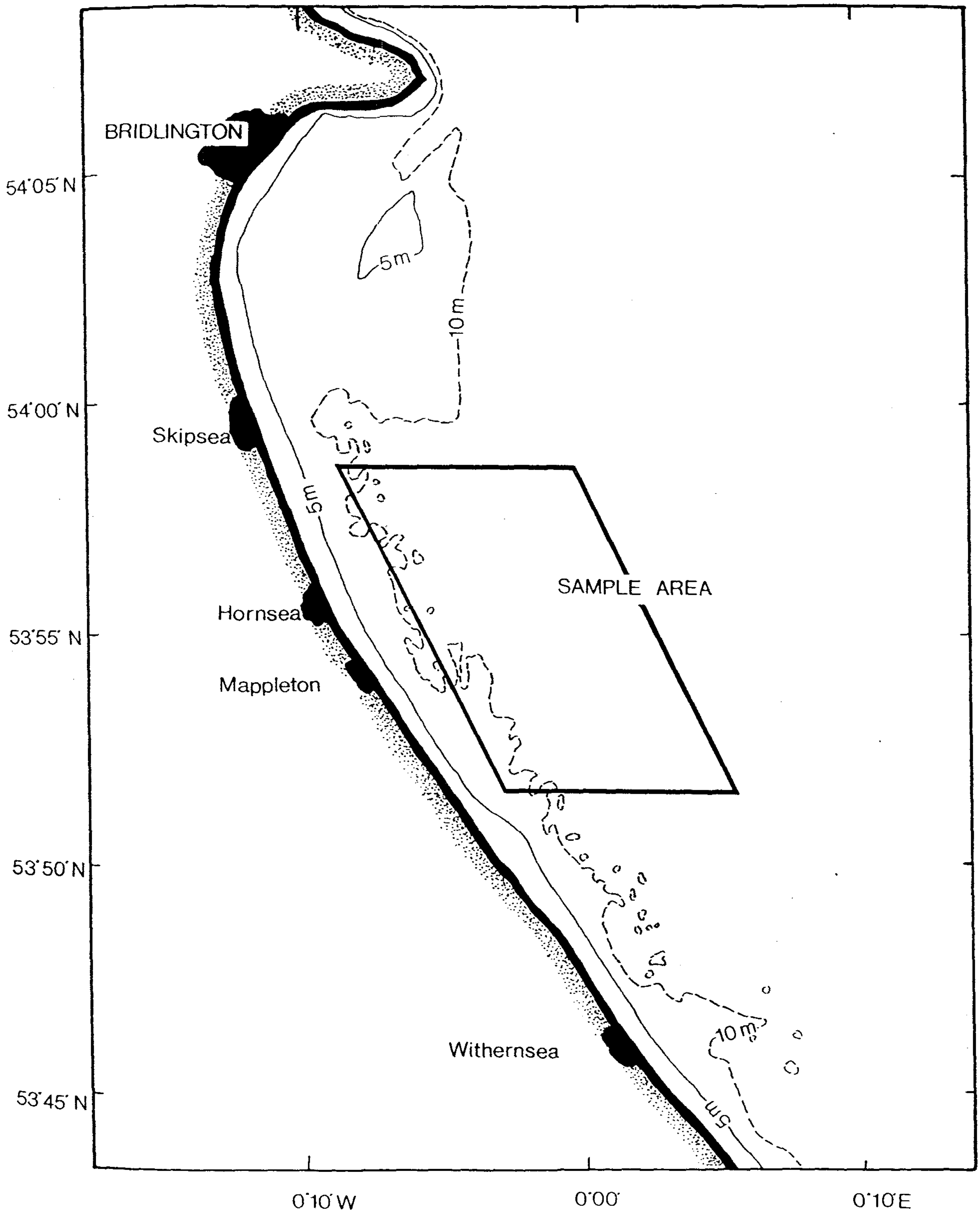


Figure 2.4 Chart showing the area covered by sampling in Bridlington Bay, Yorkshire

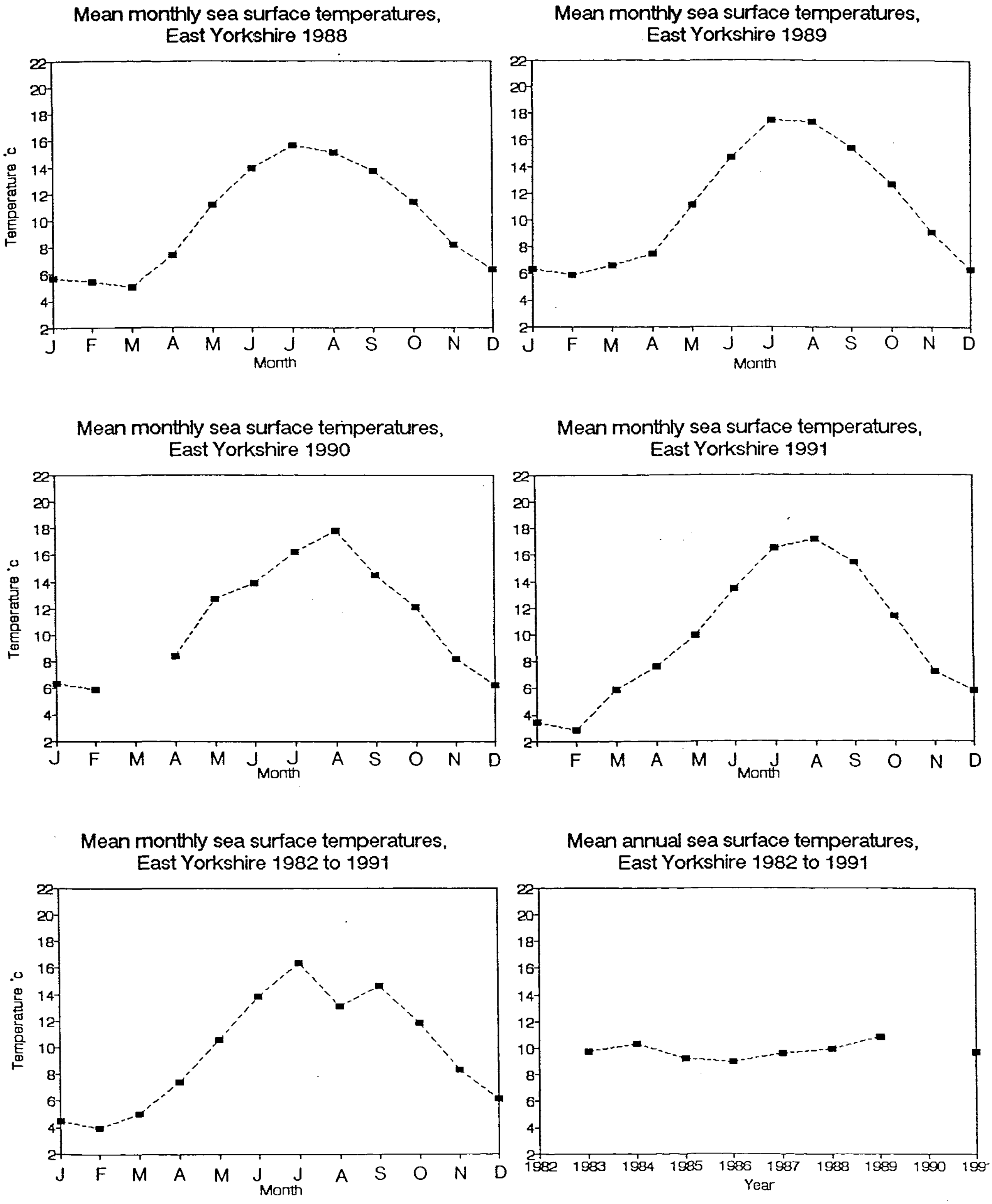
2.1.2. Dale

Although in 1990 only 97.02 tonnes of lobsters were landed in Wales compared with 495 tonnes around the English coast, lobster fisheries are important in their local areas. The three Pembroke ports of St. Davids, Fishguard and Milford Haven landed 7.4% of the total English and Welsh lobsters between 1986 and 1990. A decline in traditional inshore stocks, presumably from a reduction in catch per unit effort (C.P.U.E), forced fishermen to exploit previously un-fished offshore stocks and as a result an improvement in landings was observed during the 1980's. Catch records from the region since 1960 are shown in Figure 2.11.

Sampling trips from Dale took place in 1989 from the commercial fishing vessel F.V. "Castle Bay of Dale". F.V. "Castle Bay of Dale" is a 12 metre purpose-built boat which is crewed by 3 or 4 men. The size of this vessel enables work to take place offshore, and most of the year round, in seas which are generally stronger than those in the Yorkshire or Selsey inshore fisheries. The winter catch is predominantly crab, and baiting specifically for lobster with rotten fish (especially skate) takes place between May to October. Weather conditions sometimes enforce a closed season, usually in the Autumn, and winter fishing may be reduced to a fifth of the summer level because of gales.

The main fishing area is between 22 and 35 km from Dale (Figure 2.12), and comprises Grassholm Island, the "Hats", the "Barrels" and the Smalls. The "Hats" and the "Barrels" are disused explosives dumping grounds, between 10 and 40 metres deep; Grassholm Island and the Smalls are usually fished below the 30 metre contour. The distance offshore, depth and very large tidal movements in the area (2 to 3 knots neap tides, 5 knots during spring tides) have prevented any diving surveys on these sites. Admiralty charts, however, show the sea bed to consist of rock with coarse shingle, and broken shells; no more detailed information is available.

The traps used are creels, similar in size and design to parlour pots, but without an inner partition. The strings may be composed of 40, 50 or 80 pots and are usually left for 2 days soak (weather permitting). The catch is mainly crab with lobster, and occasionally crawfish *Palinurus elephas*. The dates of sampling trips to this region are shown in Appendix Table 2.2.


Mean monthly sea surface temperatures, East Yorkshire 1988

Mean monthly sea surface temperatures, East Yorkshire 1989

Mean monthly sea surface temperatures, East Yorkshire 1990

Mean monthly sea surface temperatures, East Yorkshire 1991

Mean monthly sea surface temperatures, East Yorkshire 1982 to 1991

Mean annual sea surface temperatures, East Yorkshire 1982 to 1991

Figures 2.5 to 2.10 Mean monthly and annual sea surface temperatures, Spurn Point, Yorkshire 1982 to 1991.

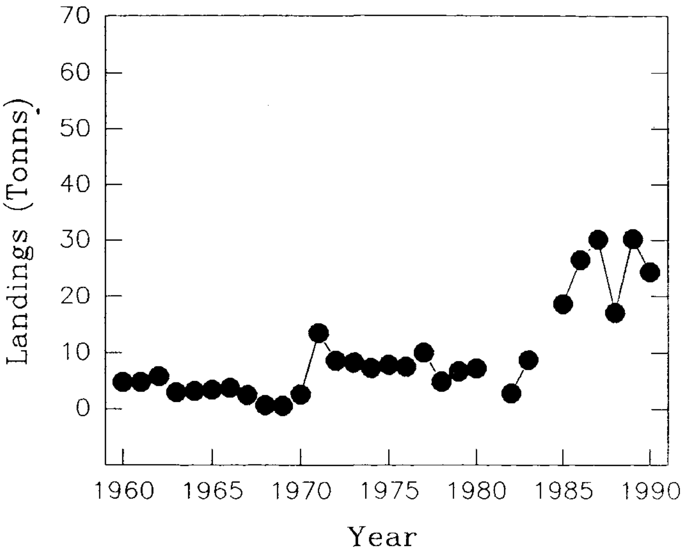


Figure 2.11 Officially recorded landings, Milford Haven, West Wales 1960 to

The mean monthly sea surface temperatures (March to November) for 1988 to 1991 inclusive and mean annual sea surface temperatures between 1982 and 1991 taken at Skomer Island and mean annual sea surface temperatures for St. Gowan light vessel are shown in Figures 2.13 to 2.17 (M.A.F.F. data, Jones and Jeffs, 1991). Skomer Island temperatures are only recorded between March and November as part of the Marine Nature Reserve research programme. These are therefore backed up by St. Gowan light vessel data (approximately 12 km South-East of Dale) (discontinued, 1987) to allow an estimation of the expected December, January and February mean temperatures.

2.1.3. Selsey

The Selsey (West Sussex) fishery has shown increased landings since the 1960's when inshore fisheries appeared to be quite depleted and an offshore lobster fishery was developed, more than 15 km out into the English Channel (fished by much larger (15-18 metre boats)). The current inshore fishery extends to less than 8 km from Selsey Bill (Figure 2.18), and is usually fished by boats of 7.5-10 metre length, moored off the Bill itself. Part time fishermen are common in the region, as are recreational divers who remove an undetermined number of lobsters during the

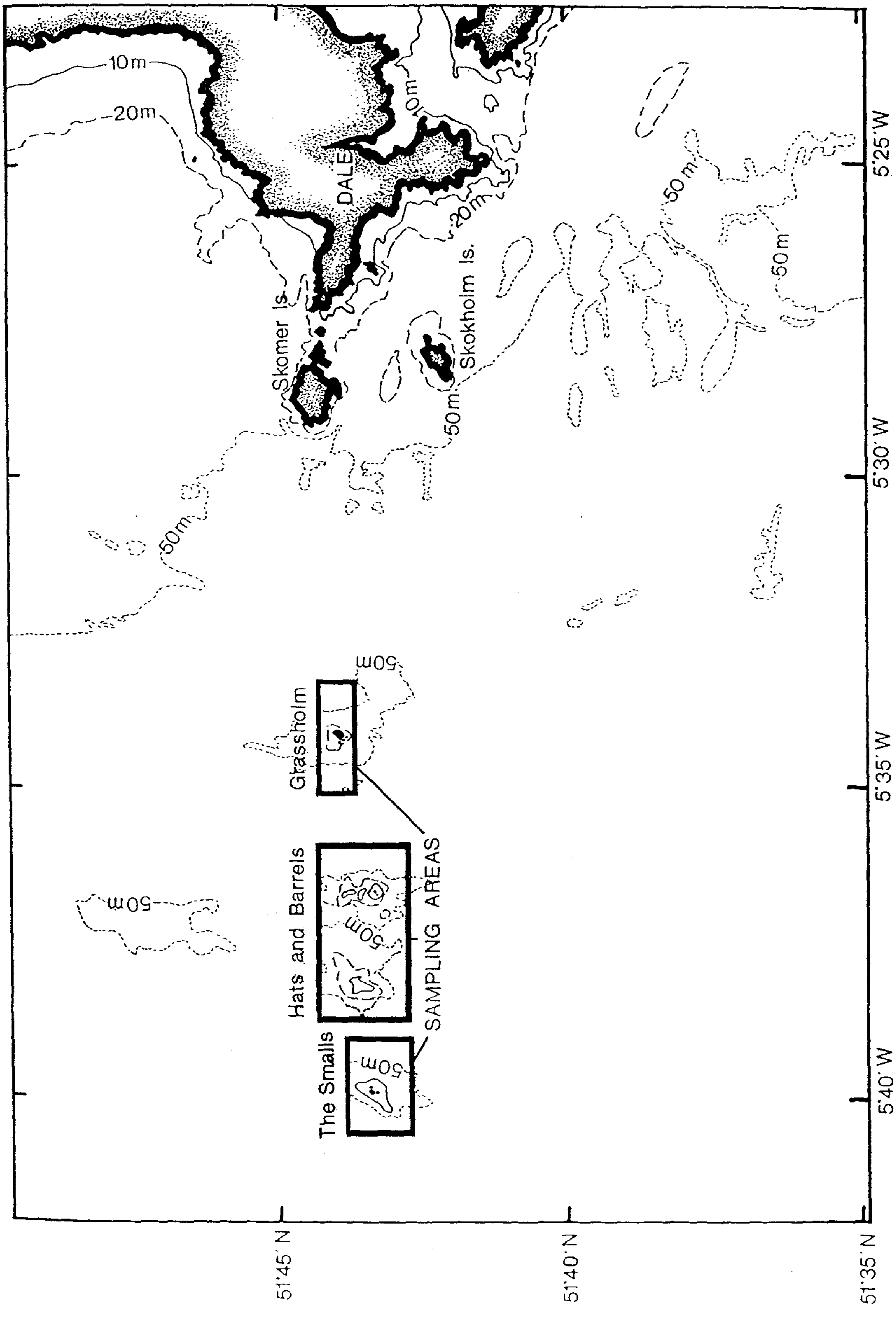
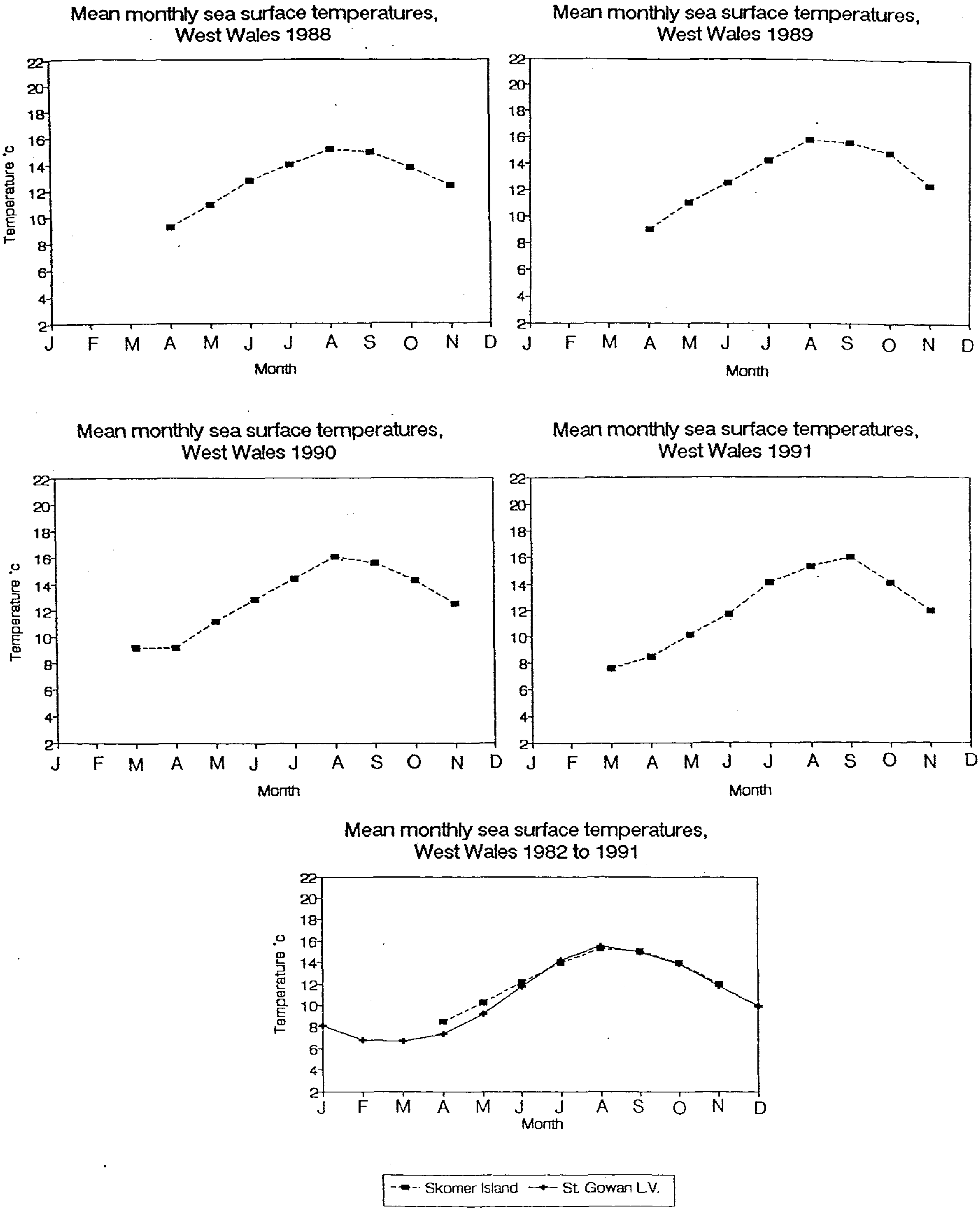


Figure 2.12 Chart showing the area covered by sampling from Dale, West Wales.



Figures 2.13 to 2.17 Mean monthly and annual sea surface temperatures, Skomer and St. Gowan L.V. 1982 to 1991.

summer months, and therefore the size and extent of the fishery may be difficult to assess. Full time fishermen often continue the fishing season throughout the winter, although the catch at this time of year is predominantly *Cancer pagurus*. The weather appears to be less restrictive on fishing activity in the area than in Bridlington. During the winter months boats are moored in the shelter of Chichester Harbour, and gear can be set closer inshore than in summer. These areas (between 100 metres and 3 km offshore) may also be fished for spider crab *Maja squinado* in the summer months if lobsters are scarce, weather is bad or if there has been an oversupply of lobster and lobster prices are relatively low. The penalty of long steam times to the winter fishery is offset by relatively high prices (up to four times peak summer prices) offered by wholesalers during the winter season.

In 1990, 31.93 tonnes of lobsters were landed at Selsey, 20% of the year's catch on the south coast (between Rochester and West Bay, Dorset). The Sussex coast fisheries, of which Selsey is by far the most important, contributed only 7% of the total official landings in England and Wales between 1986 and 1990, although this figure may be partially owing to poor records resulting from the number of part time fishermen in the area and because a large number of fishermen sell directly to the public and restaurant trade. The increase in official landings at Selsey since 1960, with the development of both the inshore and offshore fisheries, can be seen in Figure 2.19.

Sampling trips were made from Selsey in 1989 and 1990 on the fishing vessel "Romulus", a 10 metre boat crewed by 2 or 3 men. In addition, samples for fecundity studies and for investigating reproductive condition and ovarian development were collected from "Arrows" commercial storage tanks at Selsey. A list of sample dates and type are given in Appendix Table 2.2.

F.V. "Romulus" sets ink-well pots; 11 strings of 30 pots in the region shown in Figure 2.18, up to 8 km offshore. This area is 12 to 20 m deep, and according to Admiralty charts, the sea bed is dominated by rock patches, coarse shingle, gravel and pebbles. There have been no full diving studies in the area, although personal diving observations, and those of Ackers (1977), have indicated large areas of shingle banks, and occasional limestone reefs or limestone rock caps protecting blue clay sediments, and loose clay stones frequently populated by

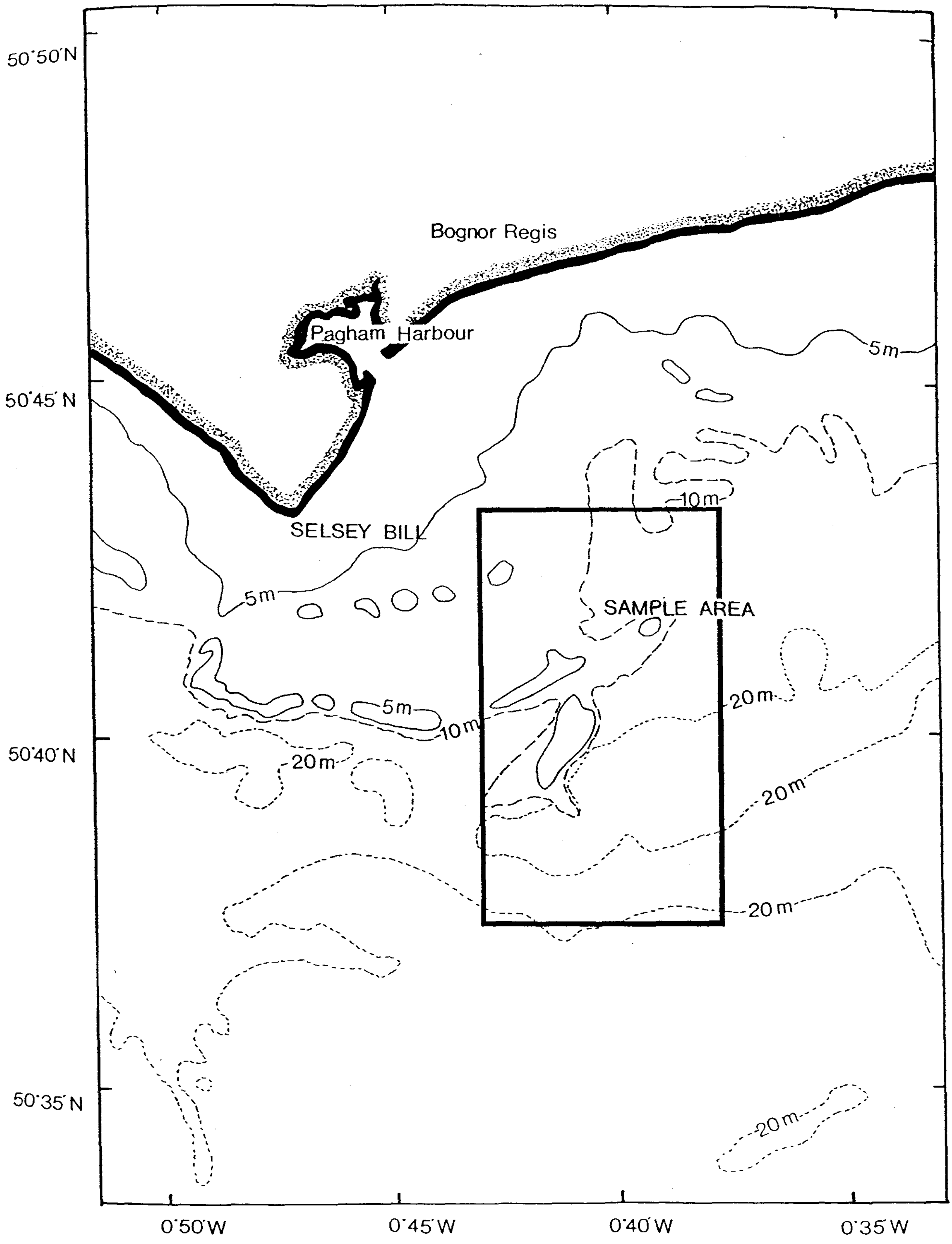


Figure 2.18 Chart showing the area covered by sampling in Selsey, West Sussex.

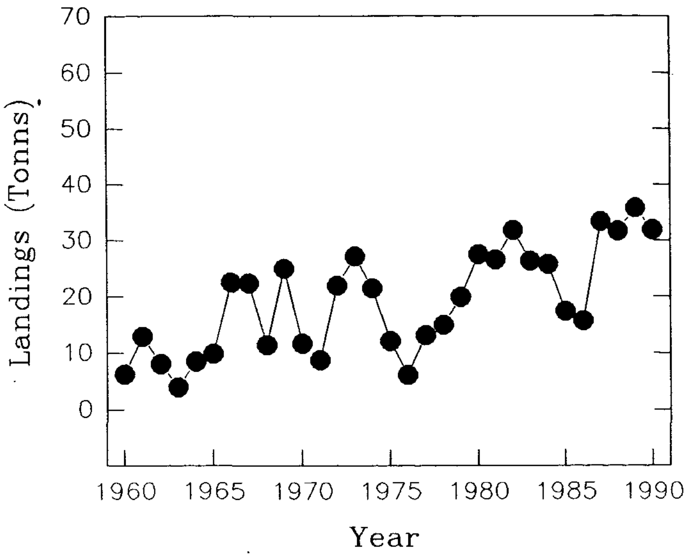


Figure 2.19 Officially recorded lobster landings, Selsey, West Sussex, 1960 to 1990.

lobsters.

When weather permits, pots are hauled 6 times a week, although this may be reduced during poor fishing periods when the catch is small or of low value. The traps are usually baited with rotten skate in summer, and fresher fish during the winter months when crabs are more common.

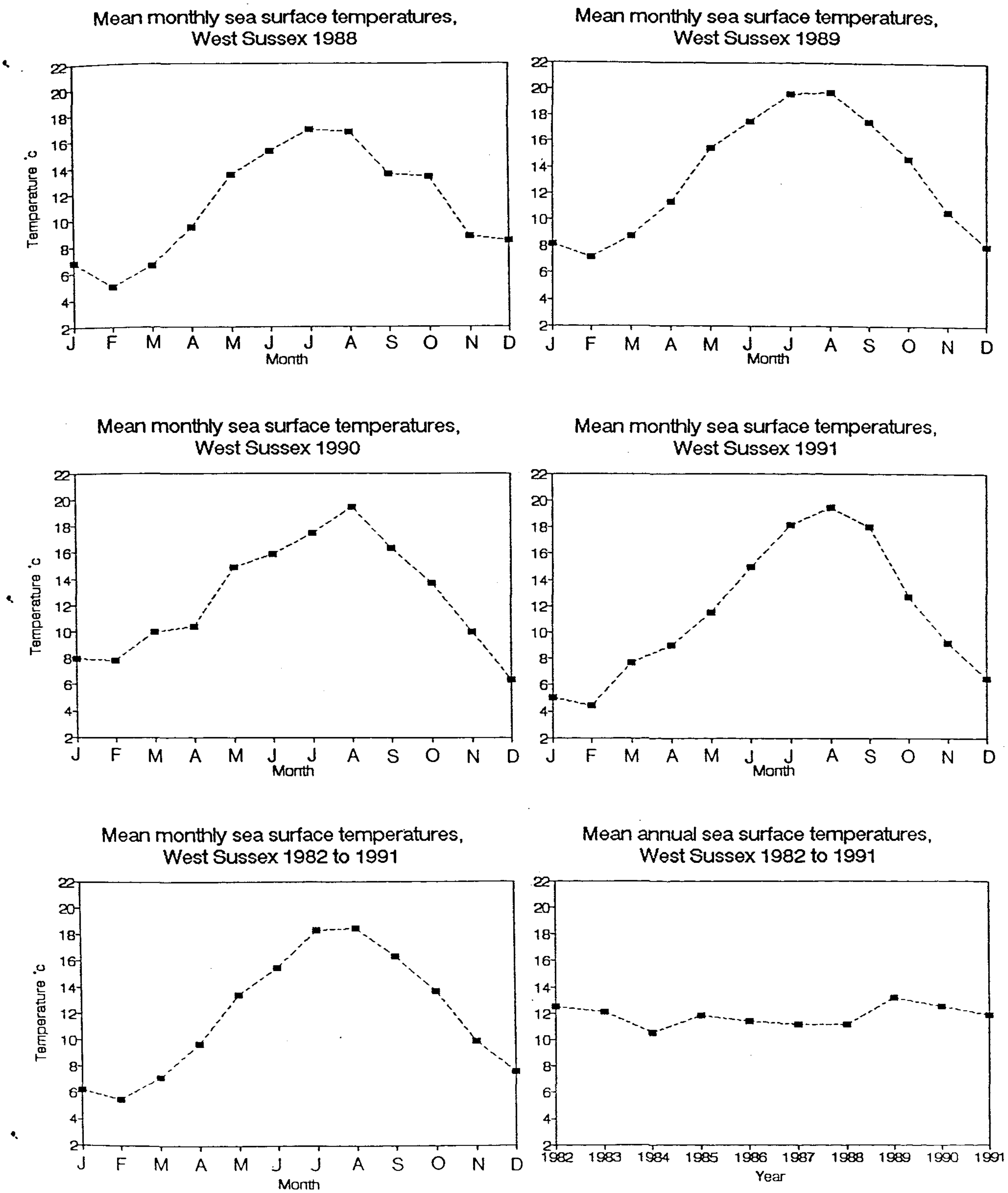
The mean monthly sea surface temperatures for 1988 to 1991 inclusive and mean annual sea surface temperatures between 1982 and 1991 taken at Shoreham (19 km East-North-East of Selsey Bill), West Sussex, are shown in Figures 2.20 to 2.25 (M.A.F.F. data, Jones and Jeffs, 1991).

2.2 Methods and data analyses

2.2.1 Collection of Data at Sea

On each field sampling occasion, the surface sea temperature and weather conditions were recorded. For each fleet hauled, the number of pots in the string, type of pot, number of days soak and the type of bait used were all noted.

Each lobster caught during the sample trip was examined and the following parameters were measured and recorded: sex, carapace length (from the rear of the


Mean monthly sea surface temperatures, West Sussex 1988

Mean monthly sea surface temperatures, West Sussex 1989

Mean monthly sea surface temperatures, West Sussex 1990

Mean monthly sea surface temperatures, West Sussex 1991

Mean monthly sea surface temperatures, West Sussex 1982 to 1991

Mean annual sea surface temperatures, West Sussex 1982 to 1991

Figures 2.20 to 2.25 Mean monthly and annual sea surface temperatures, Shoreham, West Sussex 1982 to 1991.

eye socket to the rear of the carapace, parallel to the median line), abdomen width (measured as the maximum width of the outside of the second abdominal segment (Aiken and Waddy, 1980) cf. Templeman (1939)), and chela length, width and depth (Figure 2.27). Only the larger, "crusher" chelae were gauged (Templeman, 1939; 1944), and chelae which had suffered obvious damage were not measured. Moult stages "A", "B or C_1", "C_2 or C_3" were checked for by the criteria given in Appendix A2ii.1. Ovigerous females were further examined for the development stage of their eggs. Eggs were classified into approximate developmental stages "just berried" (eggs dark green to black, no eye spots), "eyed" (eye spots visible) or "releasing" (eggs well developed with little or no yolk remaining, some egg loss apparent).

The dates of sampling trips undertaken during this study are given in Appendix A2i Tables 1 to 3.

2.2.2 Additional Data Collection

Additional data that had been collected between 1972 and 1974 were used for comparisons of current and historical population biology. Size frequency distributions of female lobsters and the monthly proportion of females berried between 1972 and 1974 from Yorkshire, Pembrokeshire (West Wales) and for the south coast of England, have been used in this study. These additional sample dates have been presented in Appendix A2i Table 4. Historical estimates of growth increments for each of the three regions (Appendix A2i Table 5) have been used for the interpretation of potential differences in size at onset of maturity (Chapter 4).

M.A.F.F. log book returns collected for the years 1987 to 1989 have been used in estimating monthly C.P.U.E. for each of the three study areas.

A representative sample of males and females covering the full size ranges of those collected on the sampling trip, were taken to the laboratory for more detailed study and for wet weight mensuration. In addition, samples for fecundity studies were purchased from wholesalers and fishermen at each of the three sites. Egg collections made for use in fecundity studies in September 1987 and June 1988 have been processed during the course of this study in addition to the 1988 to

1992 samples (Chapter 6).

Carapace length, abdomen width and claw measurements were collected on 11/09/1990 on the quayside. Female cement gland development assessment (described in Appendix A2ii.2) for onset of maturity studies (Chapters 3 and 4) were also undertaken in August 1990 at Bridlington and throughout 1990 at Selsey using animals from wholesalers stock.

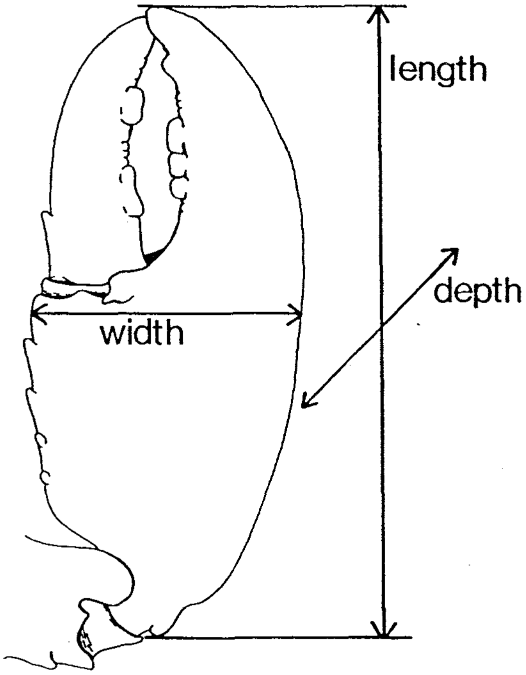


Figure 2.27 Chela propodite of *Homarus gammarus* to show the dimensions for measuring length, width and depth.

2.2.3 Data Analyses

Size frequency distributions

Size/frequency data for each site, collected between 1989 and 1991, were compared using summary statistics of the size distributions for each sample date and annual distributions for both sexes at each site, were calculated for inter-comparisons. The historical, female size/frequency data collected between 1972 and 1974 for Yorkshire, Pembrokeshire and the south English coast, have been summarised by the median and modal classes and skewness and kurtosis of the distributions only as the size/frequency data were only available in 5 mm carapace length groups. Kolmogorov-Smirnov tests (at 95 % level) were used to compare size distributions (in 5 mm CL classes) within sites for males and females and then for each sex between sites and sample years.

Length-weight relationships

The relationship between lobster carapace length (mm) and total wet weight (g) (for use in C.P.U.E estimation) was investigated by weighing those lobsters returned to the laboratory for further analysis. Total wet weight and CL were transformed into log values and their relationship assessed using linear regression analysis, after checks for data normality and homoscedacity had been carried out. The results of regression analyses (Residual sums squared, mean of Y, standard error, standard deviation of Y, R^2, r, the significance of F and coefficient values with standard error, t-statistics and significance) for each site, year and sex of lobster, in addition to female reproductive state (berried or non-berried) were compared using ANCOVA (Sokal and Rohlf, 1981). Summary statistics of the length and weight data were calculated (average, standard deviation, variation, minimum and maximum values).

Catch per unit effort

Catch per unit effort (C.P.U.E.) was standardised as catch per 100 pot hauls. Log book statistics (weight of landed lobsters) were obtained for each area. C.P.U.E. estimates for each sample date were both calculated as number of lobsters caught (above 85 mm CL and total catch) and the weight of lobsters caught (using length-weight relationships estimated in the laboratory) for each site. The percentage of the catch that was sized, for each sampling trip, was also calculated.

ANCOVAs, with month and year as covariates and data type (log book or sampling trip) as factors, were made to assess potential dissimilarity between log book C.P.U.E. data and that calculated for each sample trip (weight of lobsters landed). In addition, the variation in lobster landings (weight covarying with number and number covarying with weight), with sample dates and sites as covariates and factors respectively, was investigated using ANCOVA.

Sex ratios

The monthly sex ratios of catches and sex ratios for each sampling trip were calculated as percentage female for Bridlington, Dale and Selsey.

Percentage of females berried

The percentages of females found to be berried were calculated for both the 1972 to 1974 and 1989 to 1991 sample dates, and monthly for each site.

Percentage of lobsters soft

The percentages of lobsters of each sex noted as being soft (i.e. not stage C_4), were calculated for each sample trip.

2.3 Results

Size frequency distributions

Bridlington size frequency graphs (Figures 2.28 to 2.44) and summary statistics Appendix Table (A2iii.1) indicate that the highest catch of both males and females was on 24/05/1989. Both the size distribution of catches (and plot kurtosis) and numbers caught can be seen to vary between years, monthly and daily (e.g. 18/07/1990 and 19/07/1990).

Dale male and female size frequency distributions are not as skewed nor as kurtose as those observed on Bridlington sample trips. The relatively wide size ranges shown by the graphs (Figures 2.45 to 2.48) and Appendix Table (A2iii.2) are platykurtic. An increase in the actual number of individuals caught occurs in August 1989, possibly as a result of new recruitment, after the growing periods for males and females have ended, an increase in fishing activity, or alternatively as a result of an increase in catchability of individuals following the cessation of moult and reproduction cycle inhibitory influences. The limited number of males caught in May and June 1989 may be caused by such moult cycle influences.

Selsey size frequency graphs (Figures 2.49 to 2.54) exhibit little variation in their structure during 1989 and 1990, with the exception of a reduction in the number of individuals caught from 26/04/1989 and 06/07/1989 to 09/08/1989 and 07/09/1989. The reduction in numbers caught may simply be caused by good catches earlier in the fishing season. The catch on 19/07/1990 is quite similar to that of 06/07/1989, inferring seasonality in catch size numbers and size structure.

Catch size summary statistics from each sampling trip, indicate very slight differences in the average sizes of males and females caught at any given site between 1989 and 1991, but notable differences in the average sizes of lobsters between sites (Appendix Tables A2iii.1 to A2iii.3). The average Selsey 1989 and 1990 male and female lobsters were shorter (78.93 and 80.38 mm CL males; 81.23 and 82.24 mm CL females) than those from Bridlington in 1989, 1990 and 1991 (84.94, 86.32, 83.35 mm CL males; 84.06, 83.82, 80.23 mm CL females), which themselves were considerably shorter than those individuals caught at Dale in 1989 (males 113.25; females 111.41 mm CL). The absolute minimum and maximum sizes of animals caught also showed considerable geographical variation; the maximum and minimum sizes of Dale lobsters being larger than those at the other two sites. Unfortunately the mean sizes of female lobsters caught between 1972 and 1974 could not be calculated because the data available were classed into 5 mm CL groups. Comparisons of modal groups indicate similarities between each of the historical size distributions (with modes of between 89 and 91 mm CL) (Appendix Figs. A2.1 to A2.32; Appendix Tables A2iii.4 to A2iii.6). The Yorkshire and south coast size modes are both smaller between 1989 and 1991 than between 1972 and 1974; possibly reflecting an increase in exploitation levels within the two fisheries (although these differences may also have been caused by changes in gear type). Dale modal size for 1989 is much higher than the Pembrokeshire 1972 and 1973 figure (89 mm CL c.f. 128 mm CL), most probably because of a change in the location of the fishery from inshore to offshore regions.

Kolmogorov-Smirnov tests applied to size frequency distributions, confirm the apparent differences in the sizes of lobsters from each of the sites, shown in Figs. 2.28 to 2.54, and between dates.

Some differences between male and female size distributions are indicated

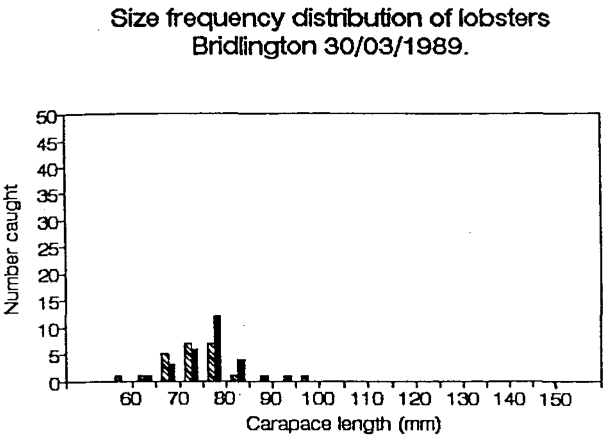

Size frequency distribution of lobsters
Bridlington 30/03/1989.

Fig.2.28

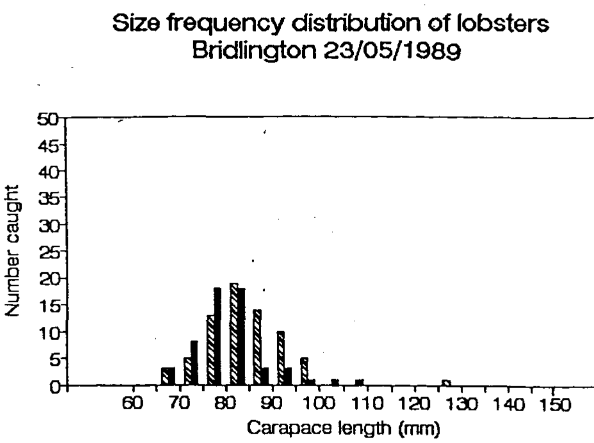

Size frequency distribution of lobsters
Bridlington 23/05/1989

Fig.2.29

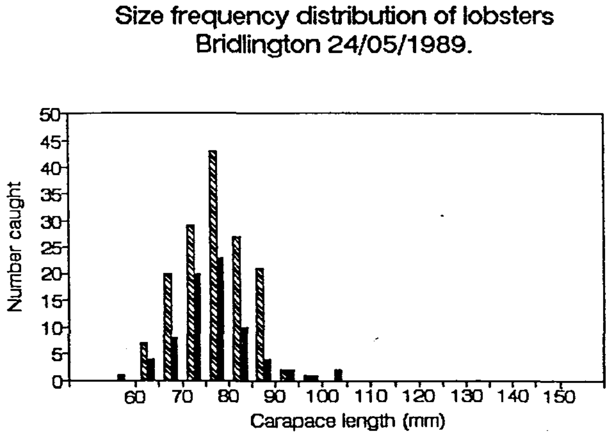

Size frequency distribution of lobsters
Bridlington 24/05/1989.

Fig.2.30

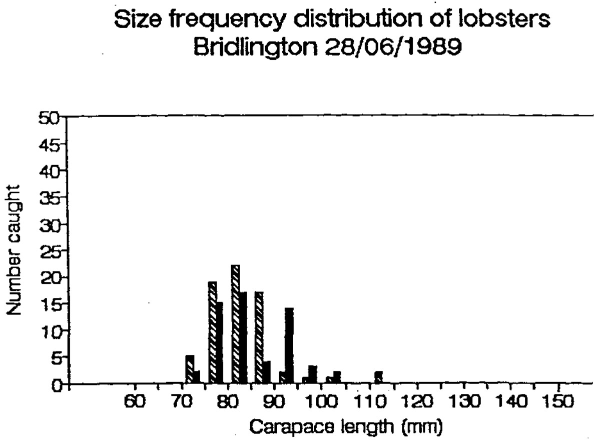

Size frequency distribution of lobsters
Bridlington 28/06/1989

Fig.2.31

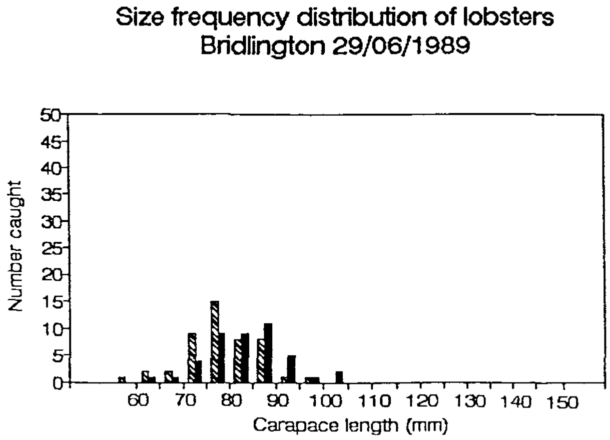

Size frequency distribution of lobsters
Bridlington 29/06/1989

Fig.2.32

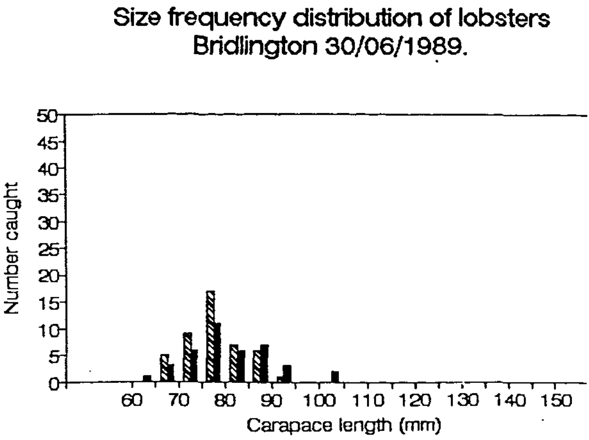

Size frequency distribution of lobsters
Bridlington 30/06/1989.

Fig.2.33

▨ Females ■ Males

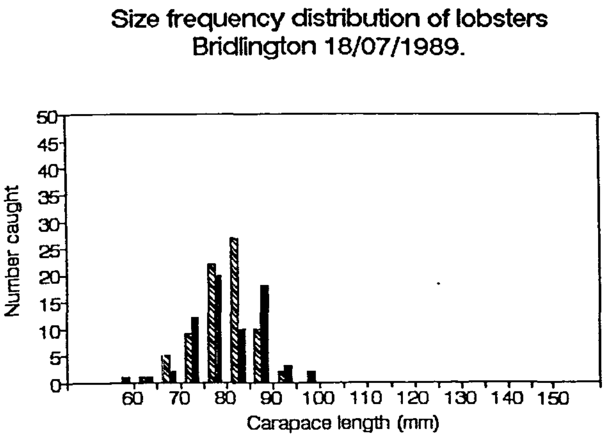


Fig.2.34

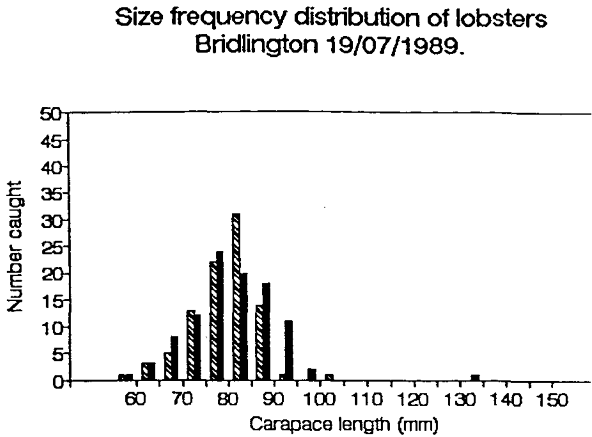


Fig.2.35

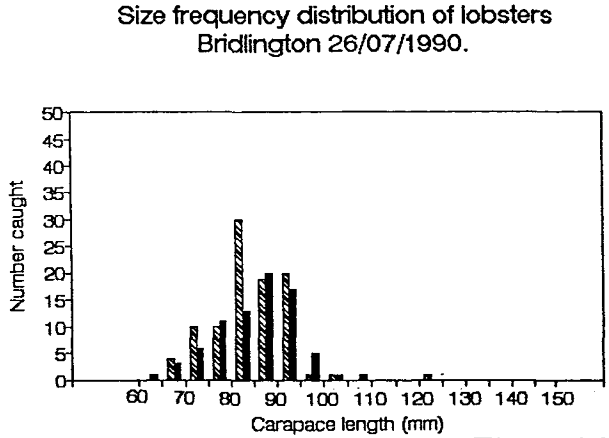


Fig. 2.36

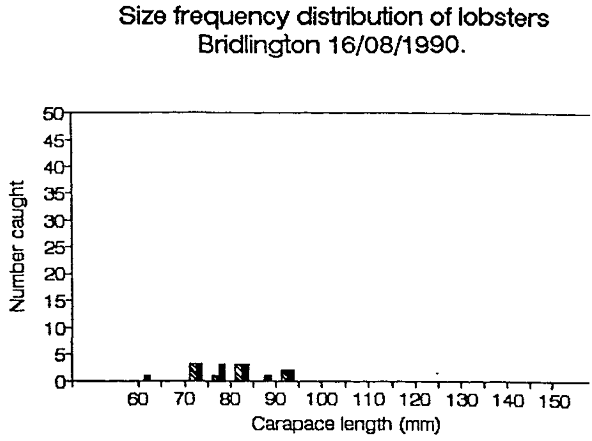


Fig.2.37

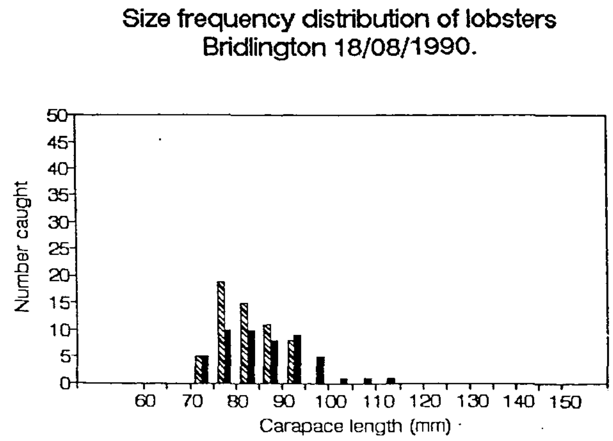


Fig. 2.38

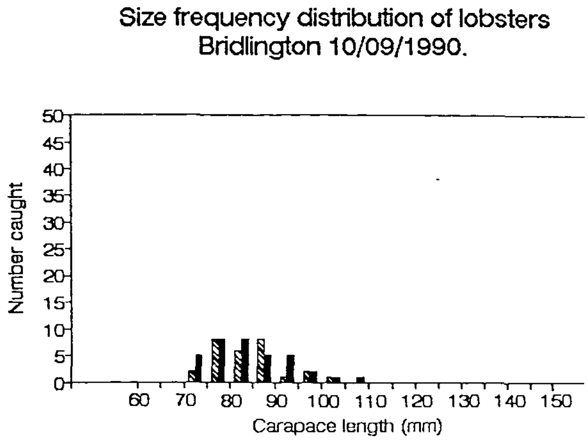


Fig.2.39

▨ Females ■ Males

Size frequency distribution of lobsters
Bridlington 11/09/1990.

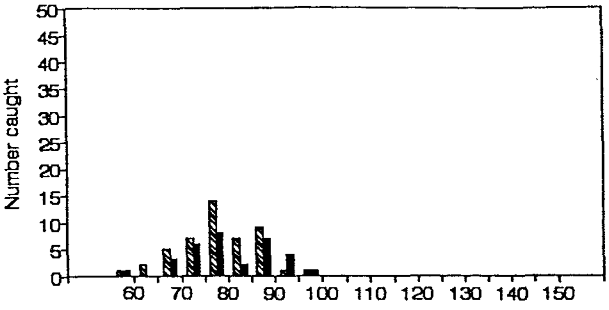


Fig.2.40

Size frequency distribution of lobsters
Bridlington 10/06/1991.

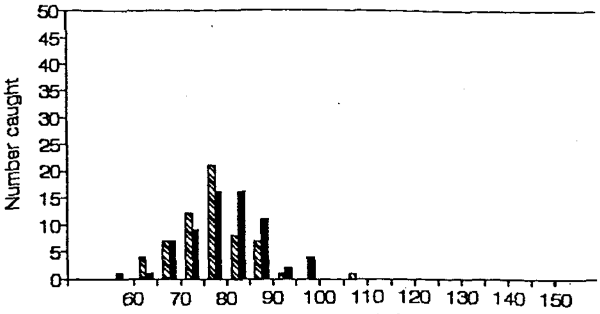


Fig.2.41

Size frequency distribution of lobsters
Bridlington 11/06/1991.

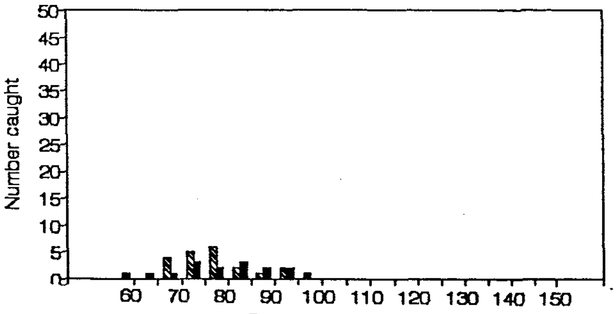


Fig.2 .42

Size frequency distribution of lobsters
Bridlington 13/06/1991.

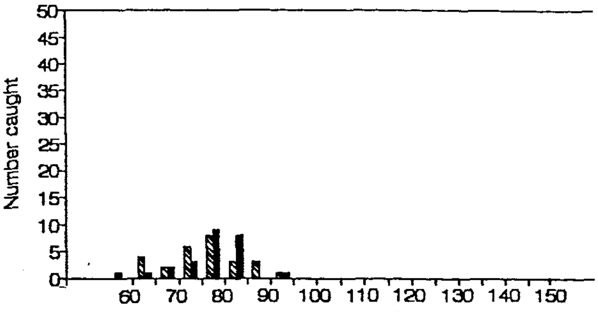


Fig.2.43

Size frequency distribution of lobsters
Bridlington 14/06/1991

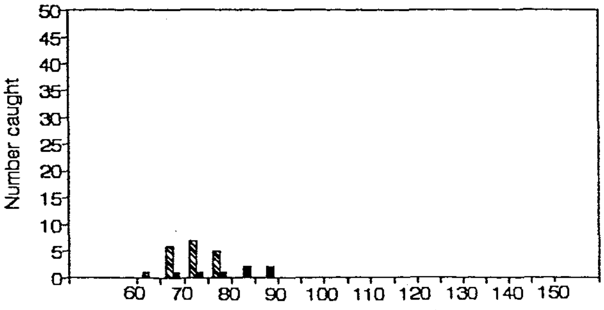
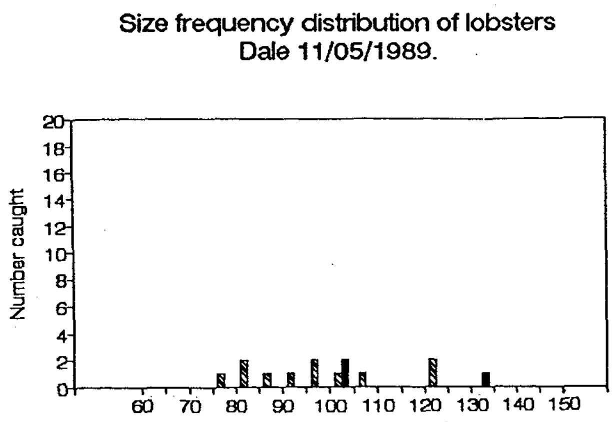


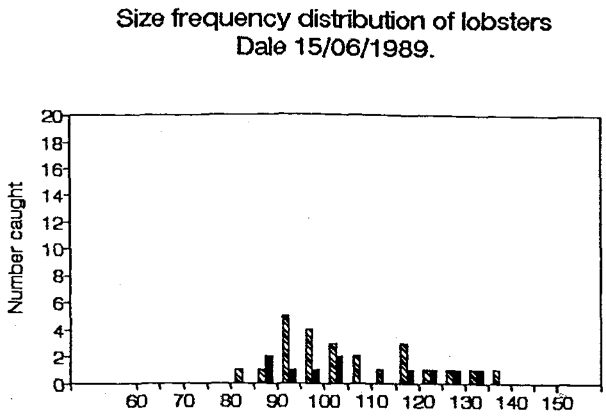
Fig.2.44

▨ Females ■ Males



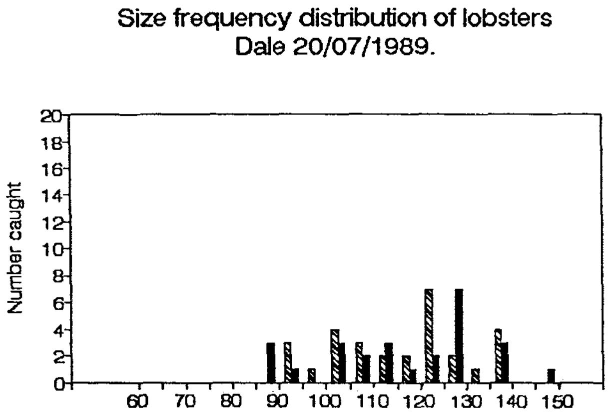
Size frequency distribution of lobsters
Dale 11/05/1989.

Fig.2.45



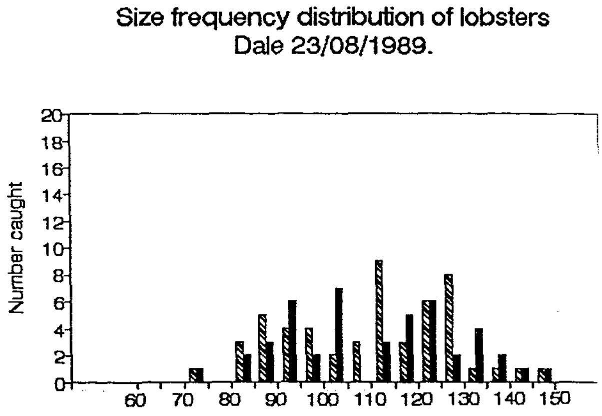
Size frequency distribution of lobsters
Dale 15/06/1989.

Fig.2.46



Size frequency distribution of lobsters
Dale 20/07/1989.

Fig.2.47



Size frequency distribution of lobsters
Dale 23/08/1989.

Fig.2.48

▨ Females ■ Males

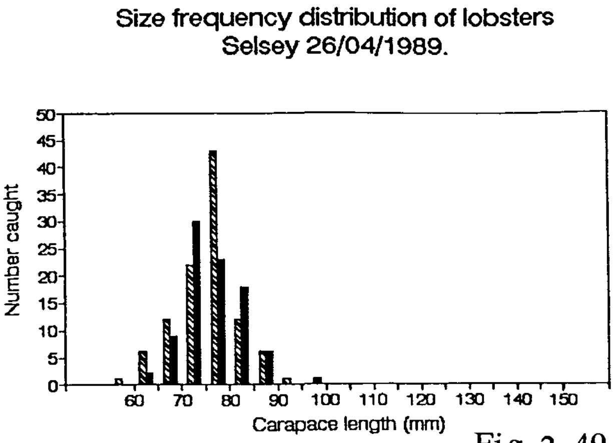


Fig.2.49

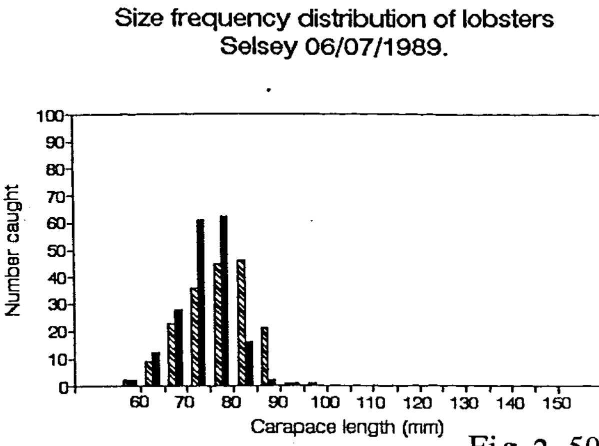


Fig.2.50

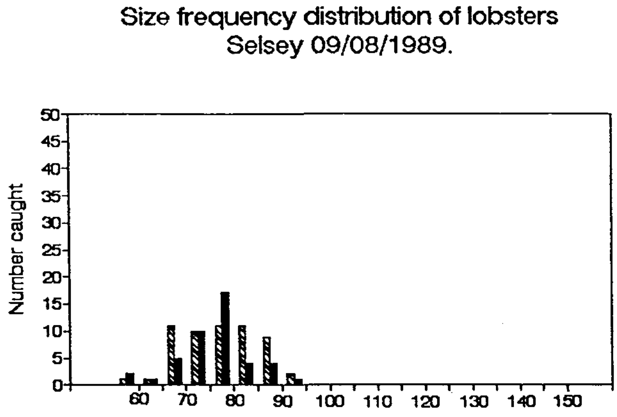


Fig.2.51

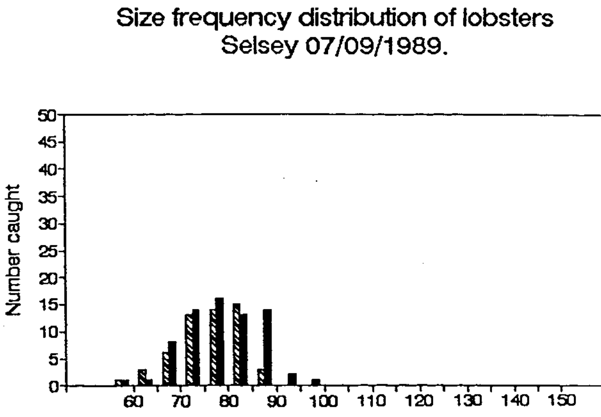


Fig.2.52

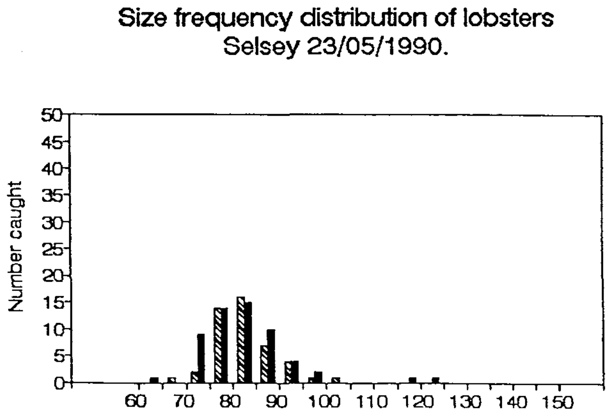


Fig.2.53

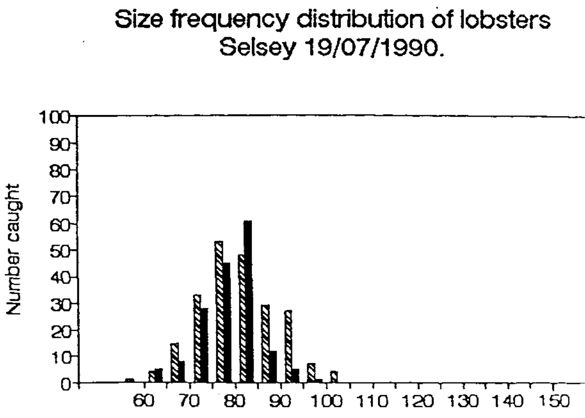
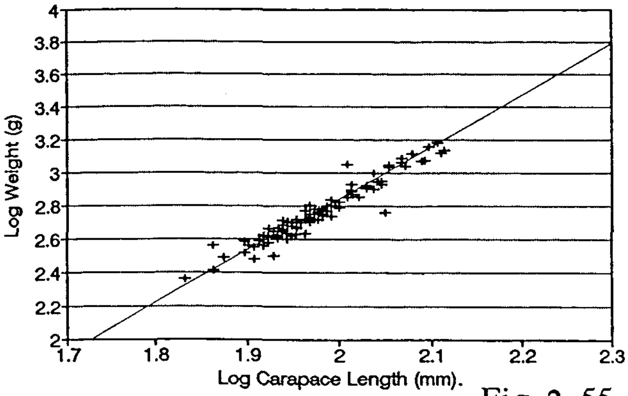


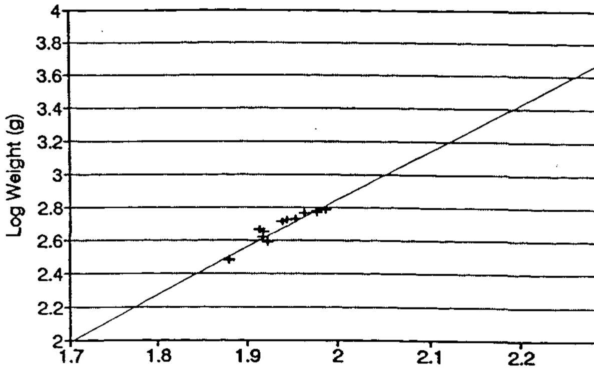
Fig.2.54

▨ Females ■ Males



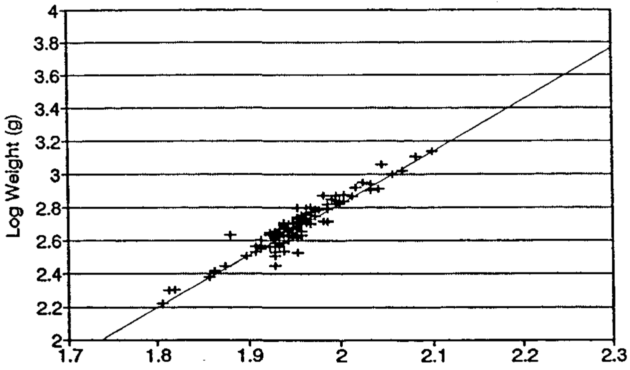
Log total weight vs log carapace length for females, Bridlington 1989 to 1991.

Fig.2.55



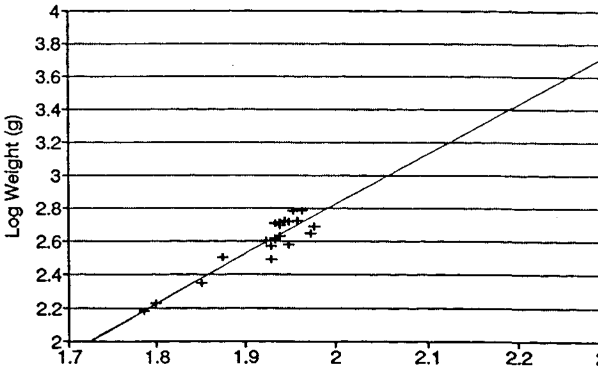
Log total weight vs log carapace length for males, Bridlington 1989 to 1991.

Fig.2.5



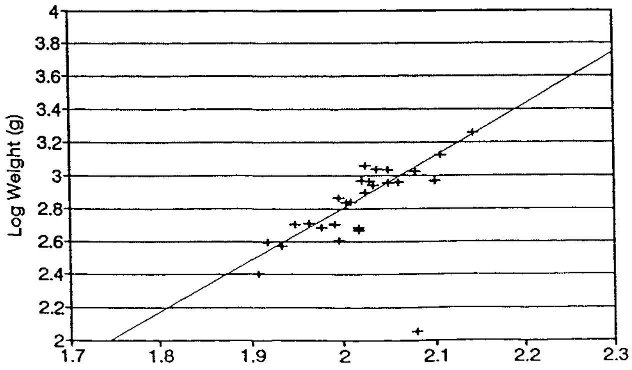
Log total weight vs log carapace length for females, Selsey 1989 to 1991.

Fig.2 .57



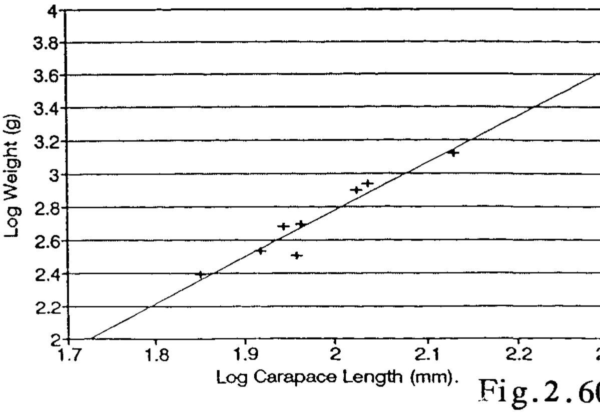
Log total weight vs log carapace length for males, Selsey 1989 to 1991.

Fig.2.5



Log total weight vs log carapace length for females, Dale 1989 and 1992.

Fig.2.59



Log total weight vs log carapace length for males, Dale 1989.

Fig.2.6

Log total weight vs log carapace length for females, Bridlington 1989.

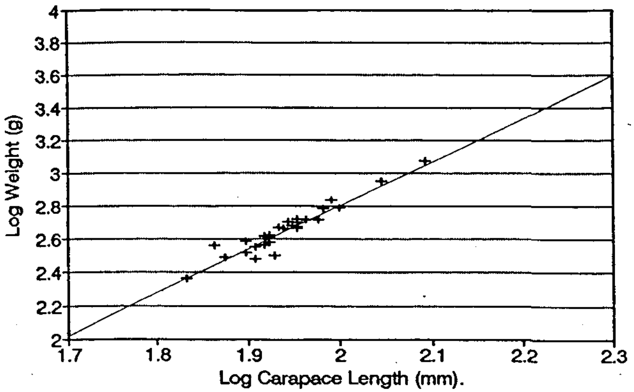


Fig.2.61

Log total weight vs log carapace length for females, Selsey 1989.

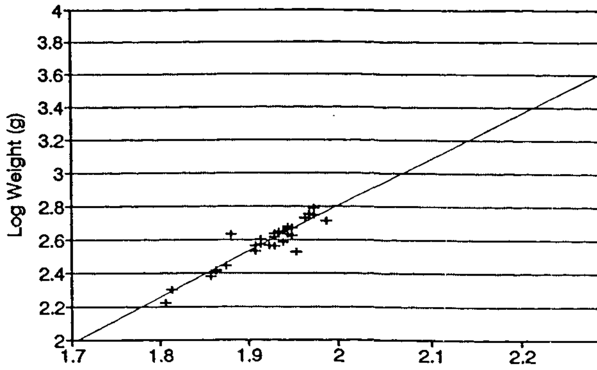


Fig.2.6

Log total weight vs log carapace length for females, Bridlington 1990.

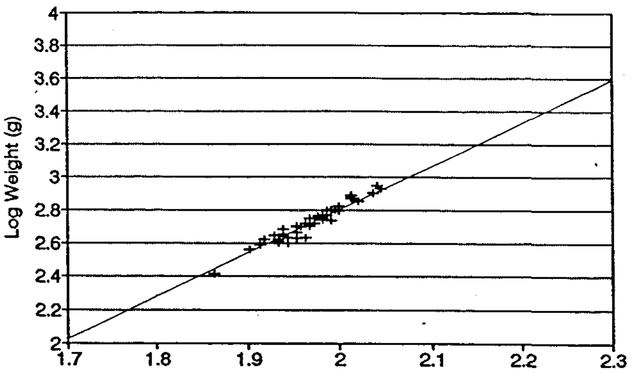


Fig.2.63

Log total weight vs log carapace length for females, Selsey 1990.

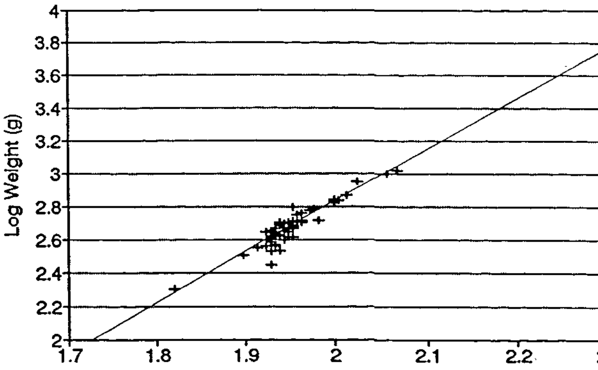


Fig.2.6

Log total weight vs log carapace length for females, Bridlington 1991.

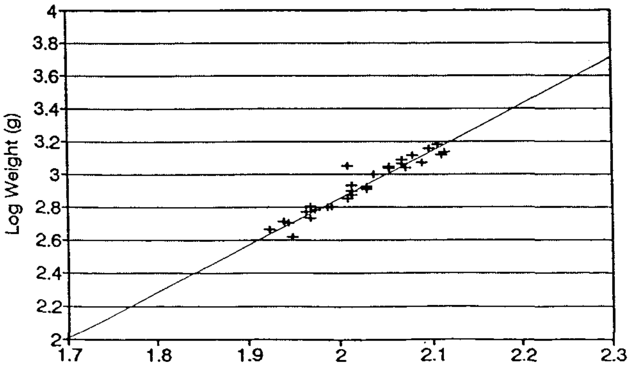


Fig.2.65

Log total weight vs log carapace length for females, Selsey 1991.

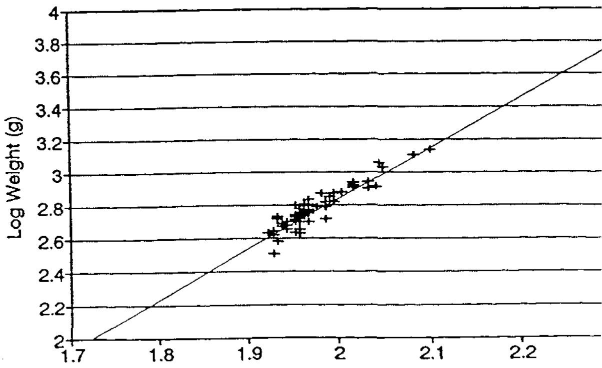
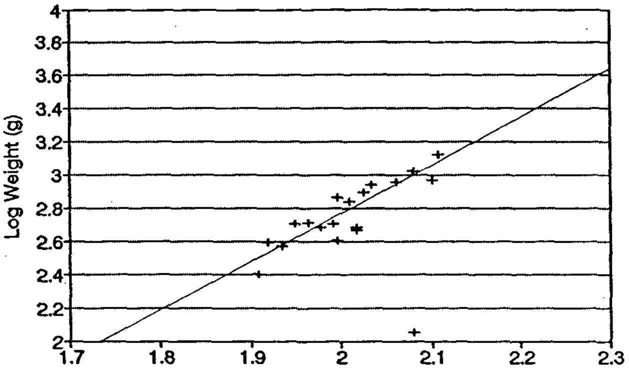
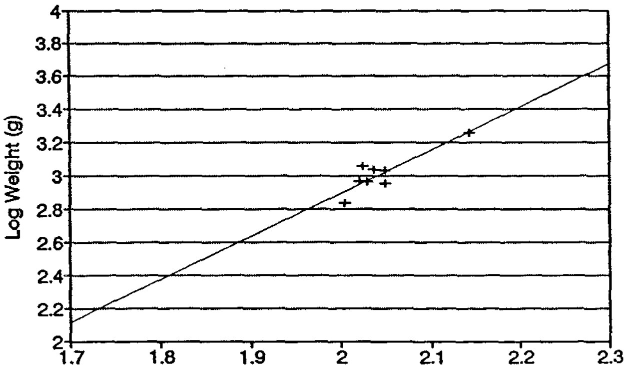


Fig.2.6



Log total weight vs log carapace length for females, Dale 1989.

Fig.2.67



Log total weight vs log carapace length for females, Dale 1992.

Fig.2.68

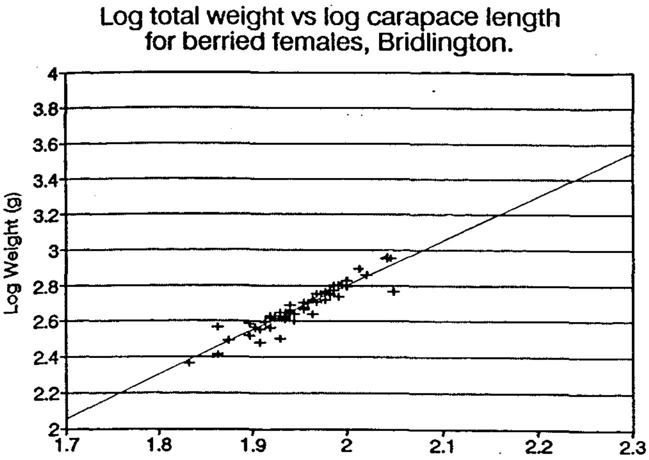

Log total weight vs log carapace length for berried females, Bridlington.

Fig.2.69

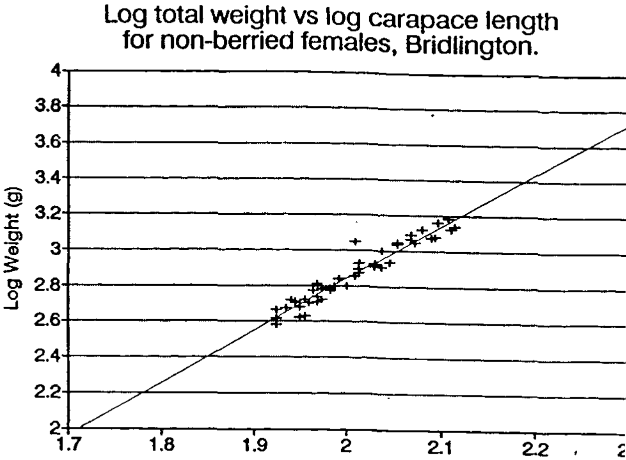

Log total weight vs log carapace length for non-berried females, Bridlington.

Fig.2.70

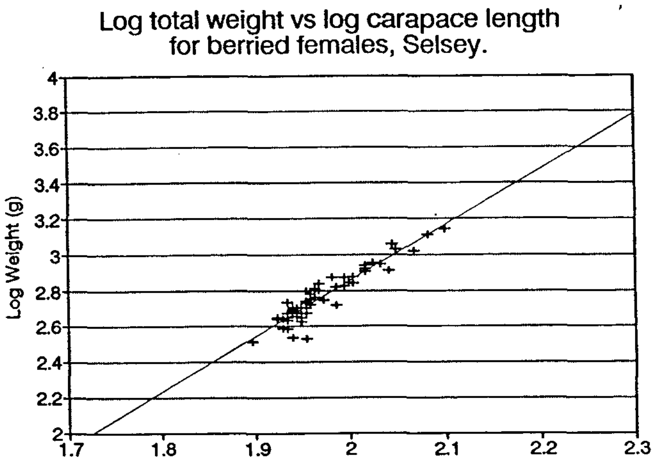

Log total weight vs log carapace length for berried females, Selsey.

Fig.2.71

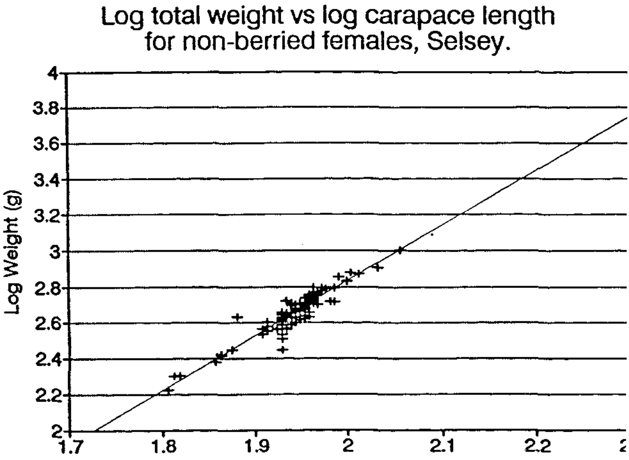

Log total weight vs log carapace length for non-berried females, Selsey.

Fig.2.72

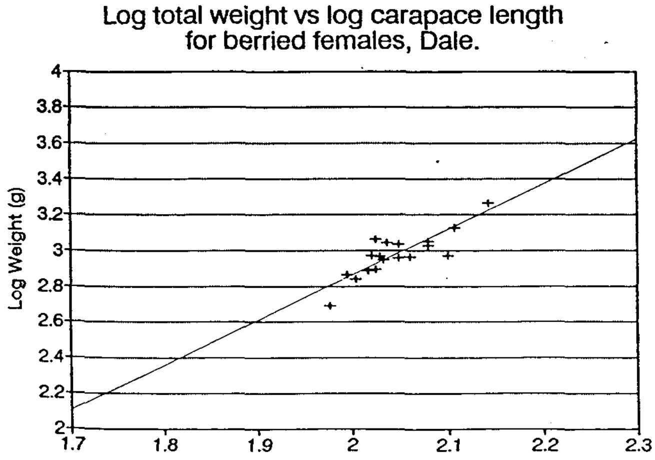

Log total weight vs log carapace length for berried females, Dale.

Fig.2.73

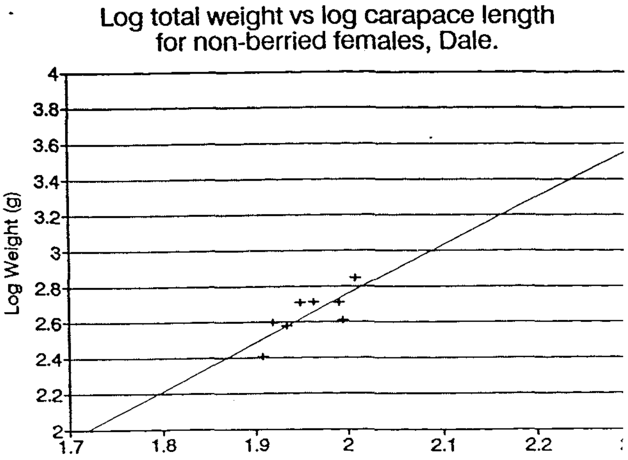

Log total weight vs log carapace length for non-berried females, Dale.

Fig.2.7

by the results from these tests (Appendix Tables A2iii.40 to A2iii.44; particularly between males and females at Bridlington, 1989 and 1990; and Selsey 1989 and 1990.

Temporal variation (between sample trips of different years) is also apparent within male and female groups at Bridlington, 1989 to 1991 and Selsey, 1989 and 1990. No sexual or temporal differences in size distribution are significant (5% level) at Dale, 1989. As no significant differences were shown between sample dates for each sex in a given year (Appendix Tables A2iii.40 to A2iii.42); sample date size distributions were collated together into year groups for between-site comparisons. Between-site analyses for each year of data, performed for males, (Appendix Table A2iii.43) revealed significant differences in the size distributions between each site. Similar analyses were carried out between sampling sites and years for female lobster size distributions, including the 1972 to 1974 data from each region. The results of these Kolmogorov-Smirnov tests, presented in Appendix Table A2iii.44, indicate significant differences at Bridlington/Yorkshire between 1972 and 1973/1974 (but not 1973 and 1974); 1972 to 1974 data and 1989 to 1991 data, but not between size distributions from 1989 to 1991. 1973 size data are not significantly different from 1989 data at Selsey/south coast, nor is there a difference between 1972 and 1990. The Dale 1989 female size frequency distribution was not significantly different from those of Pembrokeshire for 1972 and 1973. Bridlington 1990 to 1991 size distributions were not found to differ significantly from those of the south coast in 1973, nor Bridlington 1989 data from that of Pembrokeshire, 1973. Selsey 1989 and 1990 size distributions also did not differ significantly from those of Bridlington 1989 to 1991.

Length-weight relationships

Lobster log-length/log-wet weight relationship were investigated using regressions and ANCOVA. Both parameters were log transformed to conform to normality and homoscedacity assumptions of both bivariate regression and ANCOVA. A linear model, according to the equation log W = a + b log(CL in mm) was found suitable ($R^2 > 0.71$) in all cases, except for Dale non-berried females 1989 to 1992 (Appendix Tables A2iii.25 to A2iii.27). Regression coefficients were also significant for Dale berried and non-berried females and males, probably as a result of the small size of the samples used (n=18, 7 and 7 respectively). Using the regression equations produced, male lobsters of 85 mm CL can be calculated to weigh 450.85 g at Bridlington, 384.6 g at Dale and 415.645 g at Selsey; non-berried females of 85 mm CL weigh 436 g, 368.6 g and 415.9 g at Bridlington, Dale and Selsey respectively.

Regression plots (Figs. 2.56, 2.58 and 2.60) and regression coefficients (Appendix Table A2iii.25) indicate similar slopes with differing intercepts between sites for male lobster log-length/log-weight relationship: ANCOVA (Appendix Table A2iii.28) also shows the significant effect of site on this relationship. A significant effect of site on length-weight relationships was shown by ANCOVA, regression plots and regression coefficients, for female lobsters (berried and non-berried together) (Appendix Tables A2iii.27 and A2iii.28, Figs. 2.55, 2.57 and 2.59). However, the log-length/log-weight regression for Selsey berried females has quite different coefficients than those for Bridlington and Dale (Appendix Table A2iii.27) and differences between these regression relationships are shown to be significant using ANCOVA (Appendix Table A2iii.36), (Figs. 2.69, 2.71). Appendix Table A2iii.37 ANCOVA also indicates geographical differences between non-berried female log-weight/log-length equations (Figs. 2.70, 2.72 and 2.74). ANCOVA results produced in Appendix Tables A2iii.33 to A2iii.35 indicate some differences between berried and non-berried female log-length/log-weight relationships at Dale and Selsey, but not at Bridlington (also shown in Figs. 2.69 to 2.74 and Appendix Table A2iii.27). The high significance of the results for the Dale samples may be caused by the small sample size. Selsey berried and non-berried females log length log-weight regressions have similar slopes, but noticeably different intercepts, being higher for berried females.

The small sample sizes and timing of sample dates of male lobster length and weight measurements precluded separating the data into years for investigation into temporal variation of how length relates to weight. Female log-length/log-weight relationships were shown to differ at both Selsey and Bridlington between years, but not at Dale, using ANCOVA (Appendix Tables A2iii.30 to A2iii.32) as a result of dissimilarities in both slope and intercept coefficients (Figs.A2.61 to A2.68 and Appendix Table A2iii.25). An overall ANCOVA was performed for log-length/log-weight relationships between sites and sexes (Appendix Table A2iii.38), and showed variation between lobster sexes and between sexes within sites. An additional ANCOVA was performed for between sites and berried and non-berried females (Appendix Table A2iii.39) and indicated differences between berried and non berried females and between sites according to egg bearing state.

C.P.U.E.

C.P.U.E. calculated from log book returns (1987 to 1989) are presented in Appendix Table A2iii.7. Both Bridlington and Dale log book returns indicate a strong seasonal C.P.U.E. with variations between 0.87 and 26.99 and 5.995 and 25.624 kg per 100 pots respectively. Bridlington catches appear to peak in July and August, with Dale C.P.U.E. peaking July to September (1988) and May to October (1989). The Selsey fishery shows a very different pattern, with much less seasonality apparent in the catches. Selsey C.P.U.E. can be seen to be highest in July and August, but is considerably lower than C.P.U.E. for Bridlington and Dale (2.09 to 9.42 kg per 100 pots).

Monthly sample C.P.U.E. for Bridlington (with and without soak time taken into consideration) (Appendix Table A2iii.8) show a peak catch rate (weight) in July 1989. A similar pattern is reflected by C.P.U.E. expressed as numbers of lobsters caught per 100 pots (Appendix Table A2iii.11). Dale C.P.U.E., calculated without soak time, increases to August (Appendix Table A2iii.9); however, C.P.U.E. calculated with soak time can be seen to be fairly steady. This is most probably a result of an increase in catch during the summer accompanying a number of south-westerly winds which prevented daily fishing. Dale C.P.U.E. of the number of lobsters (Appendix Table A2iii.12) is lower than might be expected from the weight of animals caught as a result of the larger average size, and therefore weight, of lobsters. July had the highest C.P.U.E. (weight and numbers) at Selsey in both 1989 and 1990 (as would be expected from examination of log-book returns)(Appendix Tables A2iii.10 and A2iii.13). A very high percentage of the catch was undersized in July. Soak times vary at both Bridlington and Dale, depending on weather conditions, but Selsey pots are nearly always hauled daily. The results of ANCOVA comparing log book C.P.U.E. and sample trip C.P.U.E. (kg per 100 pots hauled) at each site, and between the three sites, are given in

CPUE for lobsters landed at Bridlington, 1987 to 1989

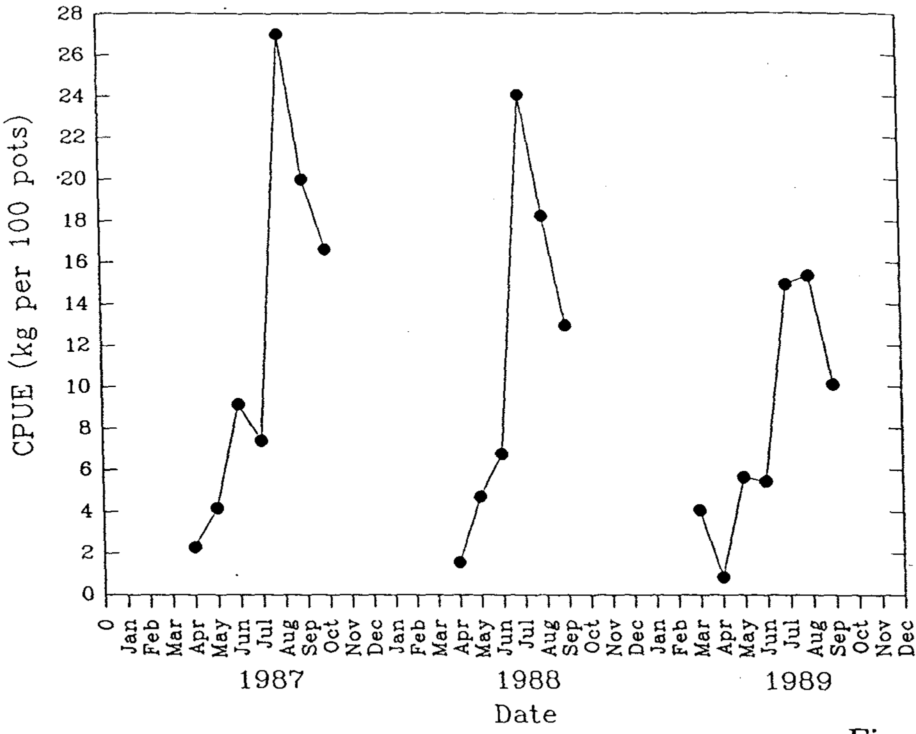


Fig.2.75

CPUE for lobsters landed at Dale, 1987 to 1989

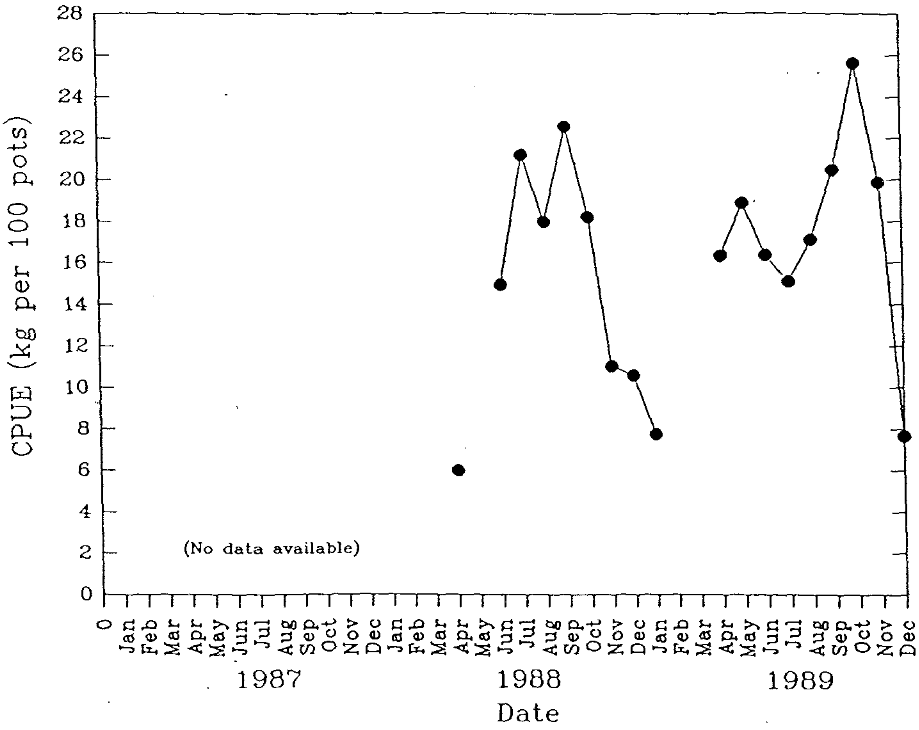


Fig.2.76

CPUE for lobsters landed at Selsey, 1987 to 1989

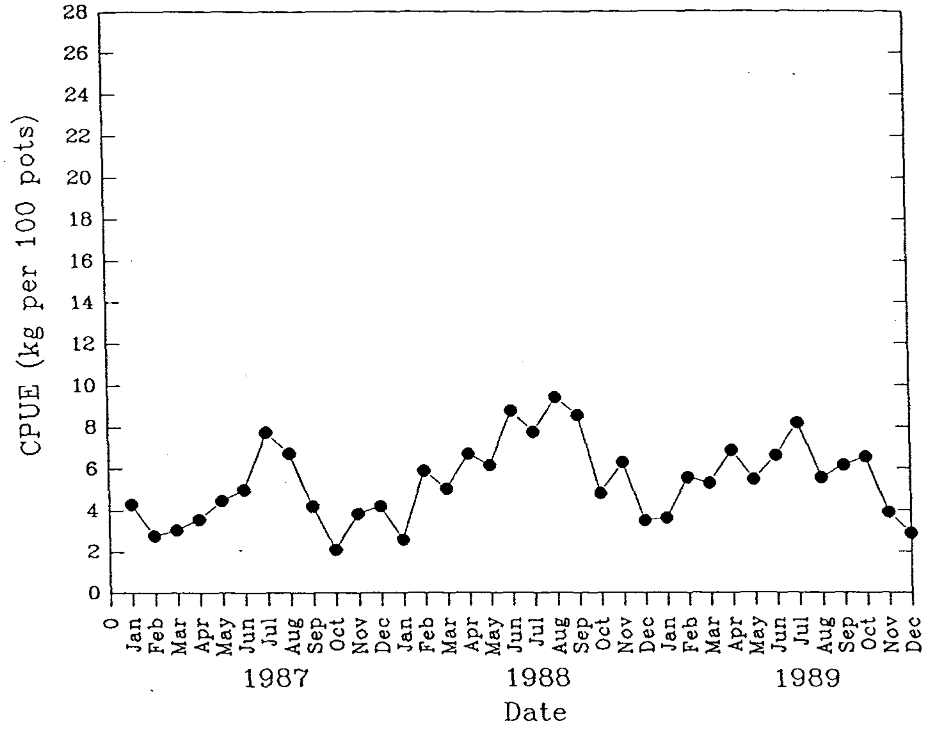


Fig.2.77

Monthly sex ratios for Bridlington, 1989

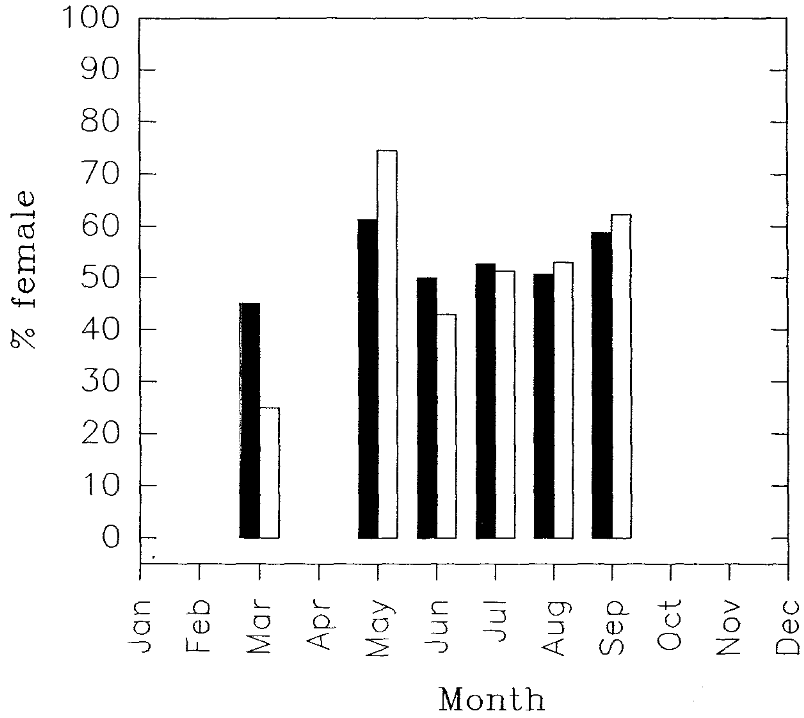


Fig.2.78

Monthly sex ratios for Bridlington, 1990

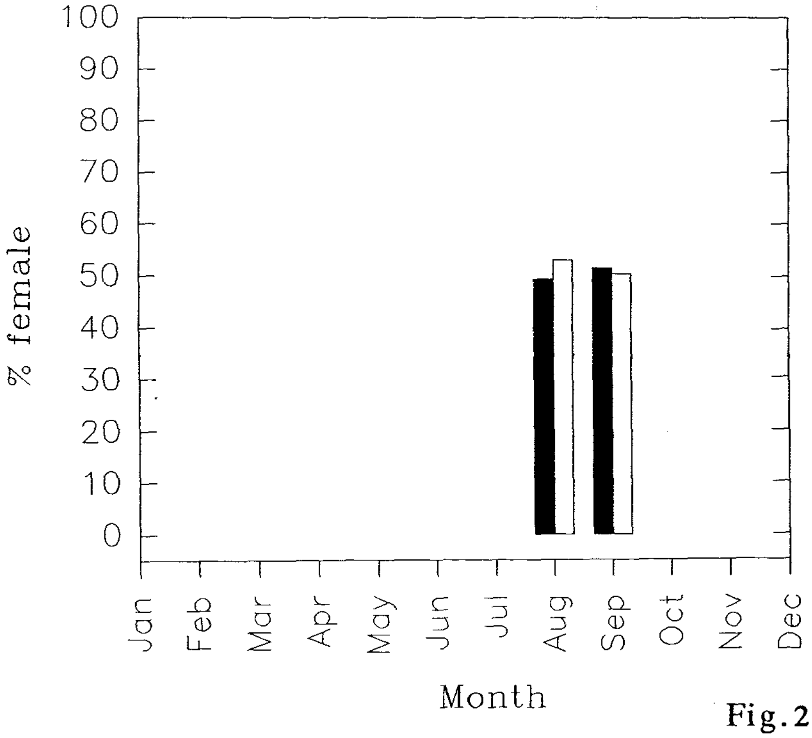


Fig.2.79

■ Total catch

□ Catch >85 mm CL

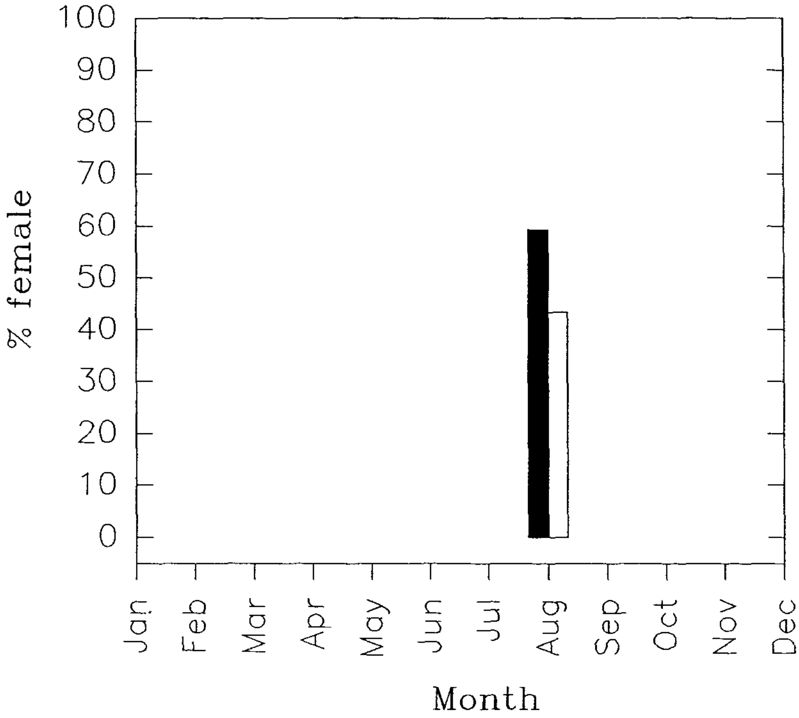

Monthly sex ratios for Bridlington, 1991

Fig.2.80

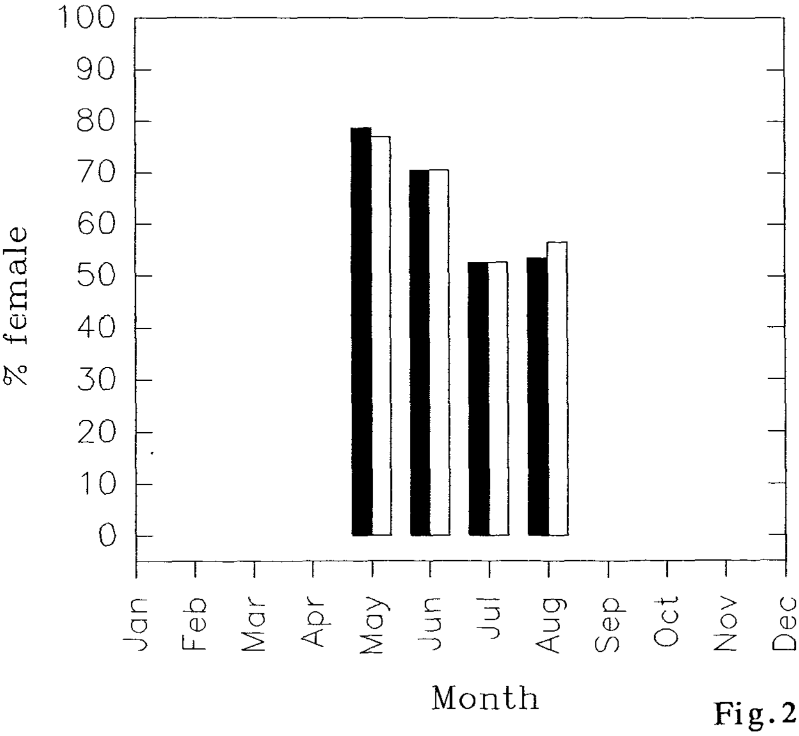

Monthly sex ratios for Dale, 1989

Fig.2.81

■ Total catch

□ Catch >85 mm CL

Monthly sex ratios for Selsey, 1989

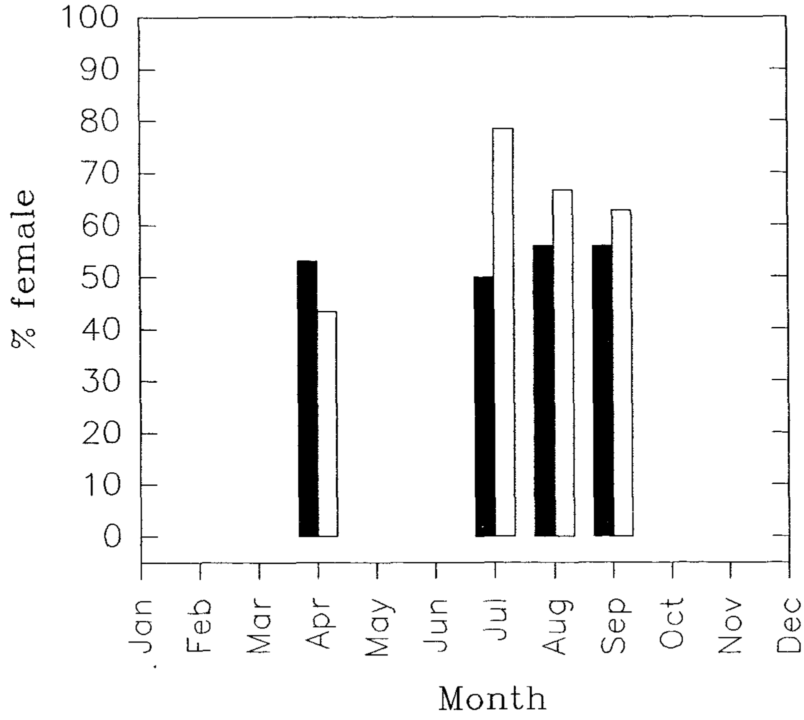


Fig.2.82

Monthly sex ratios for Selsey, 1990

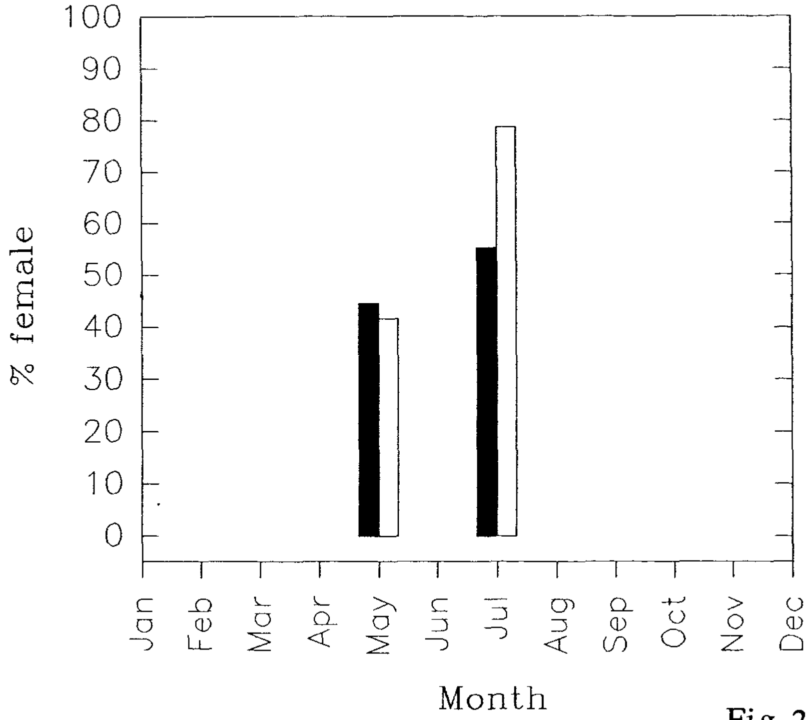


Fig.2.83

■ Total catch

□ Catch >85 mm CL

Appendix Table A2iii.45. These results do not indicate any significant difference between the two data types, but year to year variation in C.P.U.E. and a highly significant difference between sample sites. Appendix Table A2iii.46 compares sample trip C.P.U.E by weight and numbers between sites, months and years. The results indicate variation between months and years, but not between sites. Appendix Table A2iii.47 displays the results of ANCOVA shows C.P.U.E. by number covarying with C.P.U.E. by weight and comparisons between sites, months and years. Table A2iii.47 indicates more variation between the number of animals caught within all three sites than the between the weight of lobsters caught within all three sites. This is most probably caused by the variation in lobster average size (and therefore weight) between Bridlington, Dale and Selsey. The lack of strong significant differences in sample trip C.P.U.E. between sites, may be because of the lack of winter sample trips, when the greatest differences can be seen between the three sites using log-book C.P.U.E.

Sex ratios

The results of sample trip sex ratio calculations for both undersized (< 85 mm CL) and sized lobsters are presented in Table A2iii.18 to A2iii.20. Bridlington sex ratios for undersized animals show day to day variation (e.g. 23/05/1989, 45.2% and 24/05/1989, 64.52%), although the percentage female of undersized lobsters shown monthly in Figs 2.78 to 2.80, seems to decrease between May and June and increase towards October. The pattern of sex ratio for sized animals is more distinct than that for undersized individuals at Bridlington. Only 25% of lobsters sampled were female in March 1989; this percentage rapidly increased in May, decreased to below 50% in June and increased again to >50% and onto 60% in July 1989 and September 1989 respectively. The four 1991 June sampling trips also reflect this lack of sized females at that time of year (between 34 and 50% female).

All the lobsters below 85 mm CL caught at Dale were found to be female. Sized animals were also mainly female (52.7% to 78.6%), with the lowest proportion of females in July and August 1989 (Table A2iii.19, Fig. 2.81).

The Selsey sex ratios of undersized individuals (Table A2iii.20, Figs. 2.82 and 2.83) show either an approximate 1:1 sex ratio, fewer males in April 1989 or fewer females in May 1990, and July 1989 and 1990. Sized animals showed greater variability in the proportion of females (41.7% to 78.6% sized compared with 41% to 56% undersized). The highest proportions of females were observed in the catches of July and August 1989 and 1990; the lowest in April 1989 and May 1990.

Percentage berried

Table A2iii.14 presents the percentage of females found to be berried during each sample trip made in this study. The stages of eggs present on the captured females are shown in Chapter 6.

In Bridlington 1989, berried females may be assumed to be present all year round, although the percentage berried declined in July and August. No berried females were present in the August 1990 and June 1991 samples. The highest percentage of females caught berried on any one sample trip was 37.3%.

All four Dale 1989 samples showed moderate proportions of females to be berried (between 18.75 and 36.4%).

The Selsey samples had very few females carrying eggs in July (0% and 0.5% in July 1989 and 1990 respectively). The highest proportion of berried females was seen in September 1989, the beginning of the incubation period, with relatively few animals berried in May 1990 (8.7%).

The monthly percentage berried for both the current study and historical data collected for the three areas between 1972 and 1974 are shown in Appendix Tables A2iii.15 to A2iii.17 and Figures 2.84 to 2.86. The monthly percentage berried at Bridlington between 1972 and 1974 reflect similar proportions of berried females being caught, for each of the sample months, as for the 1989 to 1991 samples. In 1972, 1973 and 1974 the main egg incubation period appears to end in July, (with up to 22.1% of females berried) and begin again in October. The monthly percentages of females berried in Pembrokeshire, 1972 and 1973, imply more seasonality in the incubation period than shown in the 1989 samples. 44% of females were berried in May 1973, declining to only 3.6% in July 1973, and increasing to 13.1% in September 1973.

Over 40% of the females caught from Selsey in April 1972 and 1973 were berried. The 1972 and 1973 Selsey samples infer an egg incubation period from

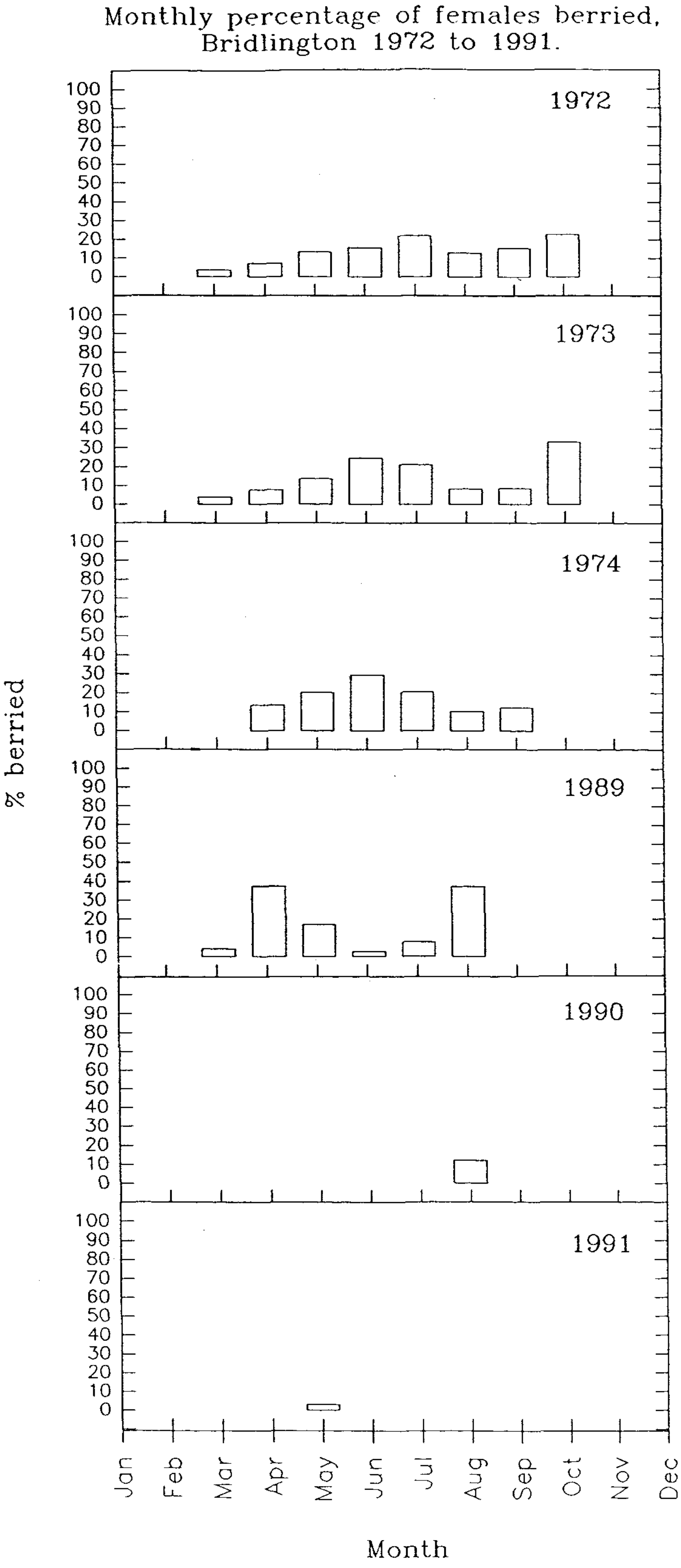

Monthly percentage of females berried,
Bridlington 1972 to 1991.
% berried
100
90
80
70
60
50
40
30
20
10
0
1972
1973
1974
1989
1990
1991
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Month

Fig.2.84

Monthly percentage of females berried,
Dale, 1972 to 1989

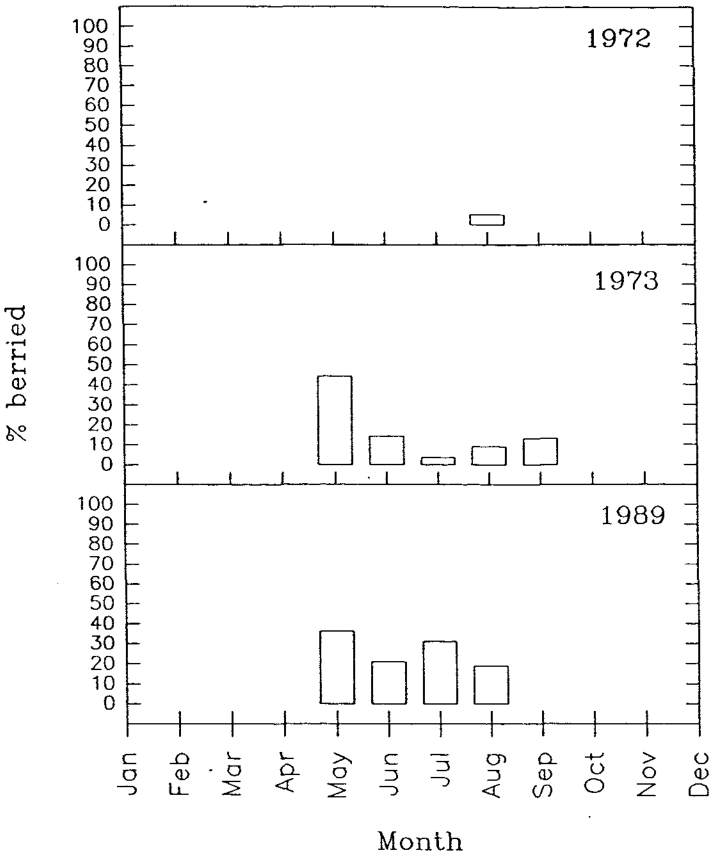


Fig.2.85

Monthly percentage of females berried,
Selsey 1972 to 1990

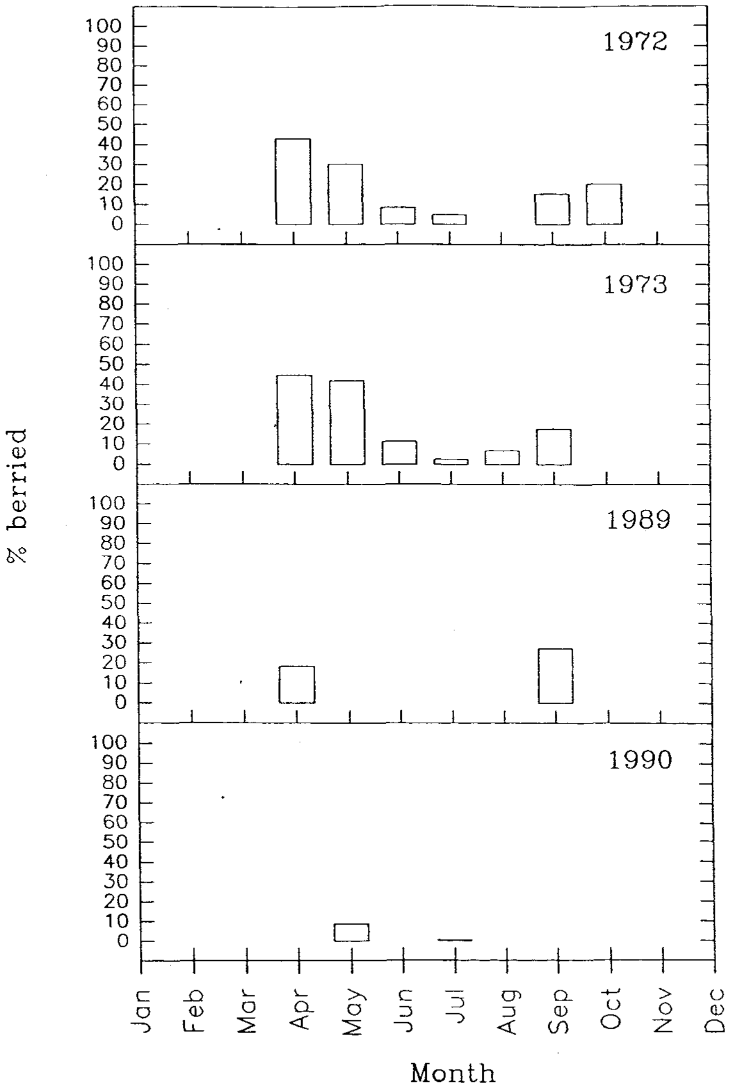


Fig.2.86

September to May/ June, similar to that implied from 1989 and 1990 data.

Percentage soft

The proportion of soft lobsters present in the catches was originally assessed as the number of individuals of each of the moult stages A to C_3 (Aiken, 1980). Only a limited number of non- intermoult animals were sampled, and the results of the field trips have, therefore, been presented as percentage soft (i.e. percentage of lobsters between moult stages A and C_3) for males and females on each sampling date.

No Bridlington females were caught soft in the 1989 March, May nor July samples (Appendix Table A2iii.21). 11.6% of females were soft in June 1989. The timing of male moulting can be seen to be more variable than that apparent for females, with two main moulting periods at the end of March 1989 and the end of June (coinciding with female moult). Surprisingly, no soft females nor males were captured in Dale (May to August 1989). The absence of moulting females from the 1989 and 1990 Selsey samples may be caused be the lack of June samples. A small proportion of males (less than 4%) were found to be soft in April 1989 and August/September 1990, suggesting two male moulting periods between April and October (although not necessarily that individuals will moult twice during this time

Growth rate estimates suggest smaller increments at moult for females than males at all three locations (Appendix Table A2i.5). Yorkshire and Selsey growth increments are approximately equal (slightly lower at Yorkshire for females)(11.3 and 9.15 mm CL, 11.25 and 9.65 mm CL at Yorkshire and Selsey for males and females respectively); however, West Wales male and female lobsters have smaller moult increments (10.5 mm and 8 mm respectively).

Cement gland Development

The results of the attempt to assess cement gland development, for use in size at maturity and proportion of females berried estimates, are given and discussed in Chapters 3 and 4.

2.4 Discussion

The three study sites differ quite markedly, by the nature of their fisheries, temperature regimes and population biology. Bridlington and Selsey are both long term, heavily exploited inshore fishery areas (depths between 10 to 20 m) whilst the Dale fishery is a relatively recently exploited offshore stock (depths between 20 and 40 m). The landing figures for Yorkshire, show a rapid increase from 1985 to 1990 (possibly as a result of an increase in offshore fishing by both potting and trawling vessels with the decline of inshore stocks), compared to a more steady increase in landing figures for the Selsey and Milford Haven fisheries. All landings fluctuate markedly between years, most probably as a result of weather restrictions on fishing activities, or temperature effects on lobster availability/catchability (Bennett, 1974; Dow *et al*, 1975; Dow, 1978; Bennett and Brown, 1979; Cooper and Uzmann, 1980; Fogarty, 1988; Krouse, 1989; Campbell *et al*, 1991).

Temperature regimes also differ between the three study areas with Selsey and Bridlington mean monthly sea temperatures, between 1982 and 1991, showing similar variation between high and low seasonal temperatures (with Selsey temperatures between 2° and 3° C higher than those for Bridlington), and Dale exhibiting a much reduced seasonal temperature fluctuation (less than 10° compared to 12.5° and 13.5° C for Bridlington and Selsey respectively).

Campbell (1989) suggested that most inshore *H. americanus* landings are composed of new recruits to the fishery. This is possibly also the case at Selsey (with its very truncated size distribution) so that annual landings for such fisheries are reasonable estimates of recruitment into the whole fishery. Bannister (1986) suggested that size composition is related to fishing mortality (F) in *H. gammarus*, although changes in F, and therefore size composition does not necessarily reflect changes in fishing effort (Addison, 1986). Size distributions showing differences between the 1970's and 1989 to 1991 sampling periods at Selsey/south coast and Bridlington/Yorkshire, both by apparent reduction in CL of the modal size classes and by differences supported by Kolmogorov-Smirnov tests, may suggest an increase in fishing pressure over this time. This supposition may be reinforced by management policy changes which have seen an increase in MLS (from 80 to 85 mm CL) over this period, so that decreases in the average sizes and size distributions of animals is probably most attributable to changes in gear type or effort and fishing pressure increases (Robinson, 1980; Addison and Lovewell, 1991). Significant differences between male and female size distributions are most probably caused by sexual variations in growth rates (moult frequency and moult increment, Estrella and McKiernan, 1989) and catchability (as a result of reproductive behavioural changes (Branford, 1976; Bennett and Brown, 1979), and fishing mortality rates inferred by the differences in these two factors. Differences in growth rates between locations may only be suggested by moult increment data. Its use in assessing potential causes in variation in size distributions (and indeed size at maturity, Chapters 4 and 5), is obviously limited without moult frequency information. Temperature has been shown to affect growth rates of *H. americanus*, as has population density, although only in laboratory conditions (Aiken and Waddy, 1976; Nelson *et al*, 1980). Potential changes in temperature regimes since 1970's are unlikely to account for such differences in growth rates, and therefore, size distributions (no obvious trend in temperature changes can be seen from year to year). Although gear selectivity and changes in locations between 1970's data collection and 1989 to 1991 data collection are both potential causes of apparent temporal variations in size distributions, changes in landings figures, and general trends of increase in fishing effort over the last 25 years would imply increase in fishing mortality to be the most likely cause of changes in size composition over this time.

Differences in growth rates of deep water adult rock lobsters, with reduced temperature variability, have been found to vary with locality, and may be linked to environmental differences such as food availability (Pollock, 1973, working on *Jasus lalandii*). Moult frequency estimates are scarce for both *H. americanus* and *H. gammarus* and are obviously crucial in estimating growth rates. Mature animals are known to moult less frequently than immatures which may moult several times a year (Hepper, 1965). Mature females are also thought to moult less frequently than males, moulting once every two years (compared to the annual male moult) to tie in with their reproductive cycle (Hepper, 1965; Campbell, 1983). In addition to faster growth rates, male *H. americanus* reach a higher asymptotic size than females because of female energy allocation to egg production, as well as somatic growth (Campbell, 1983). Campbell (1983) also stated that knowledge of growth rates is crucial for understanding lobster population dynamics and therefore fisheries management. Geographical variation in growth rates have been observed in *H. americanus* and may relate to differences in moult increments or moult frequencies (Conan, 1978). Potential causes of variation in growth rates between the three sites may be caused by factors such as temperature and juvenile density affecting food availability (e.g. in *Panulirus longipes cygnus*, Chittleborough, 1974, 1976). Indirect potential causes of geographical differences in size frequency distributions therefore include habitat limitation effects (Howard, 1980; Bannister and Lovewell, 1985), variations in temperature regimes and other environmental factors such as food availability and population density.

The log-length/log-weight relationship found for *H. gammarus* in this study, has previously been investigated for *H. americanus* (Squires, Ennis and Tucker, 1974; Estrella and Mckiernan, 1989) and *H. gammarus* (Simpson, 1961; Bannister *et al* 1983). In this study, differences have been shown to exist between log-length/log-weight relationships both spatially, temporally and between sexes and according to egg bearing state. This contrasts to the work of Thomas (1973) (using sublegal sized animals only) and Briggs and Muschake (1979) for *H. americanus* who found no significant difference between log-length/ log-weight regressions for males and females. Differences between sampling years found in this study may be caused by sampling at different times of the year, as Ennis (1971) and Estrella and Mckiernan (1989) found variations in *H. americanus* length/weight relationships between seasons. Spatial variation in *H. gammarus* log-length/log-weight relationships has previously been reported by Simpson (1961) and Bannister *et al* (1983). Calculations made for the expected weight of an 85 mm CL lobster may vary because of differences in lobster size at sexual maturity. The Dale lobsters, shown in Chapter 4 of this study to have the longest size at onset of maturity, were found to weigh less than those of both Bridlington and Selsey, although the relatively small sample size of lobsters from Dale may also have affected this result.

Sexual, spatial and temporal variations in log-length/log-weight relationships may have implications for stock abundance estimates if lobster weight is used as input. Conversions of the number of lobsters caught into weight for C.P.U.E. estimates should therefore use the most appropriate length/weight equation available.

C.P.U.E. differs considerably between the three sites; seasonality is apparent in the fisheries of both Bridlington and Dale, but not strongly at Selsey. This is probably a result of restrictive winter weather conditions at Dale and Bridlington. These two fisheries also target *Cancer pagurus* between October and May when lobster availability is reduced. The Selsey fishery is less vulnerable to long periods of bad weather and the catch is therefore more steady all year round. At Selsey, lobsters tend to be the main targeted species throughout both summer and winter months because of high winter lobster prices and poor crab catches (M. Rudwick, pers. comm.). This may effect the magnitude of C.P.U.E. at Selsey, which is less than at either Bridlington or Dale, and would suggest agreement with Brown and Bennett's (1979) comments that crab catches in the eastern end of the English Channel are heavily affected by the strongly supported lobster fishery. Warmer winter temperatures off Selsey, compared with those of Bridlington, may also reduce the impact of colder temperatures on lobster feeding and therefore availability/catchability (Cooper and Uzmann, 1980). Comparisons of C.P.U.E. estimates between fisheries are complicated by differing pot soak times as the relationship between pot soak time and change in the size of catch is still poorly understood (Thomas, 1973; Bennett and Lovewell, 1977). The use of C.P.U.E. as a relative index of abundance of lobsters at the three study sites is probably not valid because of the use of different boat and gear types, as well as soak times, making it difficult to confirm the validity of the C.P.U.E estimates (Bennett and Brown, 1979) especially for potential use in stock production models or for estimates of F for yield per recruit models. However, if C.P.U.E. may be assumed to give an approximate indication of exploitation rate, Dale can be seen as the least exploited fishery, with annual C.P.U.E. at Bridlington and Selsey quite similar, reflecting their history as long-established fisheries now showing signs of sustained, heavy exploitation. The constancy of Selsey effort for each of the sampling trips, with just one day soak, infer that the changes in C.P.U.E. estimates for this site, at least, may provide indications of changes in lobster density or vulnerability to capture (Morgan, 1979).

In areas such as Selsey, where C.P.U.E. is quite low, lobsters are relatively small and fishing mortality is high, it may be assumed that the fishing intensity is high (Skud and Perkins, 1969; Cooper and Uzmann, 1980), although the inverse relationship between catch and fishing effort in trap fisheries is actually quite difficult to prove (Harding *et al*, 1983) because of the lack of a satisfactory index of fishing effort (Munro, 1974; Bennett and Brown, 1979; Skud, 1979). Bennett (1974) suggested that the relatively high spring and autumn C.P.U.E. that he found for *H. gammarus* was a result of new recruitment to the fishery at these times: this may also be true for the results of this study, although June and July (males) and August (especially females) appear to give the greatest catches for this study (succeeding their respective moult periods).

The high proportion of undersized animals at Selsey (and to some extent Bridlington) may give cause for concern regarding fisheries management policy. Legally undersized animals, thrown back after capture, may be especially vulnerable to claw loss, predation and increased mortality. This may well lead to an increase in the potential for recruitment failure, and economic loss to the fishery.

The variability in sampling dates at each of the three sites does not facilitate an accurate picture of moulting periods for either male or female lobsters caught in this study. The results of both Selsey and Bridlington calculations of the percentages of animals soft, imply two potential male moults at the beginning and middle to end of the fishing seasons (March/April and June or August/September). Female moulting was restricted to June during the sampling periods, theoretically closely preceding the main mating period. All percentages of animals moulting were relatively low (less than 16%, and most commonly less than 5%), probably reflecting decreases in lobster activity and therefore catchability during ecdysis and pre-ecdysis (Stewart and Squires, 1968).

The period of egg incubation may be seen to start in September and finish in May or June for both Bridlington and Selsey between 1989 and 1991. The 1972 to 1974 samples from Bridlington suggest a later start and finish to the period of berry (mainly October to July), although no change appears to have occurred for the Selsey area. The apparent lack of seasonality in egg incubation period in the Dale 1989 samples, contrasts with the 1973 samples, with an obvious increase in the percentage berried in July and August from the 1970's data to that of 1989. This may be because the 1972 and 1973 Pembrokeshire samples being taken from an inshore fishery area as the offshore Dale fishery used for this study was not exploited at that time. Seasonality of moult and therefore egg bearing cycles have been noted before, in *H. americanus* (Conan, 1985).

Variations in sex ratios of sized animals especially, may be related to moult and reproductive cycles, both of which are known to affect lobster catchability (Branford, 1977). The inferred male moult in Bridlington, March 1989 (10.7%), is not apparent in sex ratios, as only 25% of the sized animals are female; this may be complicated by a lower catchability by berried females, caused by their reduced feeding (Branford, 1977). However, the suggested August/September moult, is reflected by an increase in the number of females found in the catch at that time. These results suggest that being berried has a greater effect on catchability than the lobsters being soft, although more data would be required to confirm this. The female moult period in June 1989 is most probably the cause in the reduction in the percentage of females caught at this time. If moult period does affect sex ratio, it may be that males at Dale mainly moult in May and June, although other factors such as migration may effect the sex ratios of offshore stocks (Cooper and Uzmann, 1980; Estrella and McKiernan, 1989). The relative stability of the proportion of Dale females berried does not allow for any conclusions to be drawn on the effect of catchability caused by egg incubation in this offshore stock. The Selsey April 1989 (and possibly May 1990) sex ratio appears to show a similar effect of egg incubation and male moult on sex ratio as the Bridlington March 1989 sample. Although soft males were present in the sample, more males were caught than females, probably as a result of a reduction in catchability of berried females. On those sampling occasions when few females are known to be berried or are just becoming berried, and males are in moult, the sex ratio tends towards females (August and September 1989). The very high percentage of females captured in July 1989 and 1990 may follow female moult in June; the truncated size distribution of animals off of Selsey may result in males being captured quickly after their moult to >85 mm CL, and after the more delineated female June moult, an influx of females into the fishery may appear quickly, thus biasing sex ratios, and being caught and landed soon after. Previous workers such as Skud and Perkins (1969) have suggested that there is an increase in female to male sex ratio above 80 mm CL, but below 130 mm CL (*H. americanus*) as a result of the influence of the reduced moult frequency of larger females.

Greater variability in undersized sex ratios may be caused by a lack of reproductive cycle in small females, and by more frequent and less defined moult cycles in both sexes. The results of this study contrast with those of Thomas (1954) who did not find any regular variation in either the sex ratio, nor the size composition of south-east Scottish lobsters, and suggest that those of Scarratt (1968), Cooper, (1970) and Stewart (1972), who suggested equal proportions of male and female *Homarus* below 80 mm CL, are correct. Unfortunately, *in situ* sex ratio estimates are difficult to obtain, and the effects of moult and reproduction cycles complicate the assessment of lobster sex ratios. Potential differences in sex ratio at any given size of individual may effect mortality estimates, as both males and females of any given size may be effected differently by fishing pressure (Smith, 1944; Skud, 1976; Cooper and Uzmann, 1980).

CHAPTER 3 INTRODUCTION TO REPRODUCTIVE BIOLOGY

Although *Homarus spp.* have been of considerable commercial importance for over a century, and aspects of their reproductive biology were first described in the late 19th century (Herrick, 1894, 1895; Fullarton, 1895; Garman, 1895), it is only in the last twenty years that the science of the reproduction of *Homarus spp.* has emerged from the descriptive phase.

3.1. Female Reproduction

3.1.1. The Ovary and Ovarian Development

Ovary morphology

The ovaries of both *H. gammarus* and *H. americanus* consist of paired cylindrical rods united by a transverse bridge located ventral to the heart. A short oviduct descends from each lobe of the ovary to the genital aperture on the coxa of the third pereiopods. In the cases of mature ovaries, each lobe may extend from the anterior end of the stomach to the fifth abdominal segment (Aiken and Waddy, 1980; Phillips *et al*, 1980). The ovary wall is thin, consisting of an outer epithelium, central connective tissues, blood vessels and sinuses. Smaller oocytes are present in the centre of the ovary, with the largest oocytes towards the ovary periphery (Kessel, 1978). Within the ovaries of crustacea, follicular cells are the only non-germinative accessory somatic cells (Adiyodi and Subramoniam, 1983). Oocytes are each surrounded by a follicle cell, until maturity at which point the envelope disintegrates, leaving the ripe ova free in the ovary (Kessel, 1968; Byard, 1975).

Ovary development

Oogenesis and vitellogenesis have been described for *H. americanus* by Aiken and Waddy (1980), Dehn, Aiken and Waddy (1983), Sastry (1983) and Krol *et al* (1992). Vitellogenesis consists of two phases; primary and secondary. Primary vitellogenesis may occur over many months, followed by secondary vitellogenisis leading to oviposition (Aiken and Waddy, 1980).

As with those of other decapods, the ovaries of *Homarus americanus*, *H.gammarus* and *Nephrops norvegicus* go through changes in colour and size during their development to maturity. In *Homarus spp.* ovarian maturation becomes macroscopically evident when ovoverdin carotenoprotein appears in the yolk mass, thus giving the ovarian tissue a green colour (Aiken and Waddy, 1980). Once maturity has been reached, such changes in colour and size also occur during succeeding reproductive cycles. Six arbitrary developmental stages (including the spent or reabsorbing state), have been assigned to the ovary of *Homarus americanus* according to oocyte size, and ovary size and colour, by Aiken and Waddy (1980) (Appendix table A3i.1) (although it should be noted that ovary development is an ongoing, continuous process).

Aiken and Waddy's work on *H. americanus* (1980), and that of Farmer (1974) on *Nephrops norvegicus*, suggest that the immature ovaries of clawed lobsters are a creamy white colour. Pre-vitellogenic development in each species results in the ovary becoming yellow, beige or gold in colour. In the case of *H. americanus*, the white, yellow or beige coloration shifts to light green during primary vitellogenesis and on towards a dark green colour (caused by ovoverdin) at maturity (Aiken and Waddy, 1980). Ovoverdin was first isolated by Stern and Salomen (1937) and Kuhn and Sörensen (1938) and has since been described as a lipoprotein rich in phospholipids, with a carbohydrate component (Cheeseman, Lee and Zagalsky, 1967). The onset of vitellogenesis in *Nephrops* results in the ovary turning pale blue and further development increases the blue pigmentation until a distinctive royal blue is reached indicating final maturity (Berry, 1969; Orsi Relini and Relini, 1985). Primary vitellogenesis, (with slow oocyte growth) is apparent by colour changes in the brachyuran crab *Paratelphusa hydrodromous* (Adiyodi and Subramonian, 1983); the initial ovary white coloration is present during protein synthesis, followed by an increase in coloration caused by an increase in pigmented lipoprotein (caroteinoproteins) content during the latter stages of primary vitellogenesis. Secondary vitellogenesis then occurs with rapid ovarian growth preceding oviposition.

3.1.2. The ovarian cycle

After sexual maturity, the growth of oocytes to maturation and ovulation results in growth and regression of the ovary, i.e. the ovarian cycle. In *H.*

americanus and *H. gammarus* the ovarian cycle may take two years to complete (Waddy and Aiken, 1979; Aiken and Waddy, 1980), although the population breeds annually. The length of time of the reproductive cycle is influenced by size; most probably a result of essential interactions with the moult cycle (Adiyodi and Adiyodi, 1970), and resource allocation between somatic and reproductive growth. Aiken and Waddy (1980) determined the time span of the ovarian cycle of the American lobster by egg extrusion, and ovary maturity and development (examined by macro-morphological and microscopical techniques).

At the prepubertal moult, females will mate (whilst the ovary is undergoing primary vitellogenesis); secondary vitellogenesis occurs in spring followed by oviposition in autumn. These females will then be "berried" (ovigerous) during the winter, hatch their eggs in summer, and then moult and mate (whist the ovary undergoes primary vitellogenesis leading to a repeat of the cycle) (Aiken and Waddy, 1980).

A number of internal indices have been developed to describe female reproductive condition (Appendix Table A3ii.1). Pillay and Nair (1971) determined temporal patterns of the ovarian cycles by the gonad index method for three tropical decapods; *Uca annulipes, Portunus pelagicus* and *Metapenaeus affinis.* Gonad indices were described for use in reproductive biology by Giese (1966) and use the ratio of gonad tissue weight to total body weight to assess the development of reproductive tissues. In conjunction with this, main storage organ indices (assessed by a similar method) may be used as indices of the condition of somatic tissues, thus creating a gonado-somatic index (Relative ovary weight, "ROW" = [Ovary weight (g)/Total wet weight (g)] x100). In decapod crustacea, this index shows a significant increase as maturation approaches, with an obvious drop, post-spawning (Harrison, 1990): therefore this method is most useful when used to assess seasonal or temporal patterns of reproductive organ development (e.g. Pillay and Nair, 1971). Aiken and Waddy (1980) developed the "ovary factor" (Ovf) as an indicator of ovarian maturation relative to body size (Ovf = [Ovary weight (mg)/CL^3 (mm)] x10). Kamiguichi (1971) suggested a proportional relationship between ovary weight and the cube of body length for the shrimp *Palaemon*. Aiken and Waddy (1980) developed this maturity indicator for use in *Homarus spp.* and found it to be effective for ovary maturity stage determination when used in conjunction with gross morphological characteristics (i.e. oocyte size and colour).

The development of "cement glands" on the pleopod endopodites (and additionally pleopod exopodites, protopodites and the sternal bars of the abdomen) of *Homarus spp.* has been shown to exhibit cyclic fluctuations with ovarian development and oviposition (Lloyd and Young, 1940; Aiken and Waddy, 1982). Although the exact role of these glands is uncertain, clear correlation has been documented between their engorgement and vitellogenesis in *H. americanus* (Aiken and Waddy, 1982). Yonge (1937) observed that the cement glands become vacuolated during oviposition after the secretion of an opaque white substance which is thought to be involved in the egg attachment process. The development of cement glands in non-ovigerous females has been classified into five stages (0 to 4) (Aiken and Waddy, 1982)(Appendix A2ii.2).

Coordination of the reproductive cycle

Steele (1980) stated that, under suitable environmental conditions, specific coordinating mechanisms are required to adjust the chronology of ovary maturation and ecdysis. The interaction between moult and reproductive cycles is suggested to be antagonistic in decapod crustacea (Bliss, 1966; Adiyodi and Adiyodi, 1970). Aiken and Waddy (1976) showed this to be the case for *H. americanus*, and it may therefore be assumed for *H. gammarus*. Normal environmental conditions (especially temperature) are thought to synchronize the complex hormonal coordination of the two cycles (Sastry 1983). Six hormones are thought to function in the coordination of decapod reproduction, including two that are primarily concerned with the moult cycle. Prior to initial gonad development, cyclic fluctuations in Gonad Inhibiting Hormone (GIH) and Moult Inhibiting Hormone (MIH) are synchronized. This synchrony shifts to antagony with gonad maturation, to allow the demands for organic reserves for moult to be temporally separated from those for ovarian development (Adiyodi and Adiyodi, 1970). GIH was found to prevent precocious ovary maturation in *Palaemon serratus* (Panouse, 1943), and its cyclic occurrence in decapods is thought to regulate primary vitellogenesis by preventing the ovary from taking up FSP (Female Specific Hormone). GSH (Gonad Stimulating Hormone) promotes vitellogenesis and suppresses entry in to the premoult ecdysal condition (Adiyodi and Adiyodi, 1970; Sastry, 1983).

The hormonal coordination of moult and reproductive cycles is crucial for the successful completion of egg incubation in female *Homarus spp.*. Most female *Homarus spp.* mate shortly after their moult (soft shell condition), with a male in intermoult or premoult condition, although mating can occur at any moult stage (Aiken and Waddy, 1980; 1991). Inter-moult mating has been observed in laboratory held *H.americanus* (Dunham and Skinner-Jacobs, 1978; Aiken and Waddy, 1990), but the frequency of its occurrence is unknown in nature. Aiken and Waddy (1990) suggested that female lobster receptivity to mating is most likely to be determined by the presence (or absence) of stored sperm, rather than moult stage, and that males are able to distinguish between mature and immature females, and whether or not they have been inseminated. Phillips *et al* (1980) suggested that the cyclic nature of the reproductive cycle, (and its duration) is imposed on the female lobster to enable copulation, and successful completion of the period in-berry without moult. Premoult development is not inhibited whilst *H. americanus* is in berry, and ecdysis frequently occurs directly after the larvae are hatched (Aiken, 1980). Under normal environmental conditions, the moult and reproductive cycles are phased to allow the development of the eggs first (Aiken and Waddy, 1976). In laboratory studies female lobsters have been shown to moult whilst still in berry under abnormally high temperature schemes, and therefore lose their eggs (Ennis, 1975). The timing of mating and the subsequent oviposition in female *H. americanus* is therefore strongly linked to ecdysis. In *H. gammarus* populations in England and Wales adult female ecdysis usually takes place between May and July, and oviposition during August to October; eggs are then incubated over winter until hatching in spring or early summer (Hepper and Gough, 1978).

Geographical variation in the precise timing and seasonal occurrence of moult and reproductive cycle events, may occur between populations of *H. gammarus* and *H. americanus*. The timing of female moult, mating, and oviposition is thought to be controlled mainly by temperature, in addition to other factors. Laboratory studies led Aiken and Waddy (1986; 1990) to suggest that temperature is the major factor in the control of oocyte maturation. This would therefore suggest a potential variation in spawning times between areas with differing temperature regimes. Templeman (1940) first noticed a marked difference in the spawning times of *H. americanus* from various localities with varying average sea temperatures. Variations in spawning frequencies may also be caused by temperature; Ennis (1971) discovered that *H. americanus* from relatively cold Newfoundland waters might only spawn every fourth or fifth year.

Sastry (1983) reviewed other possible environmental influences on gametogenesis and other aspects of the crustacean reproductive cycle. These factors include photoperiod, food availability and social conditions (including parasitism).

The effect of photoperiod on the reproductive cycle of *H. americanus* is still uncertain. Conclusions drawn from experiments on the effect that photoperiod and temperature have on spawning were debated by Aiken and Waddy (1985a; 1985b; 1986) and Nelson (Nelson *et al*, 1983; Nelson and Hedgecock, 1985; Nelson, 1986). Nelson *et al* (1983) concluded from their work, on the potential influence of photoperiod on the spawning and induction of vitellogenesis in *H. americanus*, that photoperiod was the most important environmental cue concerned (cf. Aiken and Waddy 1986). Waddy and Aiken (1992) suggested that females will be able to spawn in response to spring temperature increases (regardless of photoperiod) after a suitably long duration of winter temperature and photoperiod conditions. Photoperiod may control the reproductive cycle of *H. americanus* in situations without potential temperature variation for the environmental control (Aiken and Waddy, 1990).

The relationship between food availability, nutrient storage and gamete production has also been studied in decapod crustacea (Sastry 1983). Oocyte growth in *H. americanus* may be arrested by dietary deficiencies in lipid or protein which may result in oocyte resorption (Aiken and Waddy, 1980; 1986). Similarly, Beyers and Goosen (1987), working on the palinurid lobster *Jasus lalandii*, showed that food availability (and quality) in the environment was a potential limiting factor on oogenesis. Gamete production may not occur at all unless a minimal amount of nutrients are available to the gonads, either directly from the environment or alternatively from a nutrient store.

3.2. Male Reproduction

3.2.1. Male sexual organs

Morphology

The reproductive organs of male *Nephrops norvegicus, H. americanus* and *H. gammarus* (Figure 3.1) consist of a pair of white, tube like testes, two vas deferens and androgenic glands (Farmer, 1974; Aiken and Waddy, 1980). The testes may extend from the anterior end of the foregut to the posterior margin of the cephalothorax, and are joined together by a transverse bridge which is located ventral to the heart (Aiken and Waddy, 1980). The proximal portion of each vas deferens emerges from the testes as a short, slightly coiled duct which runs to a gonopore on the coxae of the fifth pereiopod (Aiken and Waddy, 1980). Herrick (1909) was the first worker to describe the vas deferens of *H. americanus*, and so noted its division into three distinct sections.

The proximal portion conducts sperm mass from the site of spermatogenesis in the testes, and then leads into an enlarged, coiled, semitransparent glandular

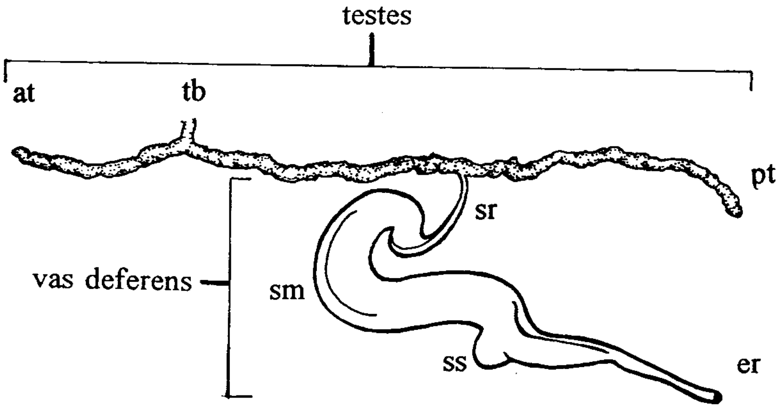


Figure 3.1 The testes and vas deferens of *H. gammarus.*

(at), anterior portion of testes; (tb), transverse bridge; (pt), posterior portion of testes; (ss), spermatophore sac of vas deferens; (sm) sphincter muscle; (sr), secretory region; (er), ejaculatory region.

section. This secretory region forms the spermatophores with the production of a jelly-like matrix; the spermatophores are then stored in the sphincter muscle and ejaculatory regions of the vas deferens until copulation (Farmer, 1974). Each spermatophore consists of a single convoluted strand of spermatozoa in a thick membrane, and is ejected to form a sperm-plug in the female, via the terminal ejaculatory duct of the vas deferens. The androgenic glands of *Homarus spp.* (which control both primary and secondary sexual characters in male crustacea) are attached to the outside of the distal region of the vas deferens (Charniaux-Cotton *et al*, 1966). The glands are sinuous and approximately 40 μm in diameter (Farmer, 1974).

3.2.2. Spermatogenesis

No seasonal pattern of spermatogenesis is thought to exist in *Homarus spp.* (Aiken and Waddy, 1980; 1986; 1991). Similarly, male *Nephrops norvegicus* have been shown to undergo spermatogenesis continuously after onset of maturity (Farmer, 1974). MacDiarmid (1989) investigated the occurrence of seasonality of spermatogenesis in *Jasus edwardsii* using spermatozoa count number in the lumen of the vas deferens. MacDiarmid's study, and similar work by Silberbauer (1971) on *Jasus lalandii* indicate potential cyclical fluctuations in spermatogenesis within male palinurid lobsters, as well as seasonal changes in the vas deferens diameter correlating to the mating period. An annual cycle of spermatogenesis has also been identified and described for the crayfish *Pontascus leptodactylus leptodactylus* (Amoto and Payen, 1978). Aiken and Waddy (1986) studied wild caught *H. americanus* and revealed a rapid growth in vas deferens size in spring, followed by regression in both mature and maturing males. However, males kept in laboratory conditions indicated a reduced rate of vas deferens growth throughout the winter, after a rapid growth increment in size during May and June (Aiken and Waddy, 1986). This change in vas deferens growth rate was consistent with somatic growth, therefore indicating the lack of a cyclic seasonal change in vas deferens size associated with mating (contrary to indications from field studies). Aiken and Waddy (1991) further stated that male lobsters are capable of mating throughout the year, also implying a lack of seasonality in male reproductive potential.

3.3. Resource allocation to reproduction

Gonad maturation and gamete production are energy-demanding processes, because of the increase in biosynthesis of necessary organic components. An organism must therefore allocate to the gonads a proportion of the energy that they have assimilated, even though there are competing demands by interrelated processes of maintenance and somatic growth (Sastry, 1983). Environmental factors including the quality and quantity of food, as well as physiological factors such as the efficiency of assimilation and metabolism, the energy requirements for somatic growth and the effect of the individual's age, all influence the amount of energy invested into reproductive processes resulting in gamete production.

In order to assess energy allocation between reproduction and somatic growth, both the calorific content and the biochemical constituents of the hepatopancreas and the reproductive tissues in both male and female decapod crustacea, may be assayed. The hepatopancreas (also known as the midgut or digestive gland), is used in such studies as it is generally considered to be the main storage organ in decapod crustaceans (Passano, 1960; Adiyodi, 1968; Heath and Barnes, 1970). Maximum hepatic reserves of organic substances occur during intermoult (C_4) (Adiyodi and Adiyodi, 1972). Adiyodi (1968) studied the storage and mobilization of both lipids and PAS-positive compounds in the hepatopancreas of the brachyuran *Paratelphusa hydrodromous* in relation to the moulting cycle, and observed large fluctuations in the concentrations of lipids. Other studies have assayed the biochemical constituents of hepatopancreas and reproductive tissues on a seasonal basis to investigate energy allocation throughout both moult and reproductive cycles (e.g. Comita *et al,* 1966; Heath and Barnes, 1970; Pillay and Nair, 1973). Total lipid assays are particularly useful in the study of seasonal changes in the major biochemical components of tissues and their relation to breeding cycles (Barnes and Blackstock, 1973).

Pillay and Nair (1973), determined the biochemical constitution of muscle tissue as well as the gonads and hepatopancreas in three tropical decapods; namely, *Uca lactea annulipes*, *Portunus pelagicus*, and *Metapenaeus affinis*. They determined seasonal lipid fluctuations in the females of all three species, relating to their respective reproductive cycles. Mature ovaries were discovered to contain more lipid than immature or spent ovaries. The hepatopancreas was shown to act as a storage organ for glycogen and lipids, before at least some of them are translocated to the ovaries for gamete production. In the males of the three species, very little seasonal fluctuation in the biochemical constituents of the testes was shown. In comparison with the ovaries which have a high lipid content, the testes were shown to have a relatively high protein content.Wallace *et al* (1967) showed that the principal protein component of the ovaries of six species of decapods is lipoprotein.

Heath and Barnes (1970) analysed seasonal changes in the biochemical composition of the temperate brachyuran *Carcinus maenas,* in relation to moult and reproductive cycles. Hepatopancreas from both male and female crabs and ovaries were used for determination of glycogen, total carbohydrate, neutral fats, protein and non-protein nitrogen, throughout the year. With regard to the hepatopancreas, no clear changes were observed in either size or composition, in relation to the reproductive cycle. It was therefore assumed that in *Carcinus*, the hepatopancreas does not act as storage for reproductive processes (Heath and Barnes, 1970). High glycogen levels in the spent ovaries also implied that some materials are not stored elsewhere within the crab, but instead are synthesized within the ovaries themselves. Lipid content of the ovaries was found to increase greatly in relation to ovary size, as a result of an increase in lipoprotein content of the ova.

3.4. Methods and data analysis

3.4.1. Initial ovary staging

Ovaries were dissected from female lobsters and then staged using their gross appearance (morphology, coloration and oocyte size). Six ovary stages were determined (1 to 6) (Table 3.1), with the "spent" ovaries of berried females described separately as parallel stages (stages 1s to 5s)(Table 3.2).

3.4.2. Histological examination of Reproductive Tissues

Ovaries were stored in buffered formalin or Bouins fixative (Appendix A3iii.1). Saunders (1949) assessed the suitability of various fixatives for the histology of lobster tissues and recommended Bouins fixative for use with most tissues including hepatopancreas and reproductive tissues. Buffered formalin was the most successful fixative used in this study, and only tissues which had been fixed by buffered formalin were used for oocyte size/frequency estimations.

Tissues were dehydrated in graded Propan-2-ol, (according to the schedule in Appendix A3iii.1), cleared in "Histoclear" and then placed paraffin wax at 60°C for 12 hours. The wax was changed, then cooled quickly to produced blocks of smaller crystalline structure for ease in sectioning with a Jung microtome at 7µm. The sections were floated out on a water bath at 35°c and picked up on glass slides.

Sections were stained with Ehrlich's haematoxylin and eosin (Cox *et al*, 1969) (Appendix A3iii.2).

Sections of ovaries from each assigned stage were used for oocyte size/ frequency analysis. At least fifty oocytes which had been sectioned through the nucleus, were measured using a TDS Digitizing tablet, and then grouped into 0.1 mm size classes for graphical presentation. Oocyte size/frequency distributions, average oocyte size (and standard deviation) were calculated for each ovary stage.

3.4.3 Ovary development and female internal condition indices

The ovary factor (Ovf), relative hepatic weight (RHW) and relative ovary weight (ROW) (Gonado-somatic index) were calculated from the wet weights of ovaries and hepatopancreas which had been washed in distilled water and blotted dry (Appendix A3ii.1). The validity of the use of the Ovf and ROW was investigated by calculating average and standard deviations of these indices, for each ovary stage, when described by gross ovary morphology. Variation in female relative hepatopancreas weight (RHW) was investigated with respect to female ovary stage. Internal maturity criteria (Ovf, ROW and RHW) were plotted against ovary stage with optimal regression lines (linear or 2nd order polynomial, determined by regression analysis) separately for non-ovigerous and berried (spent) females for each of the three study areas. Linear and polynomial regression analyses were performed for Ovf, ROW and RHW and their respective relationships to ovary development stage. Linear regression results are presented with estimates of r (correlation coefficient); R^2 (coefficient of determination) and

Sx/y (standard error of estimation) as a measure of variability about the regression line. Additionally, the regression coefficients (according to the equation $y = a+bx$), their standard error of estimation, t-statistics and their probability (P) in predicting the independent variable are tabulated. P(F), the probability of association between the independent and dependent variables, was calculated using analysis of variance (ANOVA) and is also shown. Second order polynomial regression analyses results (according to the equation $y = a+bx+cx^2$) are presented as r, R^2, coefficients and their P-values. Analyses of covariance (ANCOVA) were also made for the maturity criteria and its covariant ovary stage to investigate potential variations between berried and non-berried females at each of the three sites and additionally for collated berried female data and collated non-berried female data from all three study sites to investigate between site variation.

3.4.4 Cement gland development

Female cement gland development assessment was undertaken in August 1990 at Bridlington and throughout 1990 at Selsey. Cement gland (CG) stages were assigned using the method described in Appendix A2ii.2 (Aiken and Waddy, 1982): Female moult stage was also noted according to the method described in Chapter 2 (Appendix A2ii.1).

The relationship between CG development stage and ovary development stage was investigated using linear and second order polynomial regression analysis. The ovary factor (Ovf) and relative ovary weight (ROW) were each plotted against CG development stage. Linear and polynomial regression analyses were used to determine the relationship between Ovf and CG stage, and between ROW and CG stage.

ANCOVAs were calculated to assess potential between-site differences in the relationships of ovary development stage with CG development stage, Ovf with CG stage and ROW with CG stage.

3.4.5 Calorific content of ovaries

Ovaries dissected from female lobsters were carefully washed in distilled water, blotted and weighed, before being deep frozen. Approximately 7g of tissue was freeze-dried for water content assay, and for use in calorific determination (in those cases of ovaries of stages I - III weighing less than 7g, as much tissue was freeze-dried as was possible). Duplicates of approximately 0.5g of freeze-dried tissue were then used for ash content determination at 550°C for 20 hours. At this temperature all organic components will be combusted, the decomposition of carbonates is minimal and most major inorganic components which become volatile at 560°C (such as potassium and sodium) will not be lost (Hilton *et al*, 1984). The ash content was determined from the mean of the duplicates when the values differed by no more than 1 % (Atkinson and Wacassey, 1983).

The remaining freeze-dried tissue was ground with a pestle and mortar and triplicates of 1 g of tissue were pelleted for use in semi-microbomb calorimetry (duplicates were used when there was insufficient tissue). Those samples weighing less than 1g (minimum 0.5g) were made up to 1g weight using a known amount of Benzoic acid.

Calorific content was determined using a Janke and Kunkel IKA C4000 calorimeter, calibrated using 1g of Benzoic acid standard with a calorific value of 26456 J/g ± 20 J. Average and standard deviations of calorific values, water content (as a percentage of wet weight) and ash content (as a percentage of wet weight) were calculated for each ovary stage. Linear and polynomial regression analyses were performed for calorific values and water and ash content and their relationships with ovary development stage. ANCOVAs were calculated to investigate potential differences between calorific value, water content and ash content (each covarying with ovary development stage) for non-berried and berried (spent) females.

3.5 Results

3.5.1. Ovary staging

The results of initial *H. gammarus* ovary staging by gross morphology (ovary colour and oocyte size) are presented in Tables 3.1 and 3.2 (c.f. Appendix Table A3i.1, for *Homarus spp.*, Aiken and Waddy; 1980). White ovaries with small oocytes (<0.5 mm diameter) were classified as immature stage 1. Stage 2 ovaries were straw yellow, beige or a very pale green colour with oocytes <0.8 mm diameter. Further development to stage 3 (developing) was indicated by a light to medium green colour and oocytes up to 1.2 mm diameter. Stage 4 ovaries were medium to dark green in colour with oocytes of between 0.5 and 1.4 mm diameter. Stages 5 (developing) and 6 (ripe) were both dark green, with oocytes of 0.8 mm to 1.7 mm and 1.2 mm to 1.7 mm respectively. Spent ovaries (from berried females or females showing signs of having just released their eggs) were classified separately because of certain distinguishing features: spent ovaries (up to stage 4s) contained a number of resorbing oocytes which were a distinctive yellow colour. One non-berried female appeared to have resorbed all of her ripe ova, and had a dark green and yellow, turgid ovary with large ova (>1.4 mm diameter) (c.f. 1s ovaries which are white with large yellow and dark green ova, but flaccid). Females which had recently spawned, with non-eyed eggs (Ovary stages 1s,2s or 3s) had remnants of non-extruded ova (dark green or yellow) in the terminal portion of the oviduct. Stage 5s ovaries were distinguished from stages 5 and 6 by the presence of large white patches, especially at the centre of the ovary. In a number of cases (4 at Bridlington and 17 at Selsey), berried females had ovaries containing large dark green oocytes (<1.2 mm diameter)(inferred as stage 5s or 6s), but which were slightly flaccid or which were "veined" with an opaque white or clear fluid to making the ovaries turgid.

3.5.2. Oocyte size frequency distributions

Oocyte size frequency distributions calculated for ovary stages 1 to 6 and 2s, 3s and 4s (Appendix Tables A3iv.1 and A3iv.2, Figures 3.2 and 3.3) concur with oocyte sizes suggested by gross ovary morphology. Ovaries of stages 4, 5 and 6 have less variable oocyte size ranges than early developing ovaries (stages 1 to 3). Average oocyte diameter (fixed tissues) can be seen to increase with ovary stage (Appendix Table A3v.3 and Figures 3.4 and 3.5), to a maximum of 1.4 mm (ovary stage 6). The ovary suggested as spent 4 by gross morphology had a lower average oocyte size than that suggested as stage 3s (although it had no oocytes less than 0.18 mm diameter, c.f. those of stage 3s). This may be because only one ovary stage 4s was examined microscopically (as a result of a lack of successfully fixed tissues of stage 4s).

Table 3.1 Initial ovary development staging of *Homarus gammarus*

Ovary Stage	Description	Ovary colour	Oocyte diameter
1	Immature	White	<0.5 mm
2	Immature/ developing	Yellow, beige, or pale green	<0.8 mm
3	Developing	Light to medium green	<1.2 mm
4	Developing	Medium to dark green	0.5 to 1.4 mm
5	Developing	Dark green	0.8 to 1.7 mm
6	Ripe	Dark green	1.2 to 1.7 mm
6A	Oocytes free		
Spent/Reabsorbing (1s)		White or yellow with residual ova	

Table 3.2 Initial ovary development staging of *Homarus gammarus* (spent ovaries)

Ovary Stage	Description	Ovary colour	Oocyte diameter
1s	Spent	White or yellow (with residual yellow/green ova)	<0.5 mm
2s	Spent/ developing	Pale green, white (with residual yellow/green ova)	<0.8 mm
3s	Developing	Light to medium green (with residual yellow/green ova and white patches)	<1.2 mm
4s	Developing	Medium to dark green (with residual yellow/green ova and white patches)	0.2 to 1.4 mm
5s	Developing	Dark green	0.8 to 1.7 mm

Oocyte size frequency distrubutions (with standard deviations)
ovary development stages 1 to 6

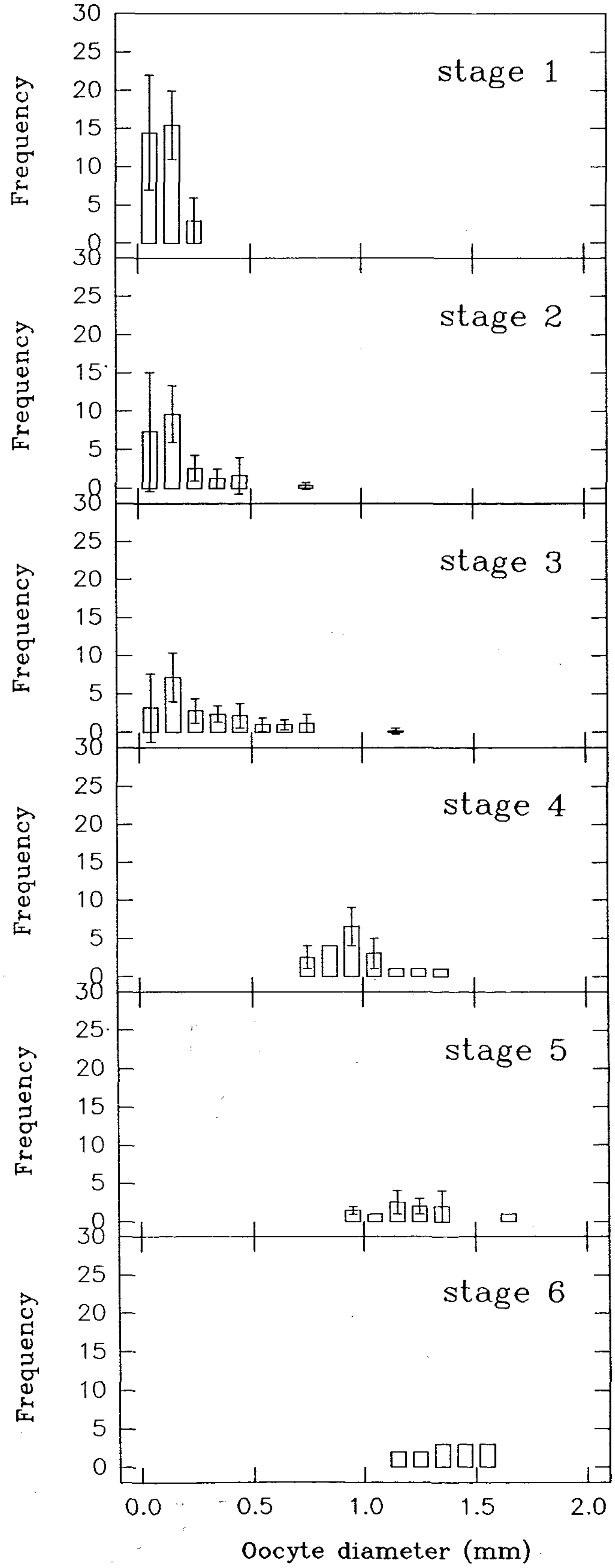


Fig. 3.2

Oocyte size frequency distrubutions (with standard deviations)
spent ovary development stages 2 to 4

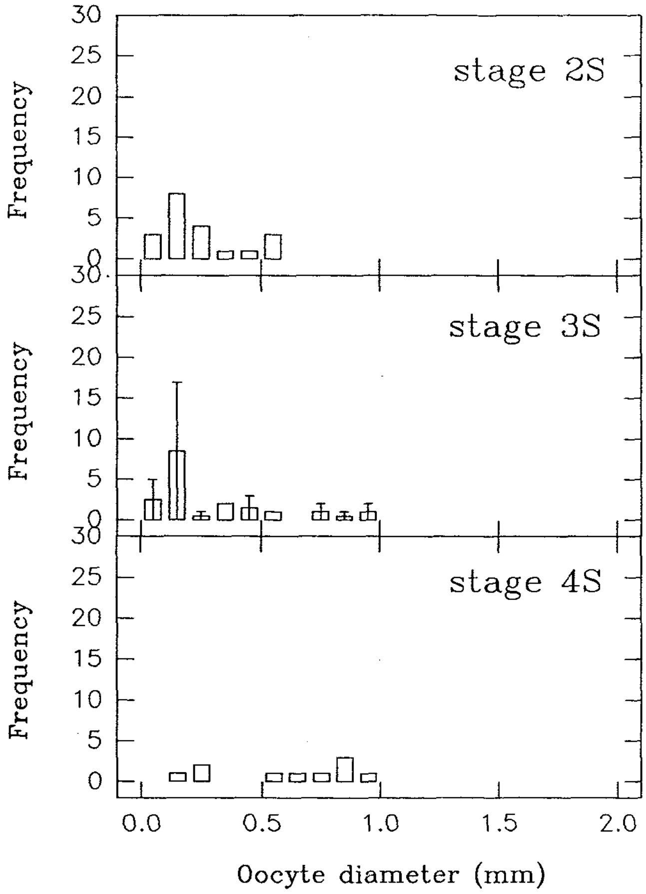


Fig. 3.3

Average oocyte size (and standard deviations) against ovary development stage

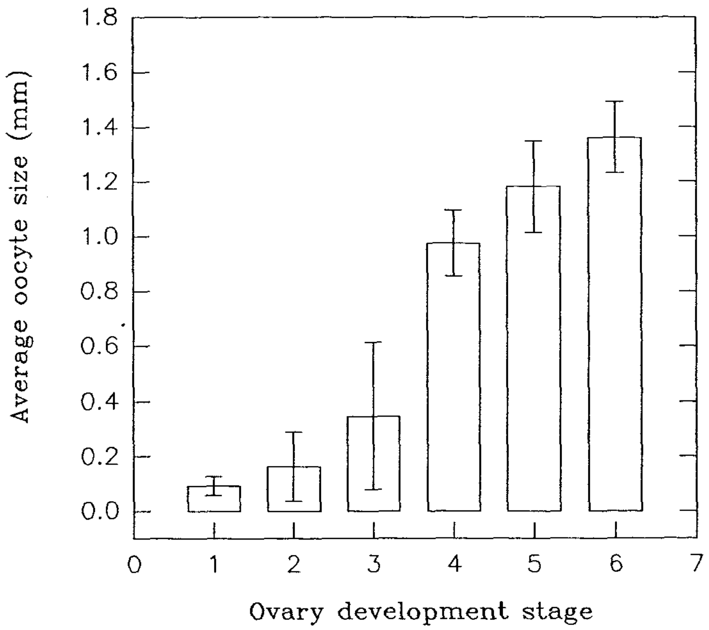


Fig. 3.4

Average oocyte size (and standard deviations) against ovary development stage (spent ovaries)

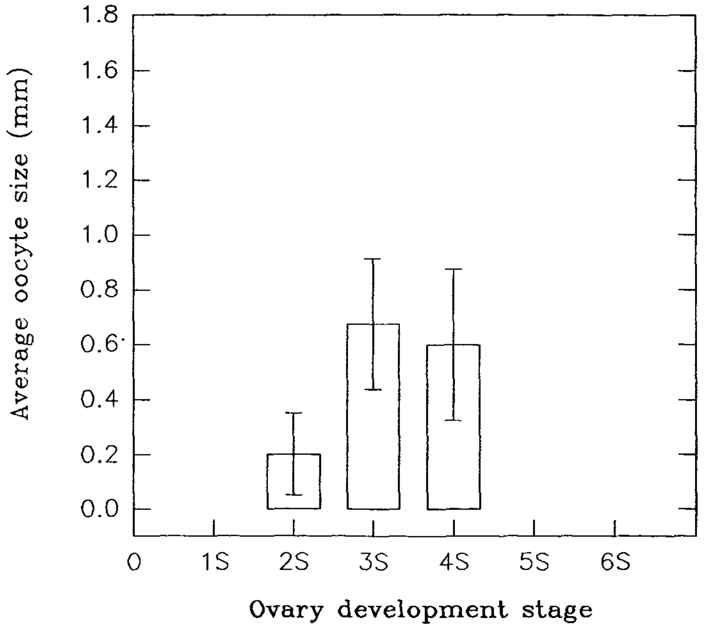


Fig. 3.5

3.5.3 Ovary development and female internal condition indices

Ovary factor

The ovary factor increases with ovary development stage (polynomial relationship)(for both berried and non-berried females) for Bridlington, Dale and Selsey lobsters (Appendix Tables A3v.1 to A3v.5)(Figs. 3.6 to 3.8). The ovary factor is correlated to ovary stage for both berried and non-berried females (R^2 0.586 to 0.817 linear model, 0.586 to 0.874 polynomial model)(Appendix Tables A3v.6 and A3v.7). ANCOVA between berried and non-berried females Ovf covarying with ovary stage indicate a difference between females of the two reproductive states (Appendix Tables A3v.18 to A3v.20). ANCOVA for Ovf/ovary stage for aggregated non-berried females (Appendix Table A3v.27), and also for berried females (Appendix Table A3v.30), indicate between-site covariation.

Relative ovary weight

Relative ovary weight increases with ovary development stage (Appendix Tables A3v.1 to A3v.5). Bridlington and Selsey data suggest a polynomial relationship between the two variables (polynomial model R^2 0.667 to 0.882, linear model R^2 0.611 to 0.816), whereas Dale data exhibit little difference between polynomial and linear model coefficients of determination (polynomial model R^2, 0.677; linear model, 0.675) (although this may be a function of the small Dale data-set, and omission of females of ovary stages 5 and 6 from sampling)(Figs. 3.6 to 3.8)(Appendix Tables A3v.8 and A3v.9). ANCOVAs between non-berried and berried females at each site (Appendix Tables A3v.24 to A3v.26) indicate differences between ROW/ovary stage covariations between spent (berried) and non-ovigerous females. Significant differences for ROW, covarying with ovary stage, were found between the three study sites (non-berried females Appendix Table A3v.29; berried females Appendix Table A3v.32).

Ovary factor and Relative ovary weight

Appendix Tables A3v.12 and A3v.13 indicate a strong correlation between Ovf and ROW (linear regression model R^2 0.813 to 0.985: polynomial model R^2 0.822 to 0.986).

Relative hepatopancreas weight

There is a poor relationship between RHW and ovary stage at Bridlington, Female internal condition indices (and standard deviations) plotted against ovary stage, Bridlington 1989 to 1991

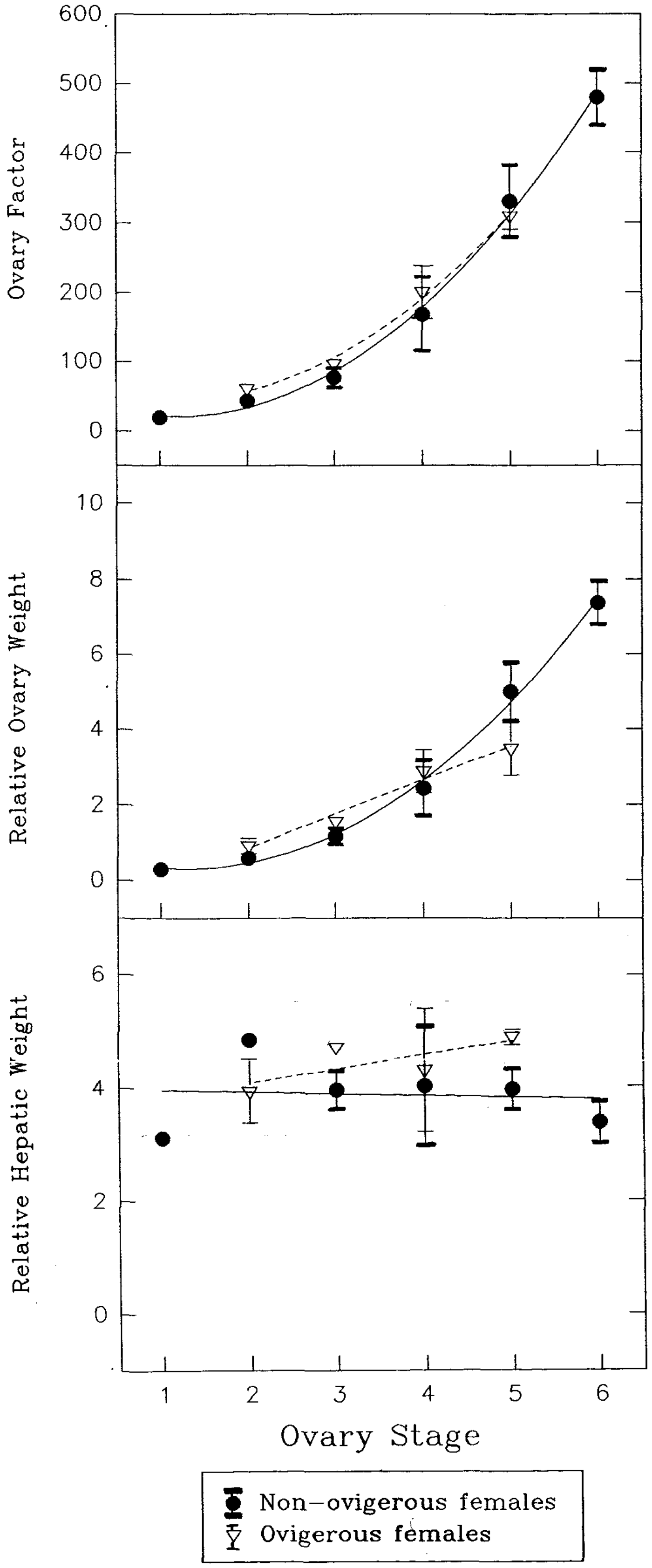


Fig. 3.6

Female internal condition indices (and standard deviations) plotted against ovary stage, Dale 1989 and 1992

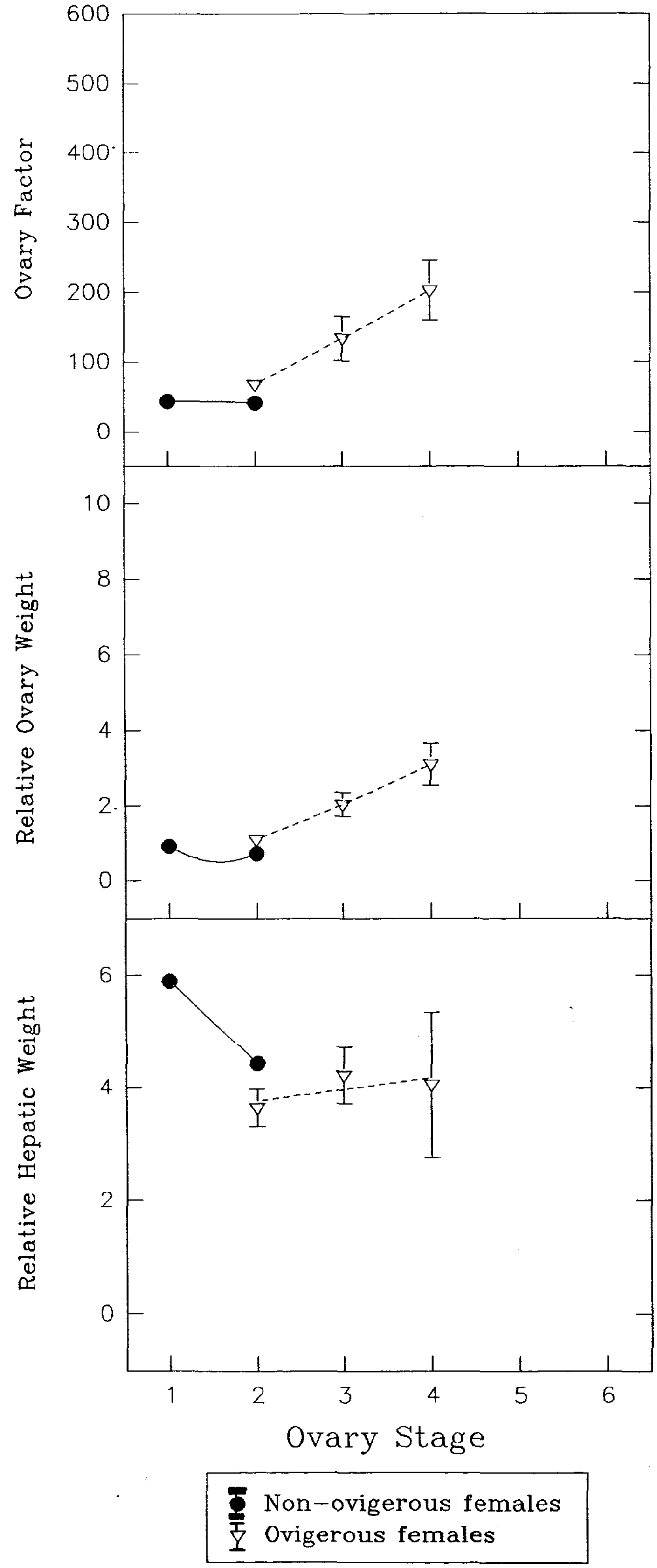


Fig. 3.7

Female internal condition indices (and standard deviations) plotted against ovary stage, Selsey 1989 to 1991

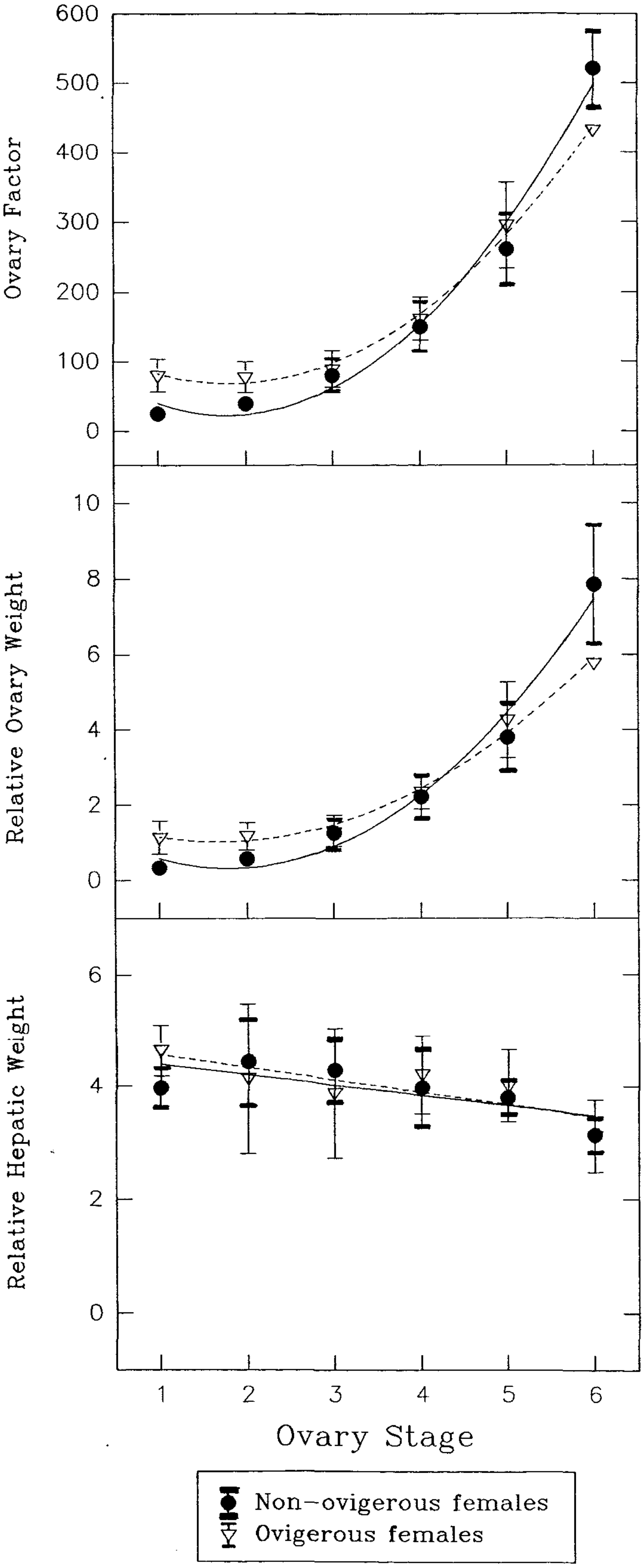


Fig. 3.8

Dale and Selsey (Figs. 3.6 to 3.8)(Appendix Tables A3v.1 to A3v.5 and A3v.10 and A3v.11)(P(F) 0.11 to 0.853, linear regression model; P(F) 0.001 to 0.813, polynomial model). ANCOVAs between berried and non-berried females also indicate poor covariance between RHW and ovary stage, as well as between-reproductive-state differences (Appendix Tables A3v.21 to A3v.23). Potential covariance between RHW and ovary development stage appears to be more likely in non-berried females than berried females (Appendix Tables A3v.28 and A3v.31: significance 0.0014 and 0.3557 respectively). ANCOVAs also indicated between-site differences for both berried females and non-berried females (Appendix Tables A3v.28 and A3v.31).

Relative hepatopancreas weight and ovary factor

Linear and polynomial regression analyses do not indicate a relationship between RHW and Ovf (R^2 0.0008 to 0.088 and 0.004 to 0.183 respectively; P(F) 0.028 to 0.812 and 0.005 to 1.08085 respectively)(Appendix Tables A3v.14 to A3v.15.

Relative hepatopancreas weight and relative ovary stage

There was no detectable relationship between RHW and ROW (Linear regression analysis R^2 <0.08; P(F) 0.038 to 0.864: polynomial regression analysis R^2<0.165; P(F) 0.1 to 0.882)(Appendix Tables A3v.16 to A3v.17).

3.5.4 Cement gland development

Cement gland development and ovary stage

CG development stage increases with ovary development stage (Appendix Table A3vi.1, Figs. 3.9 and 3.10). Females with ovaries of stage 5 had CG development stages of between 2 and 4. Females with CG stages 3 and 4 had ovaries of stage 3 or above (developing to ripe). Regression analyses do not suggest correlation between CG stage and ovary development stage (linear model $R^2 = 0.423$ and 0.427; polynomial model $R^2 = 0.473$ and 0.433 for Bridlington and Selsey respectively)(Appendix Tables A3vi.2 and A3vi.3). ANCOVA for ovary stage covarying with CG stage implies between-site variation for this relationship (significance 0.0946), although differences in sampling dates may be the cause of

Cement gland development stage plotted against ovary development stage, Bridlington 1989 to 1991

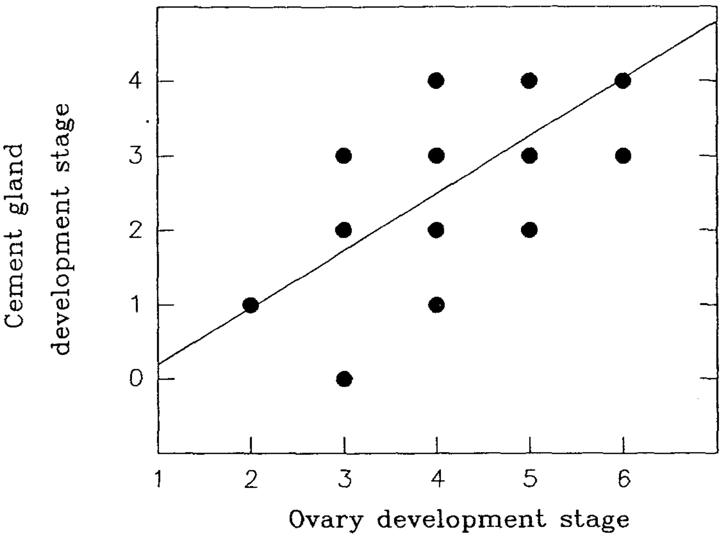


Fig. 3.9

Cement gland development stage plotted against ovary development stage, Selsey, 1989 to 1991

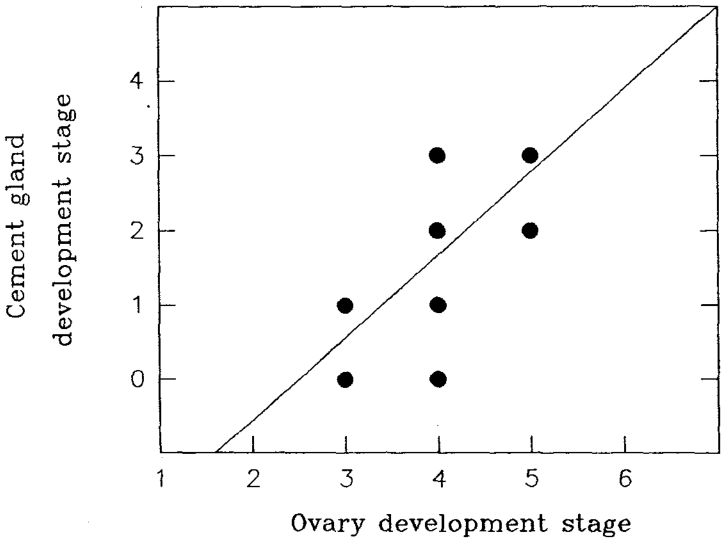


Fig. 3.10

this variation (Appendix Table A3vi.8).

Cement gland development and ovary factor

The ovary factor increases with CG development stage (Appendix Table A3vi.1, Figs. 3.11 and 3.12). Regression analysis suggests a weak correlation between Ovf and CG stage, with the polynomial model being more appropriate than the linear model (R^2 = 0.503 and 0.31, polynomial model; R^2 = 0.429 and 0.271, linear model)(Appendix Tables A3vi.4 and A3vi.5). ANCOVA for Ovf covariance with CG stage suggests a significant difference between Bridlington and Selsey data (0.6922)(Appendix Table A3vi.9).

Cement gland development and relative ovary weight

Relative ovary weight increases with CG development stage (Appendix Table A3vi.1, Figs. 3.11 and 3.12). No correlation, between ROW and CG stage, has been suggested by the results of both linear and polynomial regression analysis (R^2 0.503 and 0.174; polynomial model: R^2 0.456 and 0.149; linear model)(Appendix Tables A3vi.6 and A3vi.7). Neither of the regression models used showed a detectable relationship for Selsey data (P(F) 0.39 and 0.083 for linear and polynomial models respectively). ANCOVA suggested between-site differences in the relationship of ROW with CG stage (Appendix Table A3vi.10).

3.5.5 Calorific content of ovaries

Calorific content

Calorific values increase with ovary stages for both berried and non-berried females, ranging between 5300 and 6394 cal/g (Appendix Table A3vii.1, Fig. 3.13). Unfortunately not enough material (<0.5 g) was available for calorific determination of ovary stages 1,2,3 or 2s (1s ovaries are large and flaccid, and one such ovary was large enough for calorie assay). Regression analyses suggested a possible polynomial relationship between calorific value and ovary stage, althoughthe limited number of ovary stages used prevents statistical validation of the relationship between calorific content and ovary development stage (Appendix Tables A3vii.2 and A3vii.3). ANCOVA suggested a significant difference between non-ovigerous female's ovaries and berried female's ovaries; however this result

The ovary factor and relative ovary weight
plotted against cement gland development stage,
Bridlington 1989 to 1991

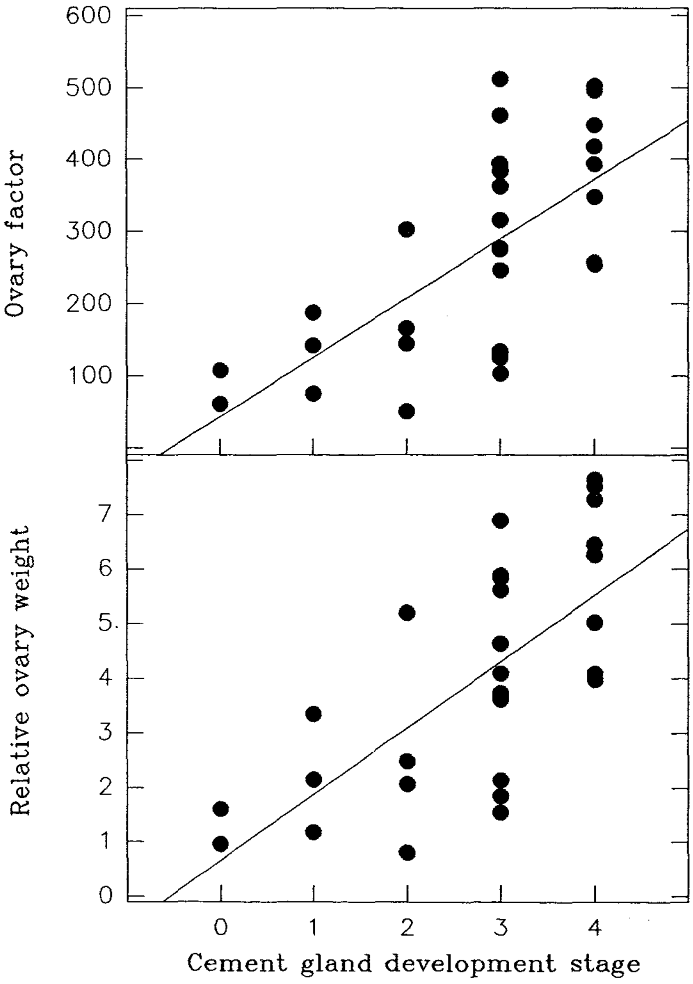


Fig. 3.11

The ovary factor and relative ovary weight
plotted against cement gland development stage,
Selsey 1989 to 1991

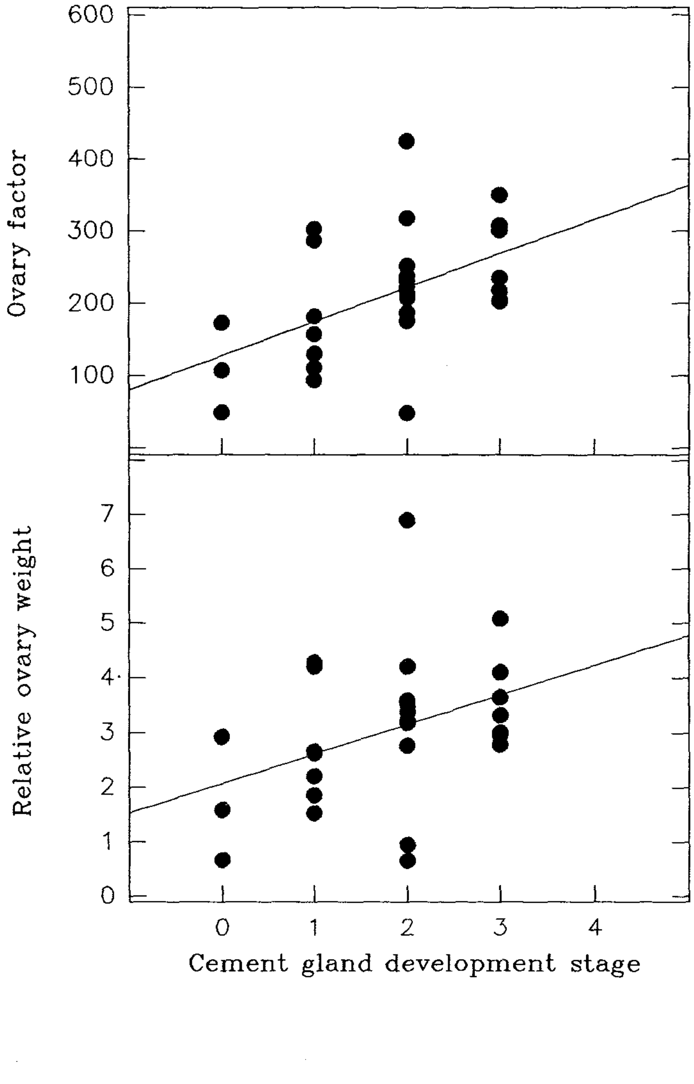


Fig. 3.12

may also be a function of the small sample size and limited covariant range (Appendix Table A3vii.8).

Water content

The results of water content analysis (expressed as water as a percentage of ovary wet weight) have been presented as averages and standard deviations per ovary stage (Appendix Table A3vii.1)(Fig. 3.13). Linear and polynomial regression results suggest a decreasing water content with increase in ovary stage (polynomial relationship with higher $R^2 = 0.493$ and 0.452 c.f. $R^2 = 0.472$ and 0.386 for non-berried and berried female ovaries, polynomial and linear models respectively) (Appendix Tables A3vii.4 and A3vii.5). ANCOVA results suggest a small significant difference between the water content of non-ovigerous female ovaries and spent ovaries, covarying with ovary stage (Appendix Table A3vii.9).

Ash content

Ash content (expressed as % of wet weight) decreases with increasing ovary development stage for both non-ovigerous female ovaries and spent ovaries (Appendix Table A3vii.1; Fig. 3.13). Both linear and polynomial regression analyses do not suggest correlation between ash content and ovary stage (Appendix A3vii.6 and A3vii.7). The results of ANCOVA suggest a significant difference between non-ovigerous ovary and spent ovary covariance with ovary development stage (Appendix Table A3vii.10)

3.6 Discussion

Knowledge of ovarian development in *H. gammarus*, and the duration and seasonality of the cycle are important for validation of external functional-sexual maturity indicators (Chapter 4). The duration of the ovarian cycle and spawning frequency affect individual fecundity, with respect to both the number of egg clutches produced and potentially the sizes of egg clutches produced (as an egg clutch produced in a second consecutive year might not be as large as the initial clutch size because of inadequate resources or limited sperm availability). Variations in the duration of the ovarian cycle and spawning frequency will affect individual fecundity. The length of ovary development time may therefore be an important consideration in selection of minimum legal landing size in order to

Average calorific content, % water and % ash (with standard deviations) plotted against ovary development stage

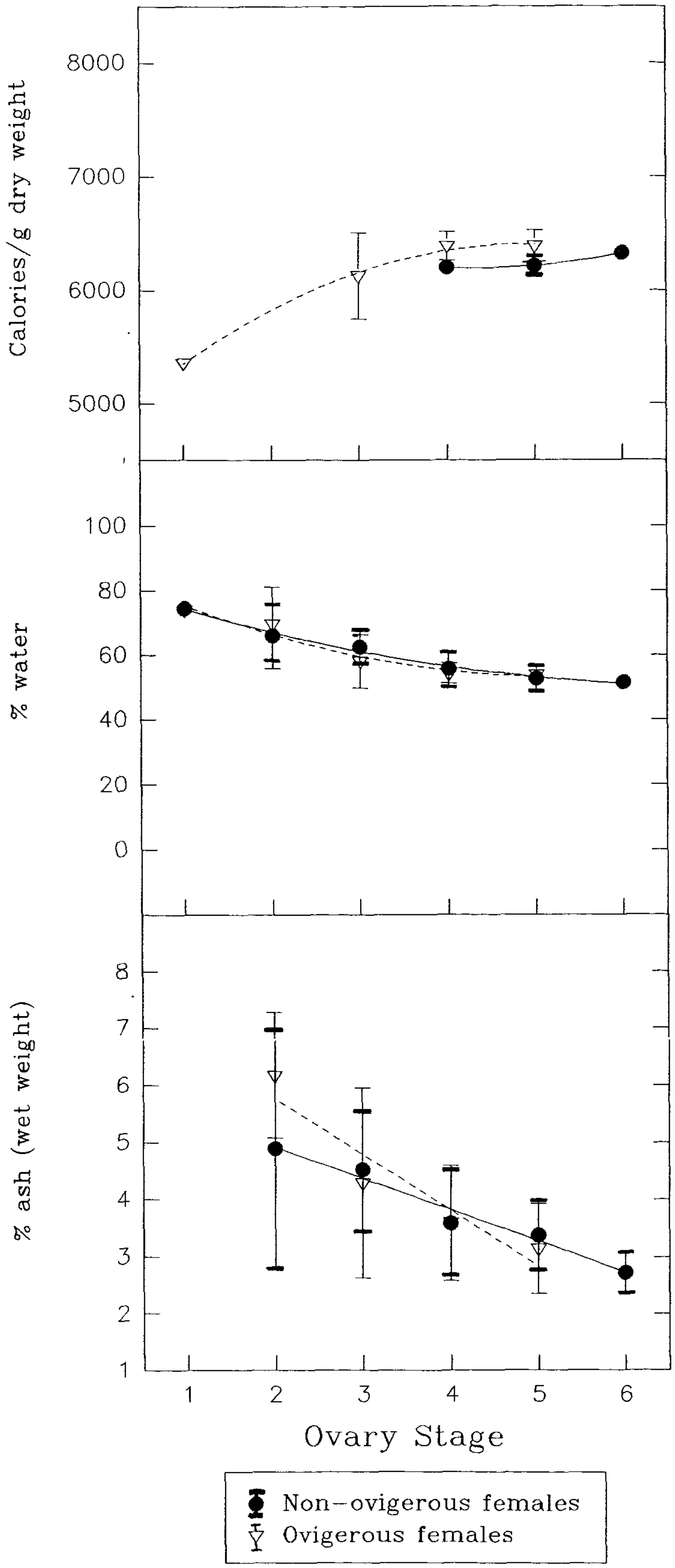


Fig. 3.13

maximise stock-reproductive potential. The effects of environmental conditions, such as temperature, on the duration of the ovary cycle may cause both spatial and temporal variations in individual fecundity and will also be of relevance for fisheries management interests.

The ovary stages of *H. gammarus* are most easily distinguished by oocyte colour and size. The smallest oocytes are found towards the centre of the ovary, as suggested by Kessel (1978). This disparity in oocyte size diminishes with ovary development stage.

This study has indicated differences between the gross morphology, and internal condition indices of ovaries developing for the first time and females known to have spawned at least once (berried females or females with indications of having just released their eggs). The presence of resorbing, non-extruded ova in spent ovaries is an obvious distinction between spent ovaries and those from non-berried females. Herrick (1911) suggested that the oocytes of *H. americanus*, which are not extruded at oviposition, take five weeks to turn from dark green to yellow, and these are thought to remain in the ovary for up to 2 years (Aiken and Waddy, 1980). This has also been suggested to be the case for *H. gammarus* in this study, and may provide an important distinction between first ovarian development and ovaries from lobsters which have spawned before.

A number of ovaries from both Bridlington and Selsey June and July samples were in development stages 5s and 6s. These ovaries may have belonged to females that were ready to spawn again that summer, although laboratory confirmation of potential successive spawnings in *H. gammarus* is required to confirm this. The females which were apparently capable of a second successive spawning were above 85 mm CL at Selsey and all above 98 mm CL at Bridlington. Ennis (1971) and Aiken and Waddy (1980; 1986; 1990) suggested that temperature and size were both important factors in determining ovary development time for *Homarus americanus* (both warmer temperature and larger female size facilitating rapid ovarian development), and this may explain why only large Bridlington females exhibited ovary stages 5s, whilst smaller Selsey females, living in relatively warmer water temperatures, could redevelop their ovaries to stages 5s or 6s within one year. Aiken and Waddy (1980) suggested that ovaries from female

H. americanus usually take 2 years to recover from oviposition, with a potential for 2 spawnings in 3 years for larger animals (Aiken and Waddy, 1986).

Both the ovary factor (Ovf) and relative ovary weight (ROW) (which are themselves closely correlated) are reasonable indicators of ovary development. As suggested by Pillay and Nair (1971) and Harrison (1990) for brachyuran decapods, ROW increases with ovary development and then drops suddenly after oviposition. Ovf also reduces rapidly after oviposition, as was shown by Aiken and Waddy (1980) for *Homarus americanus*. However, variations were observed in the relationships of both ROW and Ovf, with ovary stage, between berried and non-berried females. This will complicate the use of these indexes, as will apparent between-site variation in ROW and Ovf covarying with ovary stage. Between-site variations may be caused by potential differences in size at onset of sexual maturity (SOM, Chapter 4), and the resulting length and weight differences between females with ovaries developing for the first time. In order for these two internal indicators of maturity and ovary development stage to be calculated, individuals need to be dissected, and ovary stage assessment by gross morphology and histological methods may be a more direct and accurate method of investigating the ovarian cycle and maturation. This may be confirmed by the presence of a weak relationship between relative hepatopancreas weight (RHW) and ovary stage, compared with no detectable relationship between Ovf or ROW and RHW (although this may be a statistical phenomenon caused by the limited number of ovary stages c.f. Ovf and ROW variation).

Cement gland (CG) development was seen to stage 3 or 4 for ovaries of only development stage 3 (developing). CG development stage increases with ovary development stage but its accuracy as an indicator of functional maturity (Ennis, 1983) may be questionable for *H. gammarus*, as stage 3 ovaries are not likely to be from females spawning that year (secondary vitellogenesis, and associated colour change, are believed to occur in spring, Aiken and Waddy (1980)). Additionally, the process of CG staging is semi-destructive and difficult at sea or on the quayside, and the purpose and cyclic nature of CG development need further investigation before use for *H. gammarus*.

It may be assumed that observed increases in calorific value with increase in ovary development stage are as a result of an increase in lipid content of oocytes during primary and secondary vitellogenesis (Heath and Barnes, 1970; Pillay and Nair, 1973). Microbomb calorimetry techniques are required for assessment of the calorific content of early ovary stages because of the limited amount of tissue available for analysis. The reduction in % water content and % ash content of ovaries with their development might also be expected, concurrent with increasing egg yolk during egg development.

CHAPTER 4 FEMALE SEXUAL MATURITY

4.1 Introduction

Knowledge of the size at which sexual maturity occurs in *H. gammarus* is important in the assessment of the minimum landing size for use in management legislation. Stock reproductive potential will be affected by fishing if the size at onset of maturity is close to the minimum legal landing size (Heydorn, 1964).Templeman (1939) suggested that individuals should be allowed to reproduce at least once before being removed by fishing. Coupled with fecundity estimates (Chapter 6), size at onset of maturity may be used to model egg production potential of stocks subjected to varying levels of fishing pressure and management legislation policies (Ennis, 1984). The accurate determination of the size at maturity is additionally important in respect to changes in both moult frequency and moult increment growth factors which may occur after maturity (Simpson, 1961). The onset of maturity may also be accompanied by changes in lobster behaviour and potential changes in the nature and degree of local movements or migration in *H. gammarus* (Cooper and Uzmann, 1980; Campbell, 1986).

The size at which maturity first occurs in a given lobster population may be determined by the smallest size at which ovigerous females occur as egg bearing females are obviously mature (Aiken and Waddy, 1980). However, since not all females capable of egg extrusion will be berried at any one time, because of the complex, size-dependent timing of the reproductive cycle (Aiken and Waddy, 1980), examination of other internal and external morphological features may be required to determine maturity. The size frequency distribution of berried females and females deemed mature using other criteria, may be used to calculate the size at first maturity, size at 50% maturity and 100% maturity (the sizes at which females are first observed as mature, and at which 50% and 100% of the population are mature, respectively). Wenner, *et al* (1974), noted the lack of convention for defining minimum size of crustacean maturity, and devised a method for assessing average (50 %) minimum size of maturity for the sand crab *Emerita analoga* using the size frequency distribution of ovigerous individuals plotted on probability paper.

Those females present in the population which are capable of egg extrusion, but not berried (i.e. functionally mature) have previously been identified using a number of external and internal maturity criteria (Aiken and Waddy, 1980). However, Ennis (1980) suggested that expressed maturity (i.e. ovigerous females and those that will become berried that year) is more important than physiological female maturity for management considerations as only those females which produce eggs in any given year will contribute to that year's egg production.

The relative growth of secondary sexual characters has been widely used as an indication of sexual maturity in crustacean populations (Hartnoll, 1978). This technique has proved to be especially successful in brachyurans, such as the mud crab, *Macropthalmus hirtipes* (Simons, 1981) and the paddle crab *Ovalipes catharus* (Armstrong, 1988). Templeman (1935) observed a relative increase in the width of the second abdominal segment of *H. americanus* with the approach of the onset of sexual maturity, in order to provide a larger area underneath the abdomen for protection of the eggs during their incubation (Templeman, 1939). Later Templeman (1944) suggested that the relationship between this measure and lobster total length could be used to facilitate comparisons between the sizes of sexual maturity of lobster populations at different localities. When expressed as the percentage of the carapace length, the measure of abdominal width has been used as a maturity index, as shown by Simpson (1961), working on *H. gammarus*. Perkins and Skud (1966), plotting the width of the second abdominal segment of *H. americanus,* revealed an inflection corresponding to the segment width of the smallest ovigerous female. The equation describing the relationship between these two variables was described as cubic, of the form $y = a + bx + cx^2 + dx^3$, with an asymptote at a female size at which most individuals might be presumed mature (i.e. 100 % maturity). Further work on the relative abdomen width of *H. americanus* has revealed a strong correlation between oocyte size and the width of the second abdominal segment (Skud and Perkins, 1969). However, Squires (1970) noticed the presence of ovigerous *H. americanus* females that were smaller than the size at maturity suggested, for the population as a whole, by the relative abdomen width index (RAW). Krouse (1973) studied the abdomen width-carapace length relationship for females of a wide size range and indicated an initial acceleration of abdomen width relative growth in females of 30 to 35 mm CL, as well as a further rapid change in relative growth at maturity. In general, it has been suggested that there is a good agreement between the size at which the graphical inflection of RAW and carapace length occurs, and the smallest ovigerous females (Skud and Perkins, 1969; Krouse, 1973; Aiken and Waddy, 1980). Ennis (1980) pointed out that although a distinct inflection and then asymptote may occur when RAW is plotted against CL, the corresponding sizes at which these events occur should only be regarded as approximations of the size at onset of maturity and 100% maturity respectively within the population concerned. Originally, the maximum inside width of the second abdominal segment was measured for use in such studies. Ennis (1971) and Briggs (1976) used the maximum outside width of the segment to estimate the maturity index. This method is now preferred for its ease of use, and to increase the accuracy of the measurement, especially in field work (Aiken and Waddy, 1980).

Intersect analysis has been used successfully to determine maturity in palinurid lobsters using the leg length/CL ratios of males and females (*Palinurus cygnus*, Grey; 1979: *P. versicolor*, George and Morgan; 1980) and tail length/CL ratios for both sexes of *P. homarus* (Jayakody, 1989)

The development of "cement glands" the pleopod endopodites and exopodites (Chapter 3) of *Homarus americanus* have been used for female maturity assessments (Aiken and Waddy, 1982; Campbell and Robinson, 1983; Ennis, 1983). The four stages of cement gland development (Appendix 2ii.2) have been used to estimate the onset of maturity (Campbell and Robinson, 1983) and the percentage of females in the population which will become berried that year in *H. americanus* (Ennis, 1984). Ennis validated the technique experimentally, showing that all of the females with cement gland stages 3 or 4 would become berried during that spawning season, and that 22% of females with cement gland stage 2 would also become berried. Ennis (1984) used these results for comparisons of functional and physiological maturity (defined as females carrying eggs or with cement gland stage 3 or 4 and by ovary development respectively), with a correction factor of 22% for those females exhibiting cement gland development stage 2.

Ovary development stage (defined in Appendix A3i.1) is a reliable, but unfortunately destructive method, of determining physiological sexual maturity. Individuals which have undergone secondary vitellogenesis, with dark green oocytes larger than 1.0 mm diameter (ovary stage 4, 5 or 6) have been considered potentially mature (Squires, 1970) (c.f. Krouse, 1973 and Briggs and Mushacke, 1979, who suggested that oocytes> 0.8 mm diameter indicate maturity). Aiken and Waddy (1980) suggest that fully mature, preovigerous ovaries contain ova larger than 1.4 mm diameter and which are free in the ovary (ovary stage 5 or 6). The ovary factor, (Aiken and Waddy, 1980), developed to assist in determining ovary development stage may also assist in maturity assessments as the determinate between ovary stages 4 or 5 (Chapter 3).

The evidence of FSP (female specific hormone) may be used an external maturity indicator. FSP is immunologically identical to the major yolk protein present in the haemolymph of female *Homarus spp.* during yolk mobilisation associated with massive oocyte resorption and secondary vitellogenesis (Barlow and Ridgway, 1969; Byard, 1975). Haemolymph containing FSP is a distinctive dark green colour, which may be observed through the ventral abdominal membrane, therefore indicating the maturity of the individual concerned (Aiken and Waddy, 1980).

Ovigerous setae found on pleopod endopodites and exopodites (Appendix Fig. A2ii.2) may be an indicator of sexual maturity in *Homarus spp.*. The potential for this method has not yet been investigated, as the relationship between the appearance of these setae and female maturity and egg production is uncertain, although their development has been suggested to be parallel to the gradual broadening of the abdomen (Aiken and Waddy, 1980). There are seven groups of setae found on pleopods as secondary sexual characteristics to increase the available surface area for egg retention. The relationship between the development of ovigerous setae and the onset of functional maturity has also been examined in the palinurid lobsters *Jasus verreauxi* and *J. edwardsii* (Annala *et al*, 1980; Booth, 1984). Booth (1984) showed that although some *J. verreauxi* individuals with developed ovigerous setae did not have fully developed gonads, the use of ovigerous setae as an indicator of maturity was valid.

The presence of a spermatophoric mass in the seminal receptacle of

Homarus as an indicator of maturity is not thought to be reliable, and the method of internal investigation may cause damage to females. Many sexually mature females do not carry spermatophores, and conversely, some individuals with spermatophoric masses in their seminal receptacles do not have adequately developed ovaries to indicate their maturity (Krouse, 1973; Aiken and Waddy, 1980). Cobb and Wang (1985) stated that female clawed lobsters can mate before ovarian maturity and then store sperm for up to two years; this will obviously complicate maturity estimates using this method and implies that, unlike males, females can mate when both physiologically and functionally immature.

The sizes at onset of maturity (SOM) of both *H. americanus* and *H. gammarus* have been shown to vary between locations. The size at first maturity of the American lobster varies between 55 mm CL in the western Long Island Sound (Briggs and Muschake, 1979) and 90 mm CL in the Bay of Fundy and southern Georges Bank (Templeman, 1936). Simpson (1961) showed differences in the average size of maturity (50% SOM) between *H. gammarus* populations off the north coast of Angelsey and Pwllheli. The size at maturity was smaller in the more shallow, warmer waters of Pwllheli (77 mm CL) than those of Angelsey (91 mm CL). Gibson (1969), using egg bearing as the maturity indicator, observed different SOMs on the west and east coasts of the Irish Sea (the smallest berried female from his pooled data-set was in the 70 to 74 mm CL size class). Such spatial variation in the size of maturity has been attributed to a number of potential factors. Aiken and Waddy (1986b) stated that higher temperatures may be associated with the earlier maturation of both male and female *H. americanus*. Aiken and Waddy (1976, 1980) and Cobb and Wang (1985) suggested that high population density and the selective pressure of high fishing effort (especially in cases where MLS is smaller than SOM) may together exert a genetic pressure for maturation at a smaller size. A decrease in SOM has been suggested from 90 mm CL to 81-82 mm CL for *Panulirus argus* in Bermuda, concurrent with an increase in exploitation rate between 1950 and 1986 (Sutcliffe, 1952; Evans, 1988). Annala *et al* (1980) observed little variation in SOM of *Jasus edwardsii* between years at any given site, but considerable variation between areas. This spatial variation in SOM was suggested to be inversely related to water temperature. SOM may also be considered as a function of growth rate, age, metabolic rate, population density, food availability and other environmental factors exerting a direct pressure on SOM, as well as a function of growth rate which may influence the time taken to the onset of egg production (Annala *et al*, 1980; Sastry, 1983, Wenner *et al*, 1985). Pollock (1982) suggested that regional differences in SOM of *Jasus lalandii* are caused by variations in hydrological and physical environmental characteristics and their resultant density-dependent effects upon growth and mortality. SOM of *P. cygnus* is not thought to be temperature related, but rather SOM is smallest in areas with the highest population densities (Chittleborough, 1974; 1976). In *H. americanus*, temperature is believed to be more important in determining SOM than animal density (Aiken and Waddy, 1980).

Wenner *et al* (1985) proposed a number of potential life history and growth patterns which might explain individual and regional variation in SOM:

A) Individuals with fast and slow growth rates mature at the same size, but at different times (fast growing individuals reach maturity first).
B) Individuals with fast and slow growth rates mature at the same time, and therefore at different sizes (fast growing individuals have largest SOM).
C) Fast growing individuals mature earlier and at a smaller size than slow growing individuals.
D) Fast growing individuals mature earlier and at a larger size than slow growing individuals.
E) Fast growing individuals mature later and at a larger size than slow growing individuals.
F) Different cohorts of individuals (with similar growth rates) enter the population at different times but mature at the same time, therefore maturing at different sizes (last) cohort smallest).

Regional comparisons of SOM may need to consider the cause of potential spatial variation in maturity estimates. Individual age, size or instar may be the determinate of sexual maturity. SOM is used for fisheries management considerations, but may not be as important as growth rate if either individual age or instar number determine sexual maturity. Lipcius (1985) suggested that a combination of age and size, within a narrow range of instars will determine the onset of maturity and not purely size alone. This would suggest that knowledge of moult frequency is crucial in estimating age at maturity, and of moult increment for estimating the resultant size at maturity. This has also been suggested by the work of Hughes *et al* (1972) who raised *H. americanus* to maturity in warm waters in approximately two years, compared with 6 to 7 years in the wild.

4.2 Methods and statistical analysis

4.2.1. Assessment of female sexual maturity

The width of the second abdominal segments of both males and females were measured on lobsters from Bridlington (1989), Dale (1989) and Selsey (1989 and 1990). Relative abdomen width (RAW) was calculated as abdomen width (AW) (mm) as a percentage of CL (mm) (i.e. AW/CL x100). In addition, abdomen width (AW) and RAW data collected in 1973 for males and females from Whitby, Yorkshire, Pembrokeshire (Solva) in West Wales and Selsey and females from Staithes, Yorkshire and St. Davids in West Wales in 1980 and 1981 were also used in this study. The presence of eggs and evidence of FSP (female specific hormone detected by green abdominal colouring) were also noted on sampling trips from Bridlington (1989), Dale (1989) and Selsey (1989, 1990). Additional data of the proportions of females berried in 5 mm CL size classes, from Yorkshire, Pembrokeshire and Selsey between 1972 and 1974, was also used for size at maturity assessments.

Specimens were examined in the laboratory for cement gland development (August 1990 Bridlington and Selsey 1990) (Appendix A2ii.2; Chapter 3) and the presence of ovigerous setae on pleopod endopodites of female lobsters (Appendix A2ii.2). Dissections of female lobsters from Bridlington (1989 to 1991), Dale (1989) and Selsey (1989 to 1991) were used for assessments of sexual maturity using ovarian development stages, ovary factor (Ovf), ovary weight and relative ovary weight (Chapter 3). Hepatopancreas' dissected from females were weighed (wet) and used to ascertain any potential relationship between ovary development and somatic resources (Chapter 3), along with hepatopancreas weight and relative hepatopancreas weight (RHW) (Chapter 3) variability with female size (CL). Ovary stages 5 (late developing) and 6 (ripe), classified according to Table 3.1, were considered an indication of full sexual maturity; a comparison with maturity indicated by ovaries of stages 4 (developing) and greater, was also made.

4.2.2. Data analyses

The data of internal and external maturity from each site were used for analysis in both 5mm CL groups and for individual lobsters. 5mm CL group summary statistics (mean and standard deviation) were calculated for abdomen width (AW) and relative abdomen width (RAW) data.

Graphs of AW and RAW were each plotted against CL for each site and year for individual females, individual males and females combined and males and females combined in 5mm CL groups. Linear, log-linear and second order regression analyses were performed to assess the relationships between both AW and RAW with CL (individual lobsters and 5mm CL groups). Additionally, third order polynomial regression were performed for RAW and CL for both individual lobsters and lobsters in 5mm CL groups. Linear and log-linear regression statistics are presented with estimates of r (correlation coefficient), R^2 (coefficient of determination) and the standard error of estimation (Sx/y) as the measure of variability about the fitted regression line. The regression coefficients, their standard error, t-statistics and their probability (P) of predicting the dependent variable are also given. ANOVA (analysis of variance) was used to calculate P(F), the probability of association between the independent and dependent variables. Second order and third order polynomial regression results are presented with estimates of r, R^2, coefficients and their P-values.

The points of intersection between male and female regression lines for AW and RAW with CL were calculated using simultaneous equations. Third order polynomial regression equations were differentiated and then simultaneous equations used to ascertain the asymptote (i.e. when dy/dx =0). Potential inflexion points for AW-CL and RAW-CL were ascertained by eye when possible.

ANCOVA (analysis of covariance) were performed to assess the covariance of AW and RAW with CL between-sites, between-years and between males and females.

The percentages of females berried, per 5 mm CL size class, were calculated and plotted against CL. Lines at 25 %, 50 % and 66.67 % females berried were drawn to indicate 50 % maturity and 100 % maturity (assuming two year reproductive cycle) and 100 % maturity (assuming females being berried twice every three years). The sizes of the smallest observed ovigerous females (only available as 5 mm CL classes for 1972 to 1974 data) are presented as a representation of size at first maturity (SFM).

ANCOVA were performed to assess the covariance of the proportion of females berried with CL, between-sites, between-years, and between-sites/between-years.

Cement gland (CG) development stages were plotted against female CL (mm). Linear and polynomial regression analysis was used to assess any potential relationship between CG development stage and female CL for each of Bridlington and Selsey data-sets. An ANCOVA was performed to investigate between-site variation in CG stage/CL covariation.

Each female indicator of ovarian maturity (ovary wet weight, relative ovary weight and ovary factor) was plotted against CL for each of the three sites (Bridlington, Dale and Selsey 1989 to 1991). The nature of these plots allowed for lines to be drawn, by eye, to mark both the lower and upper limits of ovary weights, ROW and Ovf for any given CL. Linear and 2nd order polynomial regressions were calculated to assess the relationship between ovary development and CL. ANCOVAs, comparing the relationships of each of Ovf, ovary weight and relative ovary weight with CL between-sites, were also performed.

Hepatopancreas wet weight (HW) and relative hepatopancreas weight (RHW) data were plotted against CL for each site. Linear and polynomial regressions of hepatopancreas weight and RHW on CL were performed for Bridlington, Dale and Selsey. Additionally, ANCOVA was calculated to investigate between-site variations in HW with CL and RHW with CL.

Indicators of ovarian maturity (ovary stage, ovary weight, relative ovary weight and ovary factor) were each plotted against abdomen width and relative abdomen width. When possible, lines marking the lower and upper limits of plotted data-points were drawn by eye onto these figures, and were used to estimate female size at onset of ovarian development. Linear and second order regression analyses were performed to assess the relationships between AW and ovary development, and RAW and ovary development. ANCOVA was used to investigate any between-site differences in both AW-ovary maturity indicator relationships and RAW-ovary maturity indicator relationships.

Average Ovf for 5 mm CL size groups (and standard deviations) were calculated to clarify any potential Ovf/CL relationship. The percentages of females with ovaries of stages 4+, and then stages 5+, per 5 mm CL class, were also calculated by site. Average Ovfs per 5 mm size class were plotted against female CL, and Ovf/CL covariations were compared between-sites using ANCOVA. Logistic curves, of $f(x) = a/(1+\exp(b(x-c)))$, were fitted to % females with ovary stages 4+ and 5+ for each site. ANCOVA were performed on % ovary stage 4+CL and % ovary stage 5+/CL relationships to investigate potential between-site differences.

4.3 Results

4.3.1 External indicators of maturity

Abdomen width (AW) and relative abdomen width (RAW) both increase with carapace length (CL) (Figs. 4.1 to 4.56) (Appendix Tables A4ii.1 to A4ii.18). Male AW and RAW increases less rapidly with CL than female AW and RAW with CL.

Abdomen width

Regression analyses for individual lobsters suggest a linear relationship between AW and CL (linear $R^2 = 0.549$ to 0.998; log-linear $R^2 = 0.585$ to 0.988; second order polynomial = R^2 0.557 to 0.988; third order polynomial $R^2 = 0.088$ to 0.946) (Appendix Tables A4ii.19 to A4ii.21). The smallest coefficient of determination was calculated for Whitby 1973 females, which showed a very high standard deviation of AW for the 72.5 mm CL class, and may therefore contain erroneous data (Appendix Table A4ii.11). Excluding Whitby 1973 females, linear minimum R^2 was 0.767, 2nd order polynomial 0.769, 3rd order polynomial 0.326 and log-linear 0.759.

5mm CL regression results show an increase in R^2 from individual lobsters results, as a result of the reduced number of data-points and standardisation of AW per size class (Appendix Tables A4ii.22 to A4ii.25). These aggregated data suggest a log-linear relationship between AW and CL ($R^2 = 0.975$ to 0.998; linear $R^2 = 0.549$ to 0.998, second order polynomial $R^2 = 0.936$ to 0.998) (no third order regression analysis was performed because of the small number of CL classes compared with the number of degrees of freedom).

Male and female AW indices intersect at between 56.5 and 74.7mm CL (between 25.4 and 38.1mm AW) (linear model), 48.25 and 68.9mm CL (21.9 and 35.3mm AW) (second order polynomial model) and 54.3 and 75.0mm CL (26.9 and 37.3mm AW) (log-linear model) (Appendix Tables A4ii.33 to A4ii.35). Third order polynomial asymptotes (Appendix Table A4ii.39) occurred at between 31.6 and 56.5 CL, 18.1 and 32.5mm AW (minimums); 111.5 and 171.7mm CL, 65 and 106.3mm AW (maximums). The preference for linear regression models suggest that linear intersections will be most accurate. AW-CL inflexions could only be determined for Whitby 1973 (76.5mm CL) and Selsey 1973 (78mm CL)(Appendix Table A4ii.41).

ANCOVAs comparing sexual differences between the AW and CL relationship (Appendix Tables A4ii.47, A4ii.49, A4ii.57, A4ii.59, A4ii.63, A4ii.65, A4ii.67 and A4ii.69) do not suggest significant differences between male and females per year at each site. This may be a result of the spread of the data-set with most data-points occurring close to the theoretical male/female intersection point. The strong positive association between AW and CL for both males and females may also confound identification of between sex differences which are apparent from graphical evidence (Figs. 4.2, 4.8, 4.14, 4.20, 4.26, 4.32, 4.42 and 4.52), which it is felt justify identification of potential intersection points. Between-year differences in AW-CL relationships were shown for both males and females at Bridlington and Selsey (1989 and 1990) (Appendix Tables A4ii.43, A4ii.45, A4ii.53 and A4ii.55), and for between-years/between-sexes at Bridlington and Selsey (Appendix Tables A4ii.51 and A4ii.61). Between-site (and therefore year) significant differences were calculated by ANCOVA for the three Welsh sites (Appendix Tables A4ii.75 and A4ii.77), but not between Selsey 1973, 1989 and 1990 data (Appendix Tables A4ii.79 and A4ii.81) nor Yorkshire 1973, 1980, 1989 and 1990 data (Appendix Tables A4ii.71 and A4ii.73). 1989/1990 (Bridlington, Dale and Selsey) AW-CL relationships differed significantly between-years but not between-sites (Appendix Table A4ii.83) for females and between-years and between-sites for males (Appendix Table A4ii.85). No significant between-site covariation was shown for Whitby 1973, Pembrokeshire 1973, Selsey 1973, Staithes 1980 and St.Davids 1980 (Appendix Table A4ii.87 and A4ii.89).

Relative abdomen width

Relative abdomen width (RAW) has a weak correlation with CL for males; linear model $R^2 = 0.003$ to 0.25, 2nd order polynomial $R^2 = 0.003$ to 0.282, log-linear $R^2 = 0.0006$ to 0.227. The association between female RAW and CL is greater, and suggests a third order polynomial relationship between the two variables ($R^2 = 0.565$ to 0.994; linear $R^2 = 0.316$ to 0.88; 2nd order polynomial $R^2 = 0.073$ to 0.907; log-linear model $R^2 = 0.073$ to 0.875) (Appendix Tables A4ii.26 to A4ii.29). Estimates of R^2 are higher for 5mm CL groups of both male and female individuals (Appendix Tables A4ii.30 to A4ii.32). 5mm CL female R^2 estimates were calculated as; linear, 0.725 to 0.953, 2nd order polynomial 0.855 to 0.982, and log-linear 0.804 to 0.939, therefore also suggesting a polynomial relationship between RAW and CL. 5mm male estimates of R^2 suggested poor correlation between RAW and CL and were calculated as 0.017 to 0.658 (linear model), 0.019 to 0.865 (2nd order polynomial model), and 0.009 to 0.568 (log-linear model).

Despite a lack of correlation between male RAW and CL, intersect analysis were performed for male and female regression lines for each respective model (Appendix Tables A4ii.36 to A4ii.38 and A4ii.40). Male and female RAW indices intersect between 46.6 and 52.7 RAW (43.1 and 61.2 mm CL) (linear model), 46.4 and 53.3 RAW (46.2 and 76.5 mm CL) (log-linear model), and 47.4 to 50.9 RAW (46.1 to 73.3 mm CL) (2nd order polynomial model). 3rd order regression lines had a zero gradient at a minimum of between 31.6 and 52.9 RAW (2.3 and 65.3 mm CL) and at a maximum (at point of asymptote) of between 59.1 and 77.1 RAW (98.5 to 152.7 mm CL). First inflexion points, determined by eye, occurred at between 79 and 86.5 mm CL (linear plot) and between 82.7 and 86 mm CL (log-linear model). Second inflexion points occurred at 87 to 102 mm CL (linear model) and 86.6 and 101 mm CL (log-linear model) (Appendix Tables A4ii.41 and A4ii.42).

ANCOVAs comparing sexual differences between RAW-CL covariations only suggested significant differences at Selsey 1990 (Appendix Tables A4ii.48, A4ii.49, A4ii.58, A4ii.60, A4ii.64, A4ii.66, A4ii.68 and A4ii.73). This may be a result of weak correlation between male RAW and CL or most data being

Fig. 4.1 Abdomen width (mm) plotted against CL (mm) with linear regression line for Bridlington females, 1989

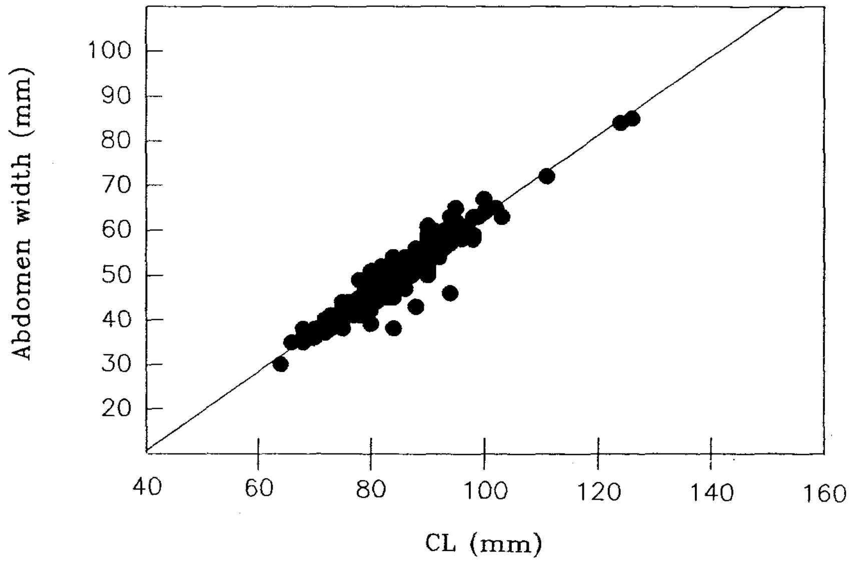


Fig. 4.2 Abdomen width (mm) plotted against CL (mm) with linear regression line for Bridlington males and females, 1989

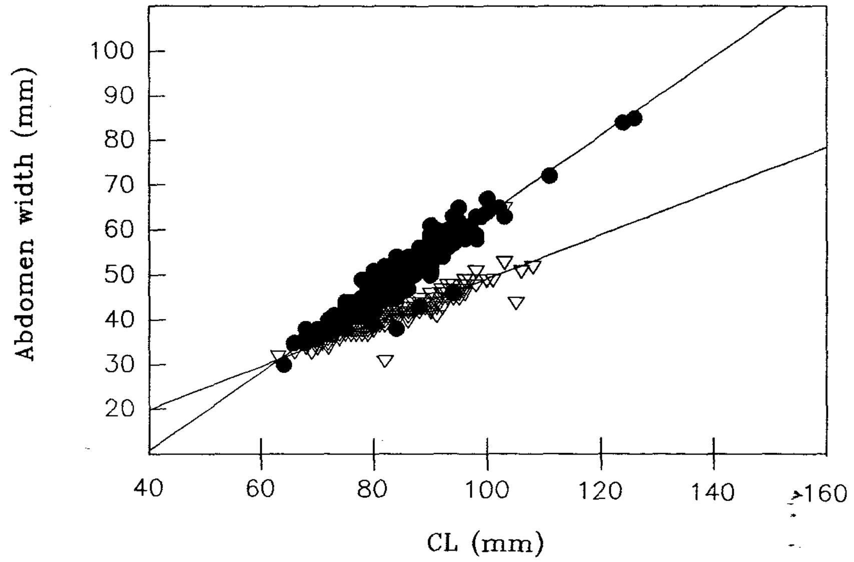


Fig. 4.3 Abdomen width (mm) plotted against CL (5 mm groups) with linear regression line for Bridlington males and females, 1989

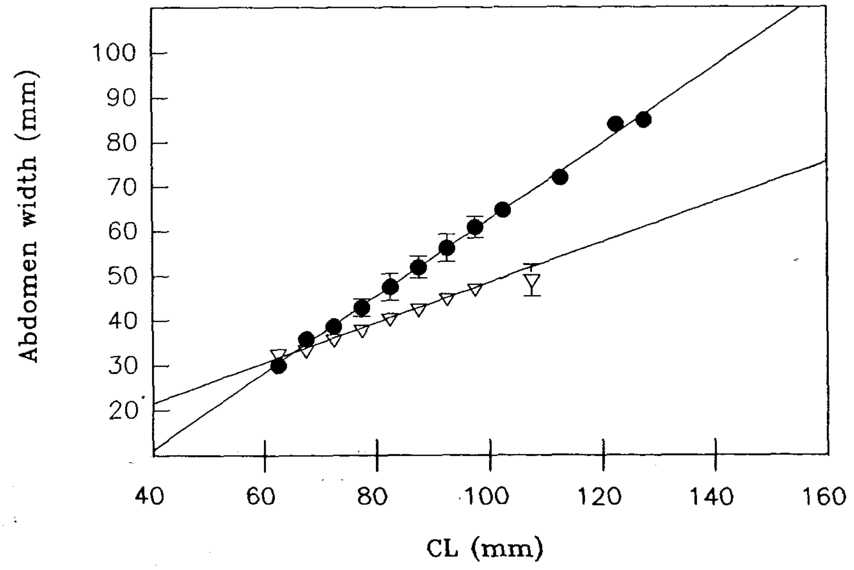


Fig. 4.4 Relative abdomen width (mm) plotted against CL (mm) with linear regression line for Bridlington females, 1989

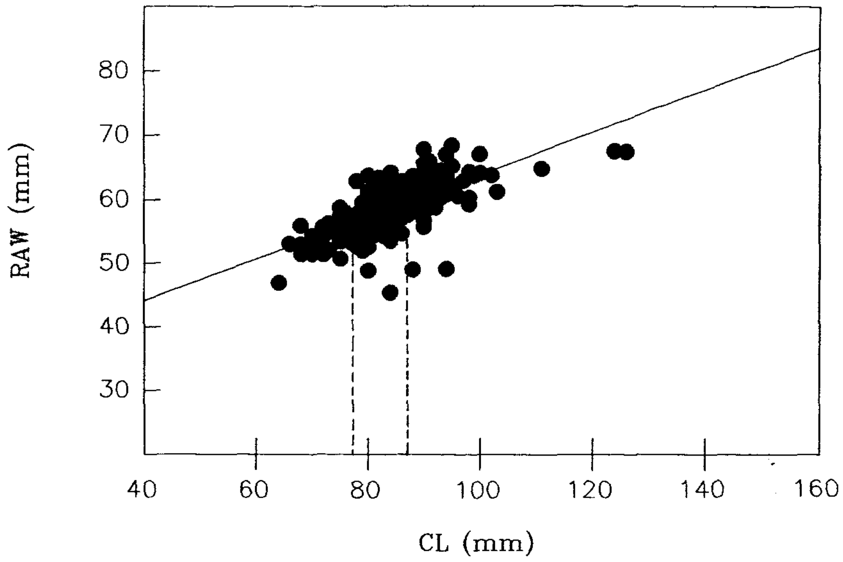


Fig. 4.5 Relative abdomen width (mm) plotted against CL (mm) with linear regression line for Bridlington males and females, 1989

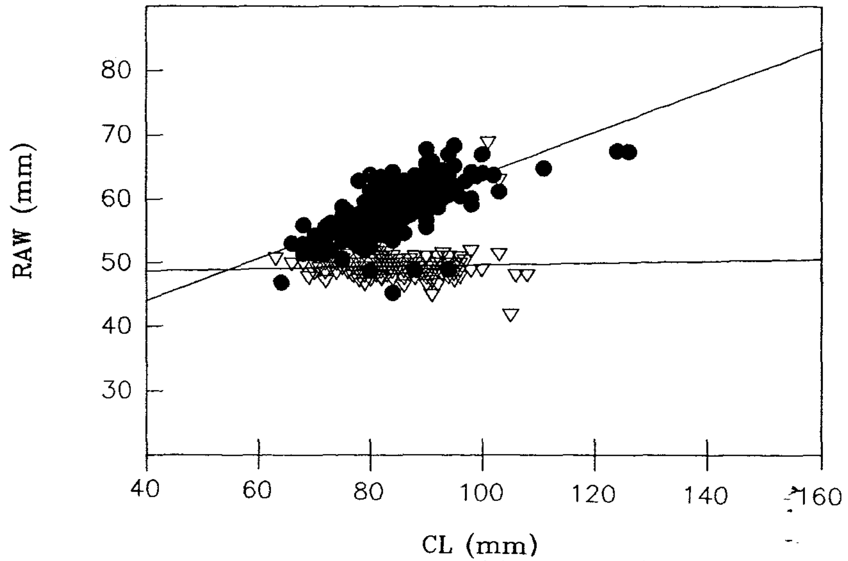


Fig. 4.6 Relative abdomen width (mm) plotted against CL (5 mm groups) with linear regression line for Bridlington males and females, 1989

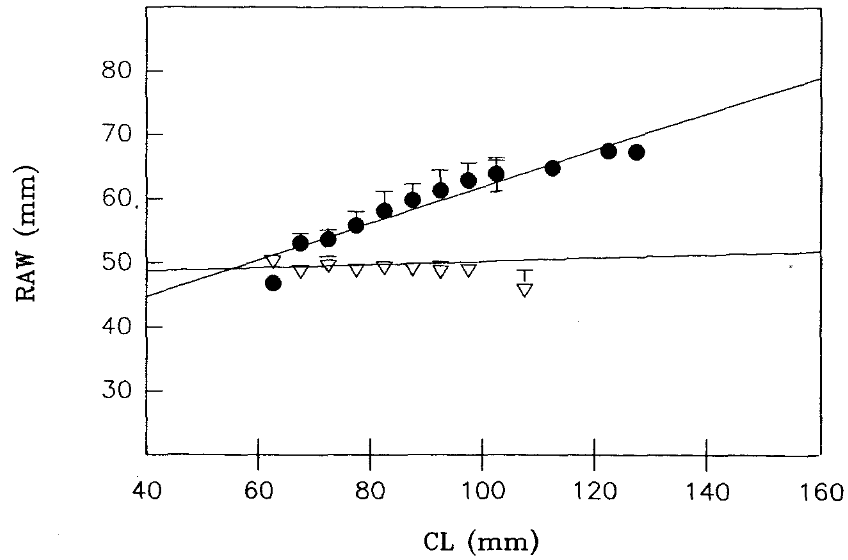


Fig. 4.7 Abdomen width (mm) plotted against CL (mm) with linear regression line for Bridlington females, 1990

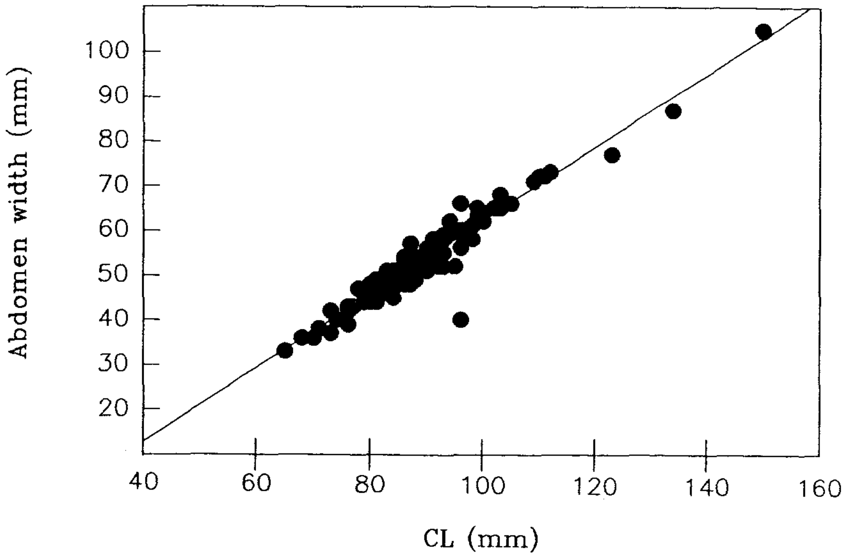


Fig. 4.8 Abdomen width (mm) plotted against CL (mm) with linear regression line for Bridlington males and females, 1990

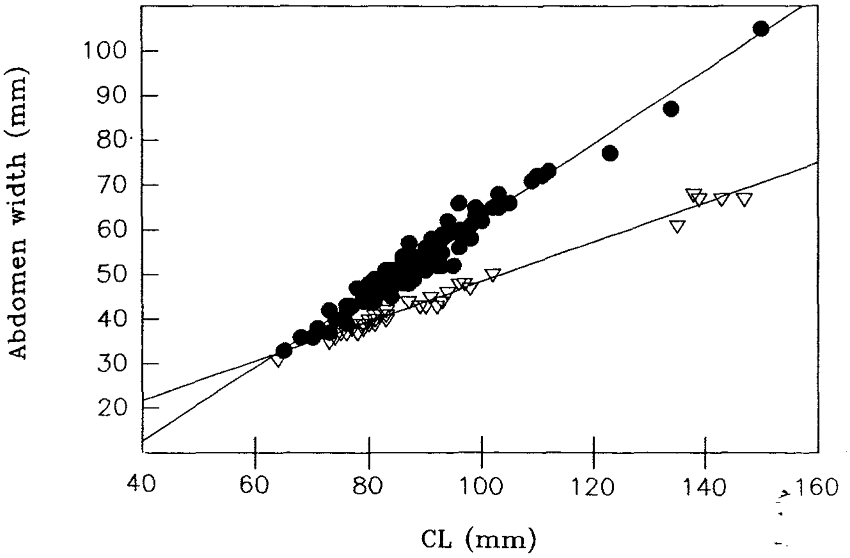


Fig. 4.9 Abdomen width (mm) plotted against CL (5 mm groups) with linear regression line for Bridlington males and females, 1990

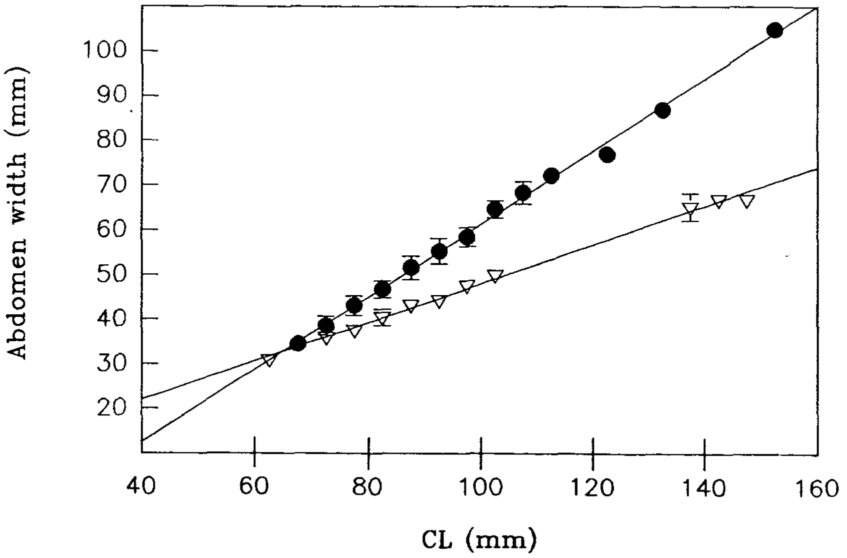


Fig. 4.10 Relative abdomen width (mm) plotted against CL (mm) with linear regression line for Bridlington females, 1990

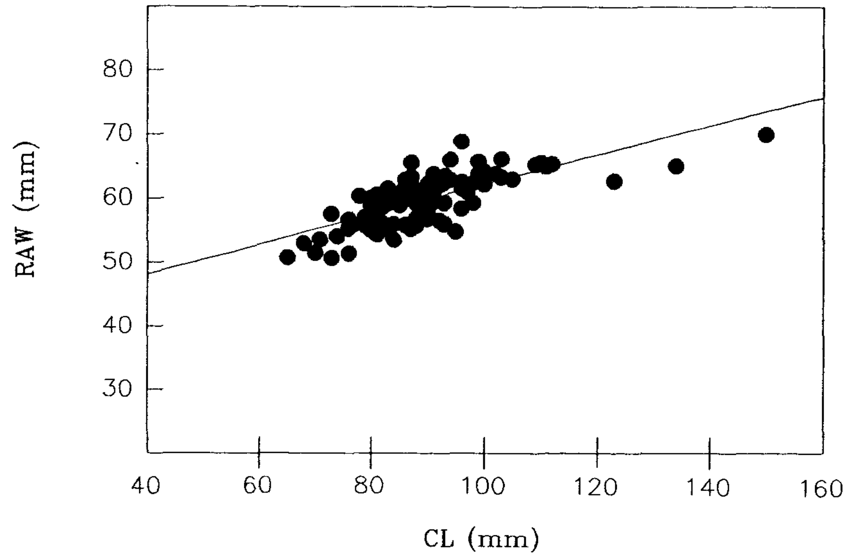


Fig. 4.11 Relative abdomen width (mm) plotted against CL (mm) with linear regression line for Bridlington males and females, 1990

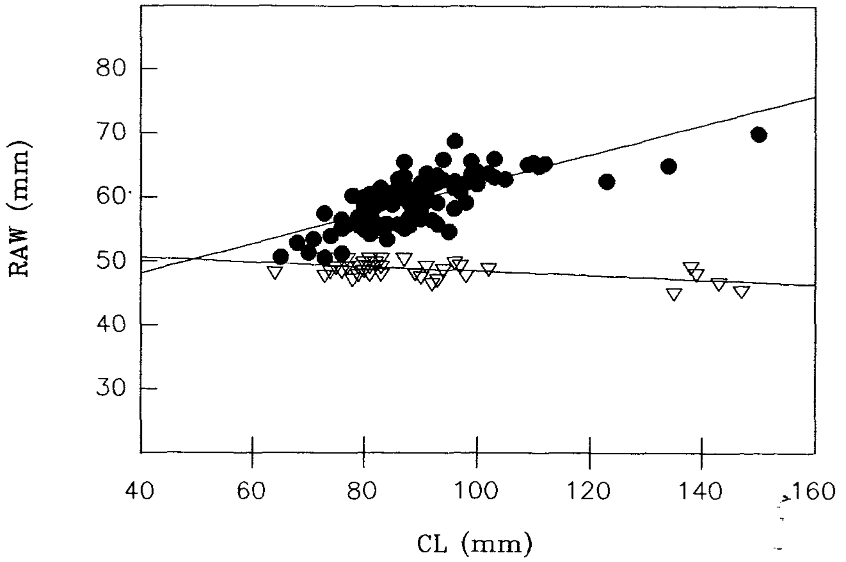


Fig. 4.12 Relative abdomen width (mm) plotted against CL (5 mm groups) with linear regression line for Bridlington males and females, 1990

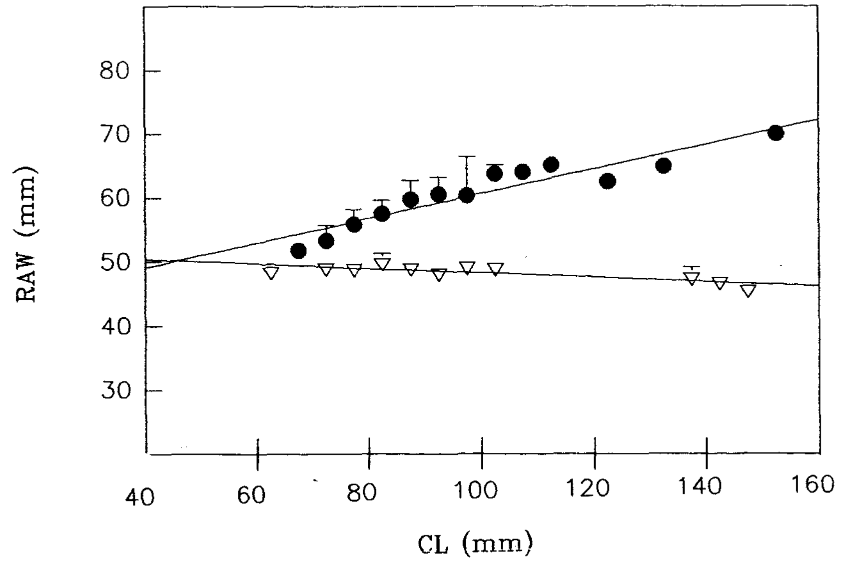


Fig. 4.13 Abdomen width (mm) plotted against CL (mm) with linear regression line for Dale females, 1989

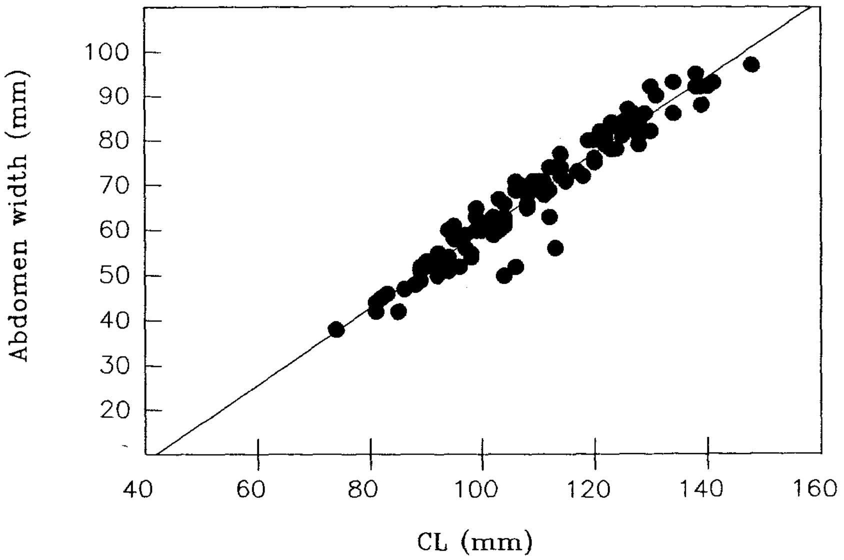


Fig. 4.14 Abdomen width (mm) plotted against CL (mm) with linear regression line for Dale males and females, 1989

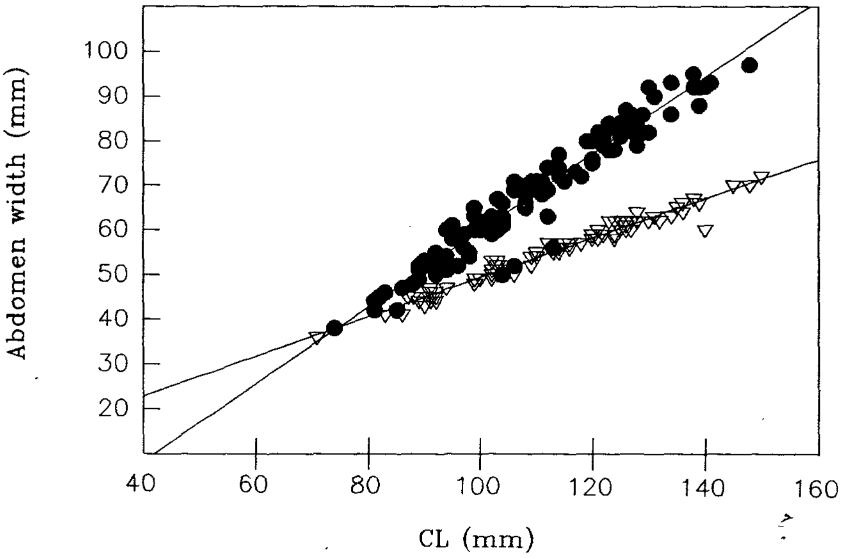


Fig. 4.15 Abdomen width (mm) plotted against CL (5 mm groups) with linear regression line for Dale males and females, 1989

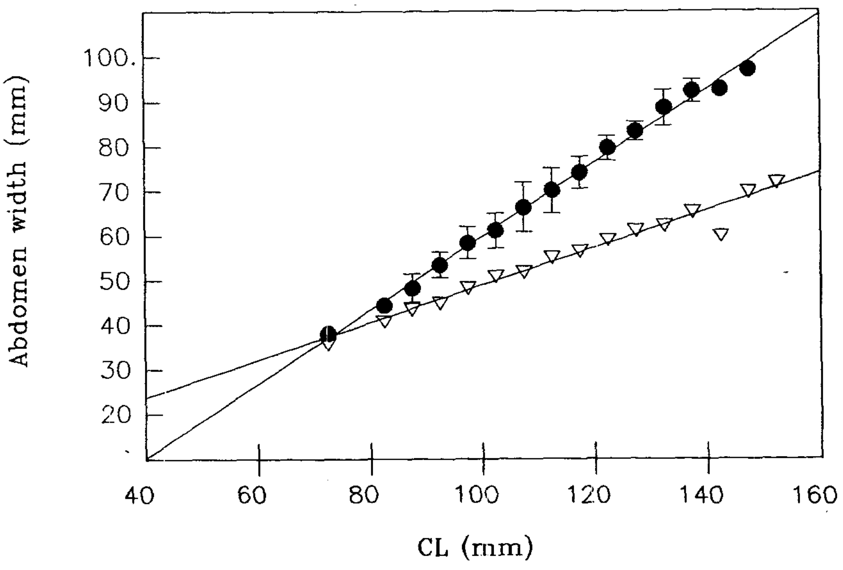


Fig. 4.16 Relative abdomen width (mm) plotted against CL (mm) with linear regression line for Dale females, 1989

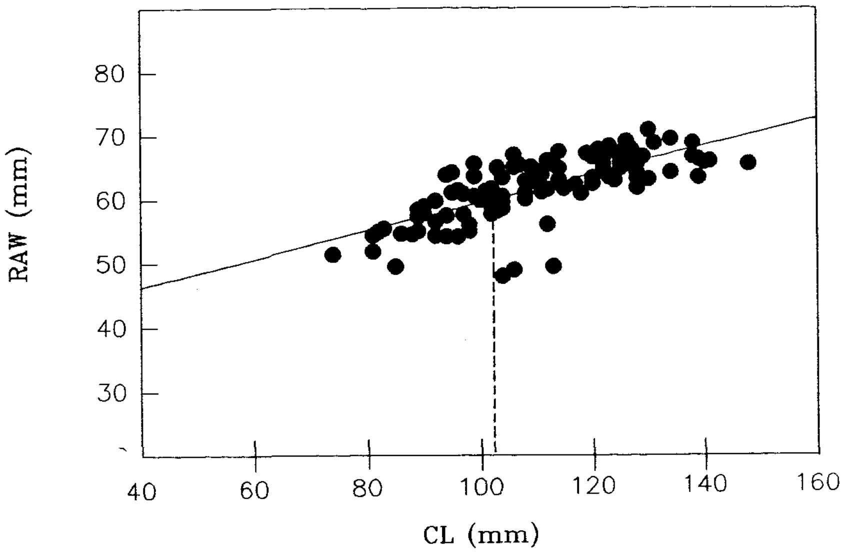


Fig. 4.17 Relative abdomen width (mm) plotted against CL (mm) with linear regression line for Dale males and females, 1989

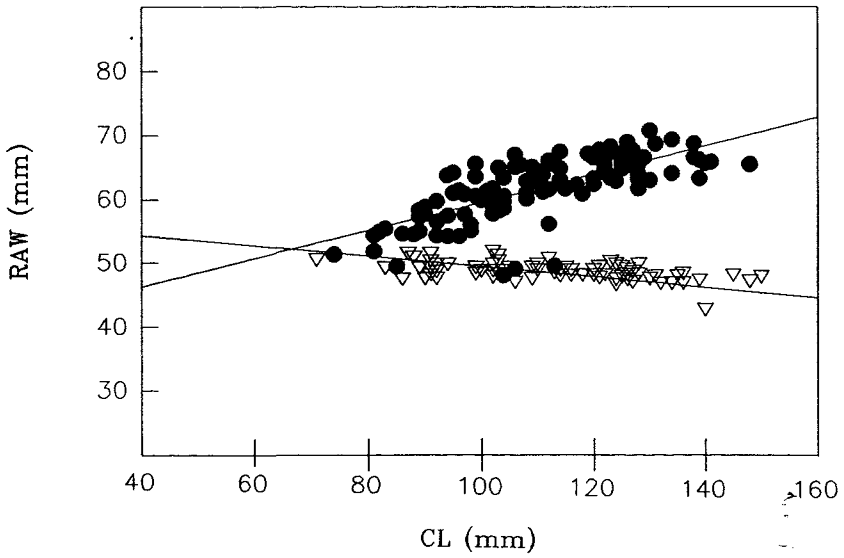


Fig. 4.18 Relative abdomen width (mm) plotted against CL (5 mm groups) with linear regression line for Dale males and females, 1989

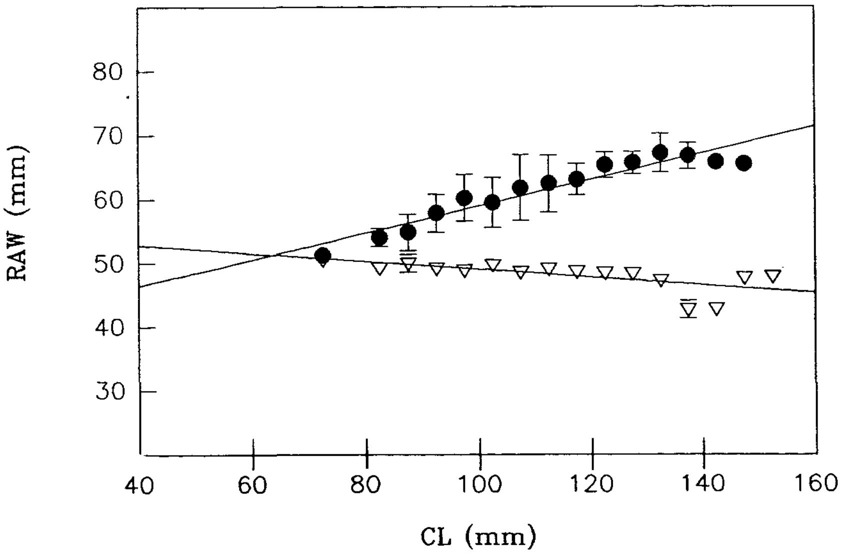


Fig. 4.19 Abdomen width (mm) plotted against CL (mm) with linear regression line for Selsey females, 1989

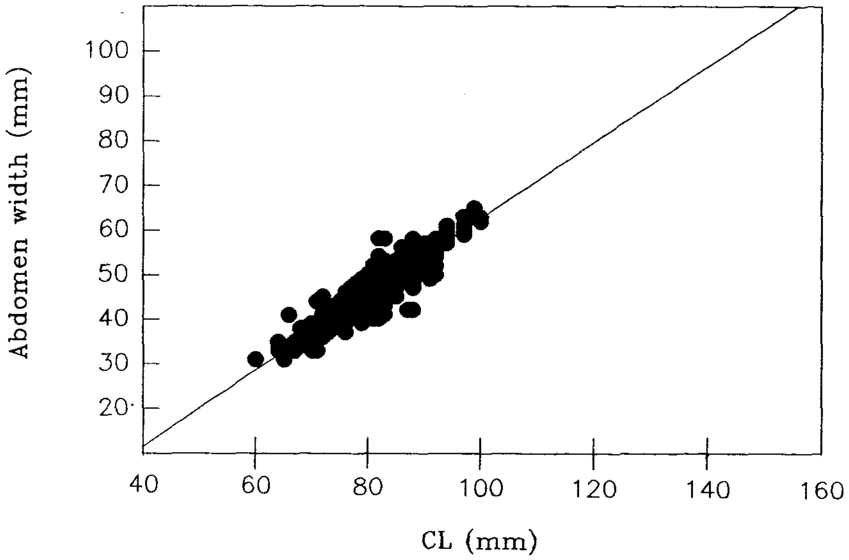


Fig. 4.20 Abdomen width (mm) plotted against CL (mm) with linear regression line for Selsey males and females, 1989

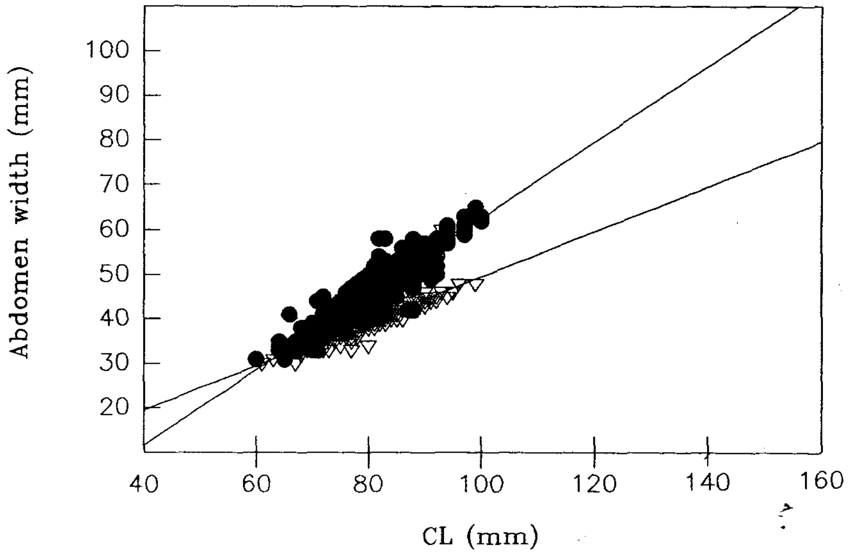


Fig. 4.21 Abdomen width (mm) plotted against CL (5 mm groups) with linear regression line for Selsey males and females, 1989

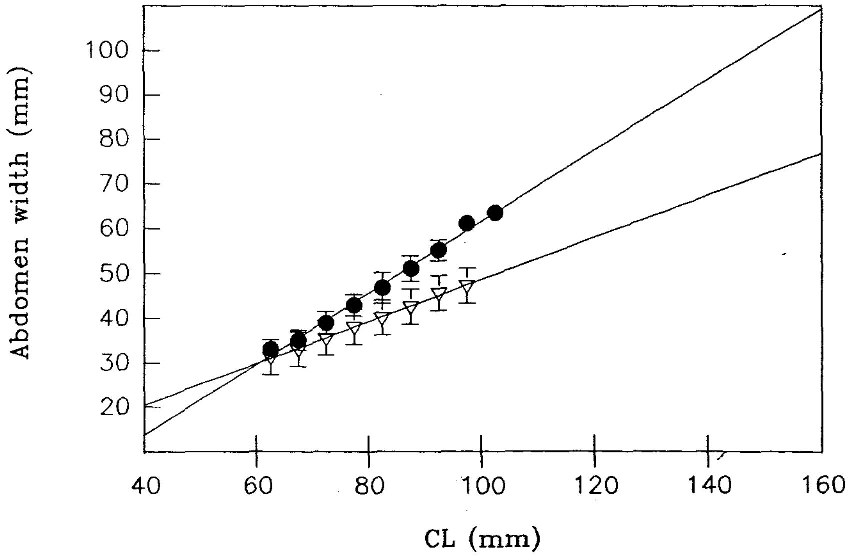


Fig. 4.22 Relative abdomen width (mm) plotted against CL (mm) with linear regression line for Selsey females, 1989

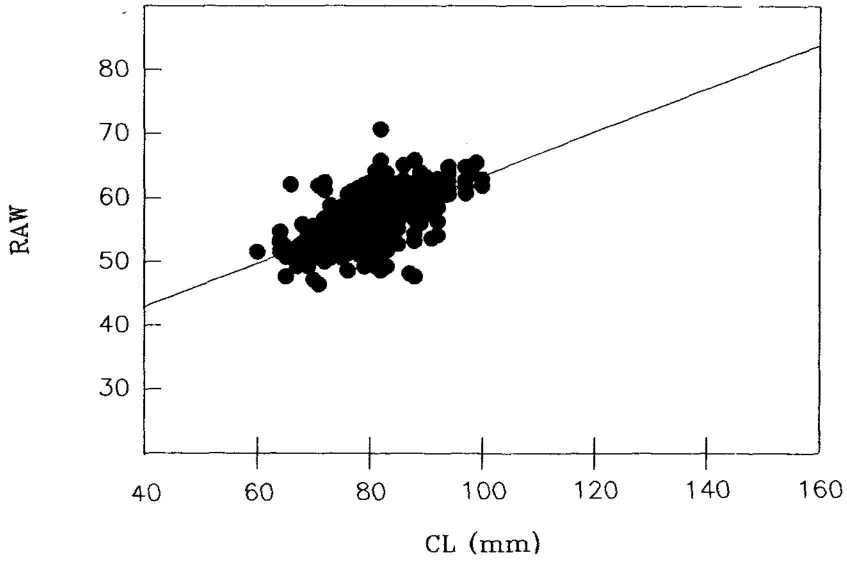


Fig. 4.23 Relative abdomen width (mm) plotted against CL (mm) with linear regression line for Selsey males and females, 1989

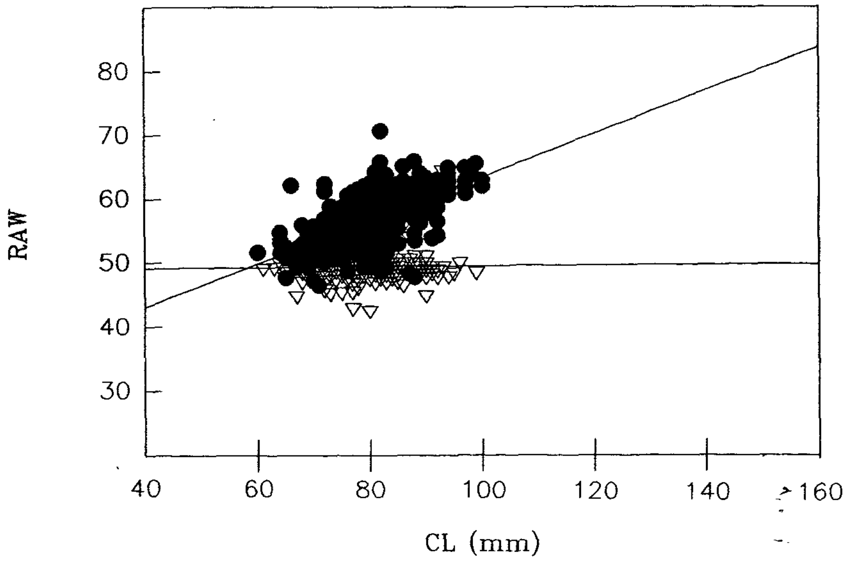


Fig. 4.24 Relative abdomen width (mm) plotted against CL (5 mm groups) with linear regression line for Selsey males and females, 1989

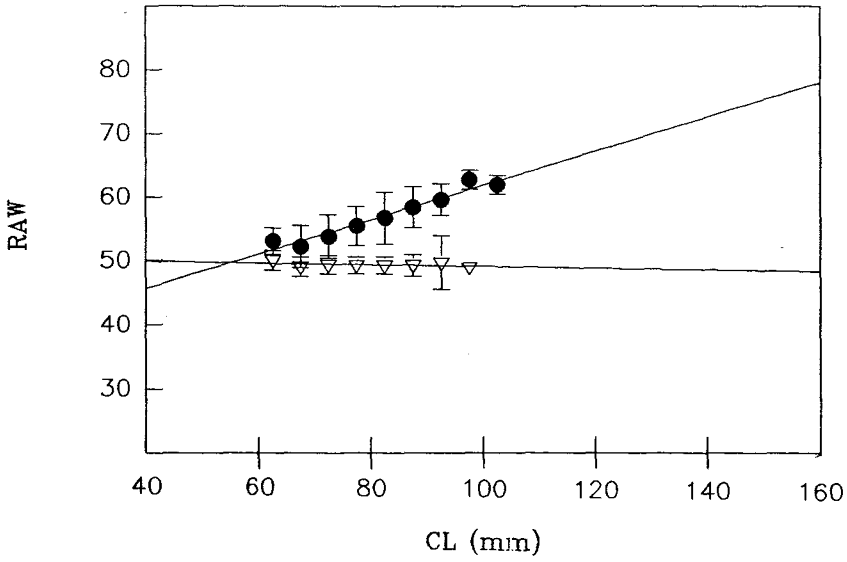


Fig. 4.25 Abdomen width (mm) plotted against CL (mm) with linear regression line for Selsey females, 1990

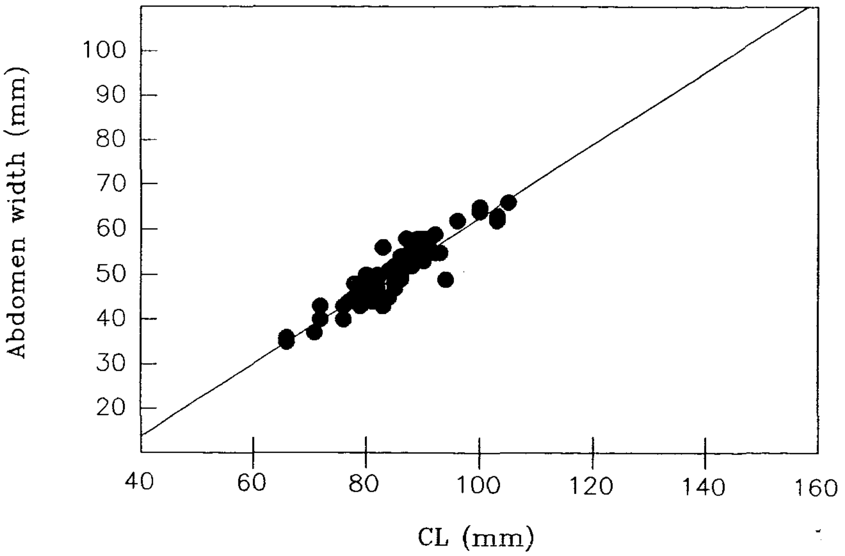


Fig. 4.26 Abdomen width (mm) plotted against CL (mm) with linear regression line for Selsey males and females, 1990

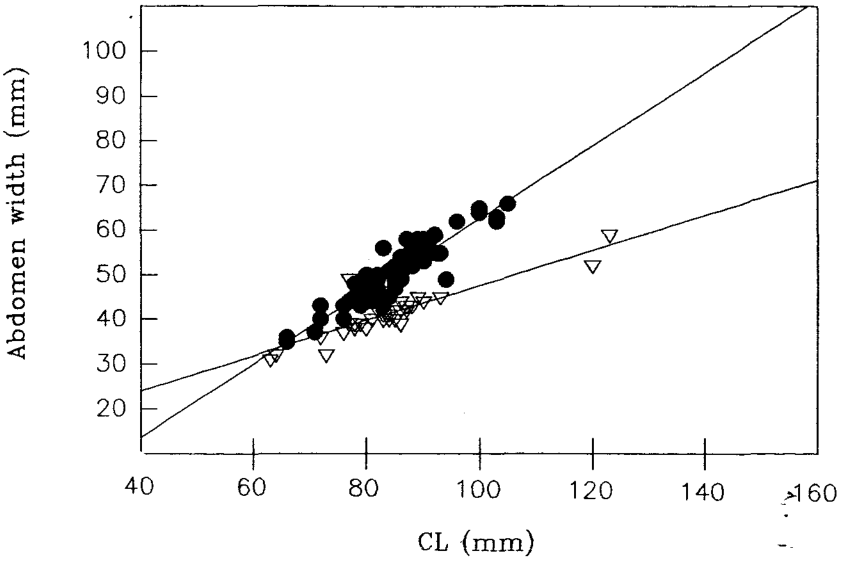


Fig. 4.27 Abdomen width (mm) plotted against CL (5 mm groups) with linear regression line for Selsey males and females, 1990

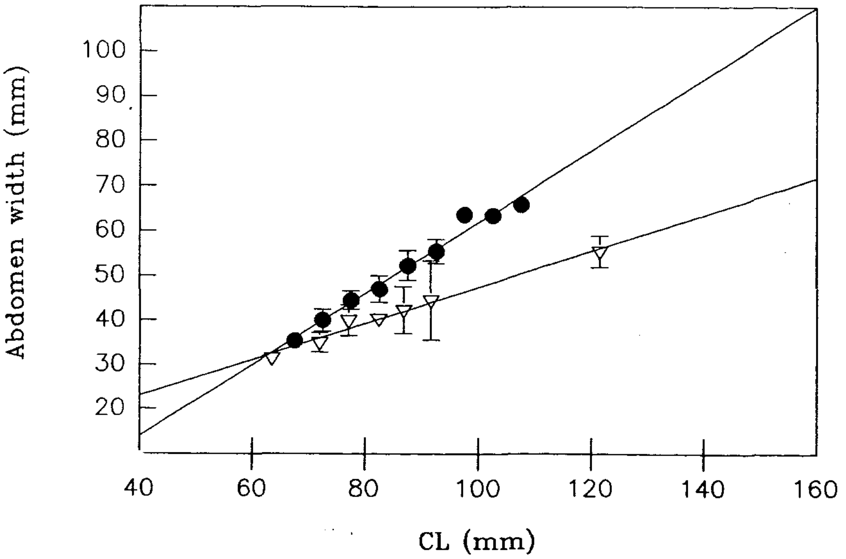


Fig. 4.28 Relative abdomen width (mm) plotted against CL (mm) with linear regression line for Selsey females, 1990

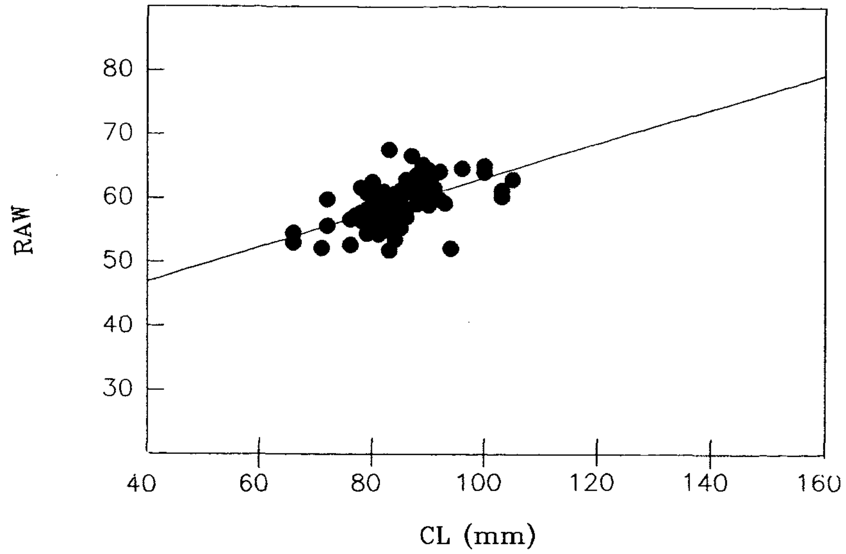


Fig. 4.29 Relative abdomen width (mm) plotted against CL (mm) with linear regression line for Selsey males and females, 1990

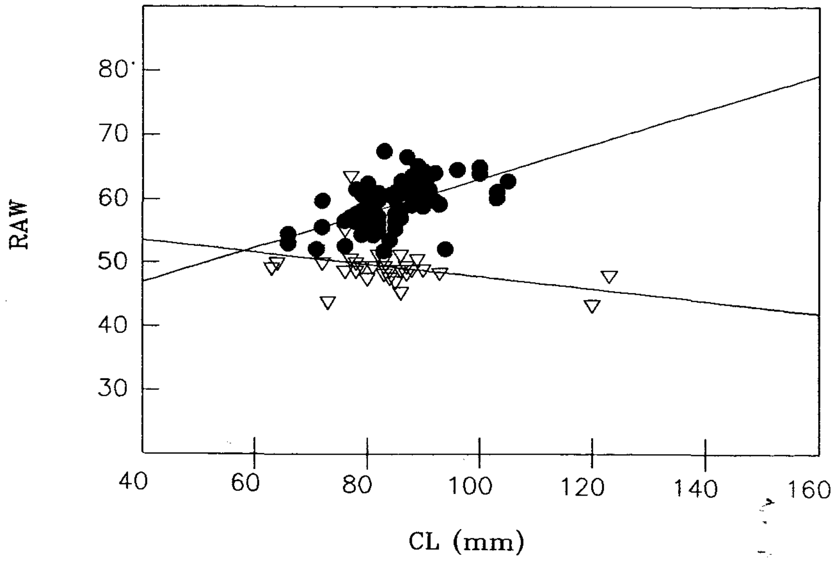


Fig. 4.30 Relative abdomen width (mm) plotted against CL (5 mm groups) with linear regression line for Selsey males and females, 1990

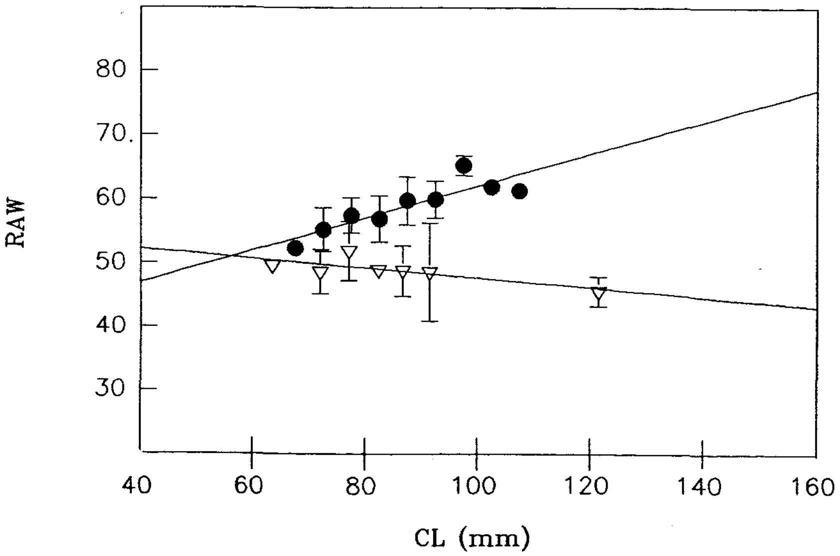


Fig. 4.31 Abdomen width (mm) plotted against CL (mm) with linear regression line for Whitby females, 1973

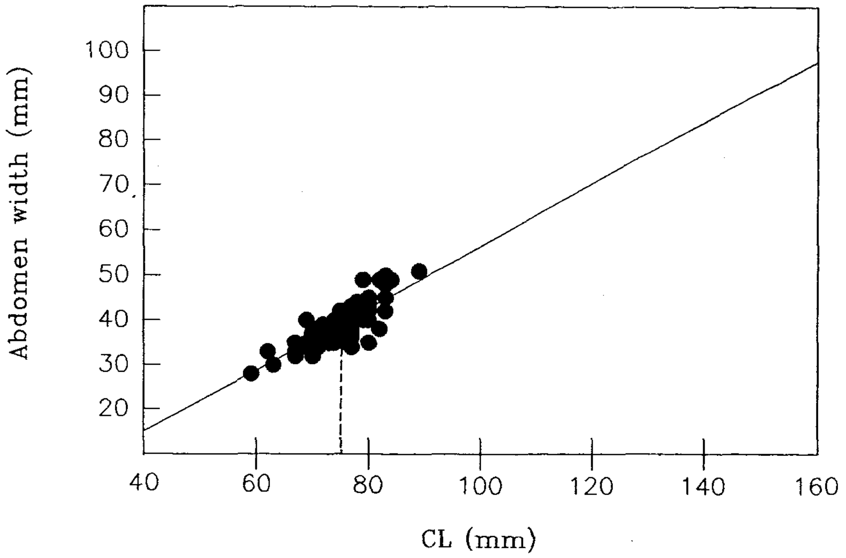


Fig. 4.32 Abdomen width (mm) plotted against CL (mm) with linear regression line for Whitby males and females, 1973

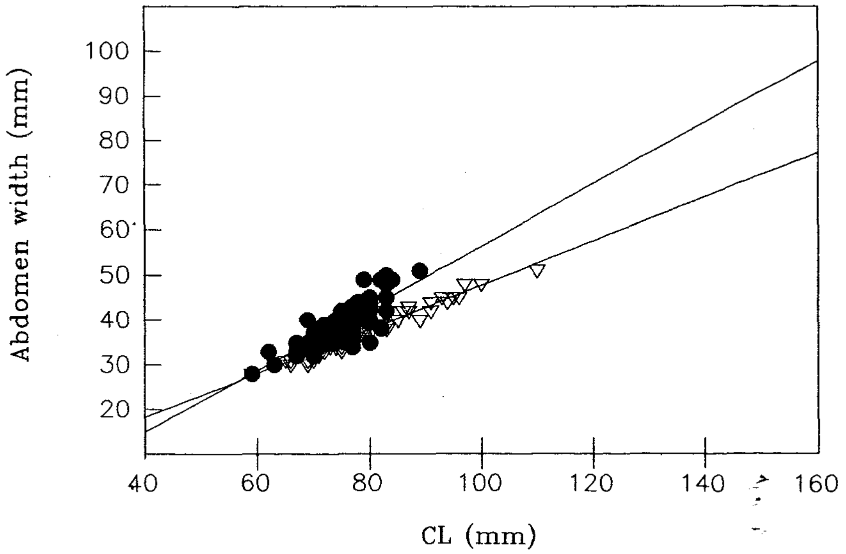


Fig. 4.33 Abdomen width (mm) plotted against CL (5 mm groups) with linear regression line for Whitby males and females, 1973

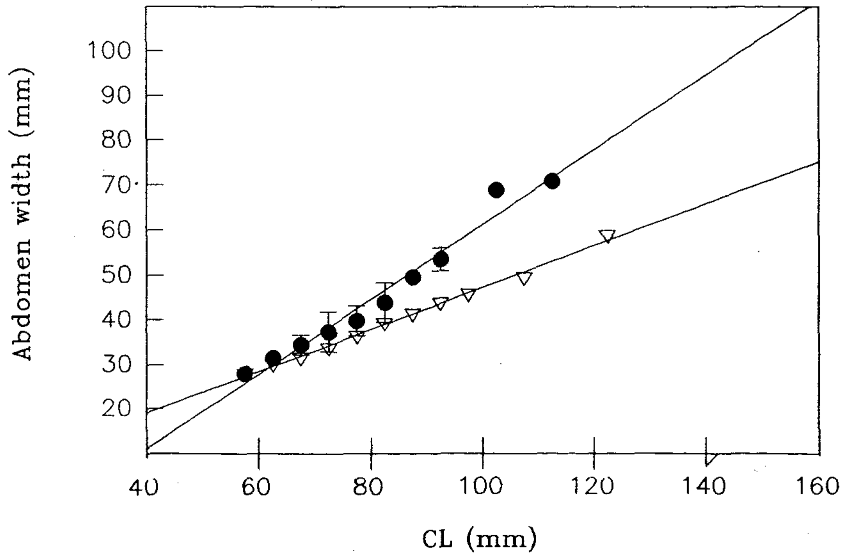


Fig. 4.34 Relative abdomen width (mm) plotted against CL (mm) with linear regression line for Whitby females, 1973

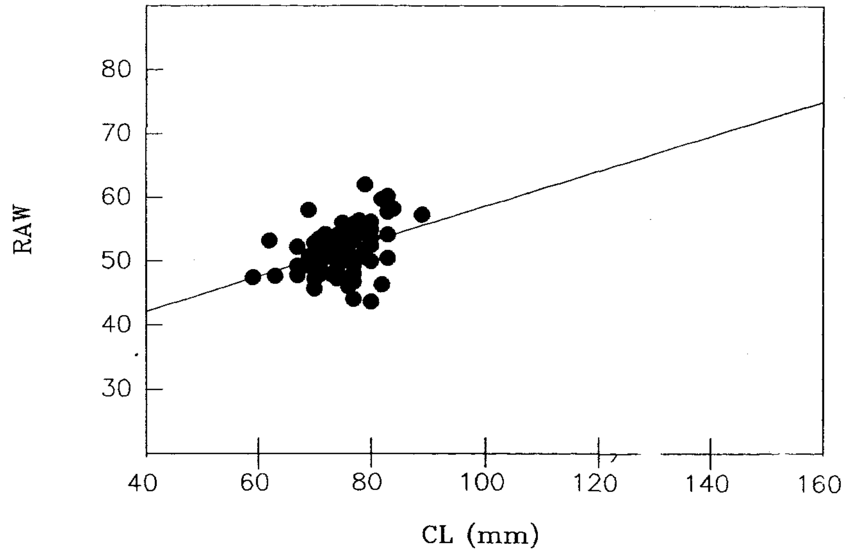


Fig. 4.35 Relative abdomen width (mm) plotted against CL (mm) with linear regression line for Whitby males and females, 1973

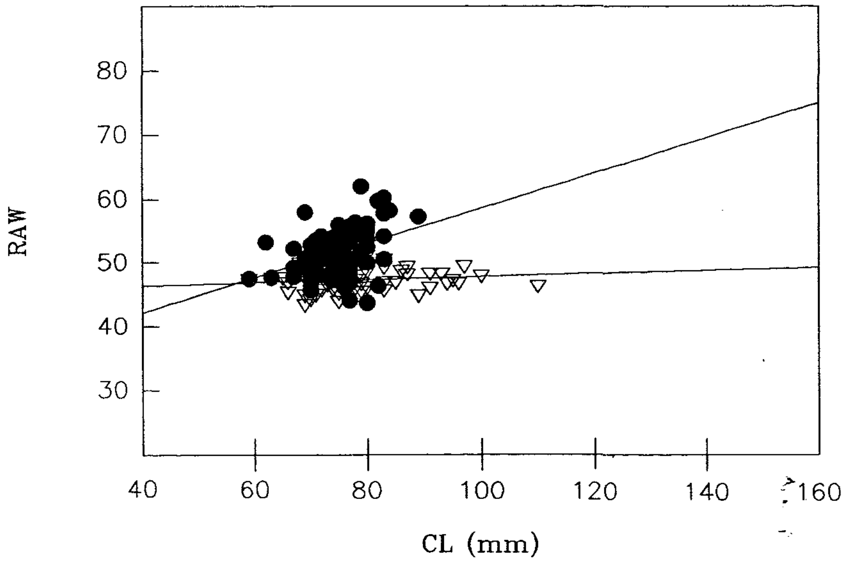


Fig. 4.36 Relative abdomen width (mm) plotted against CL (5 mm groups) with linear regression line for Whitby males and females, 1973

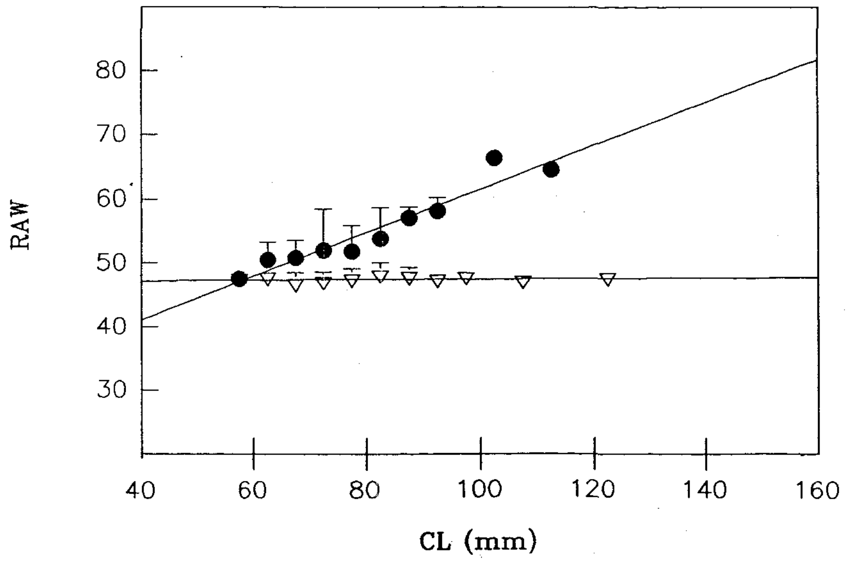


Fig. 4.37 Abdomen width (mm) plotted against CL (mm) with linear regression line for Staithes females 1980 to 1981

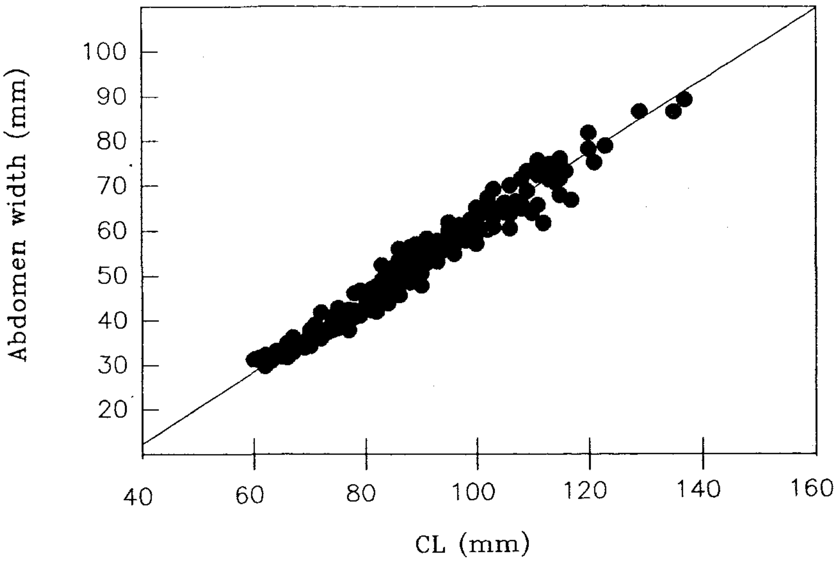


Fig. 4.38 Abdomen width (mm) plotted against CL (5 mm groups) with linear regression line for Staithes females 1980 to 1981

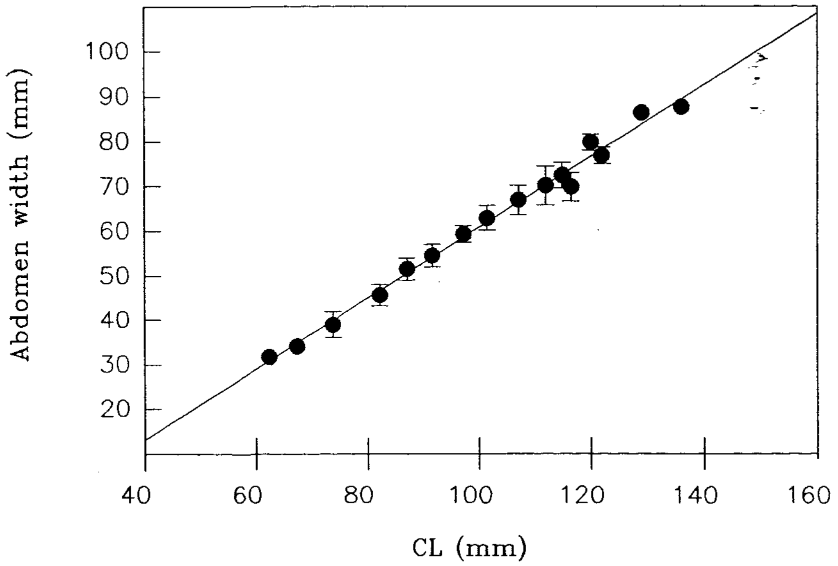


Fig. 4.39 Relative abdomen width (mm) plotted against CL (mm) with linear regression line for Staithes females 1980 to 1981

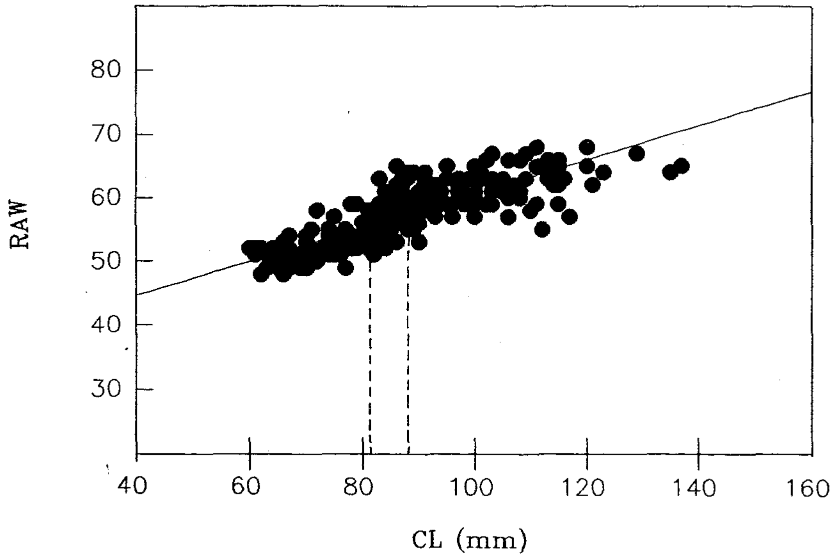


Fig. 4.40 Relative abdomen width (mm) plotted against CL (5 mm groups) with linear regression line for Staithes females 1980 to 1981

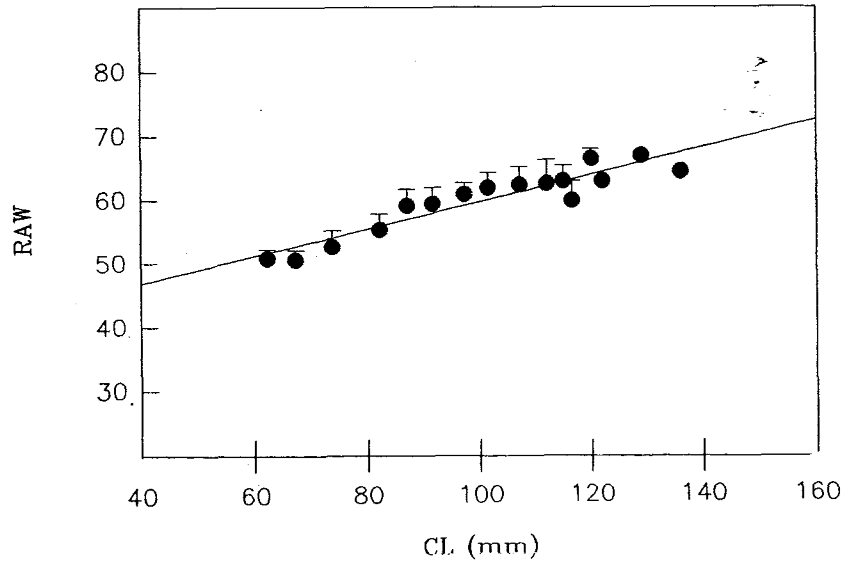


Fig. 4.41 Abdomen width (mm) plotted against CL (mm) with linear regression line for Pembrokeshire females, 1973

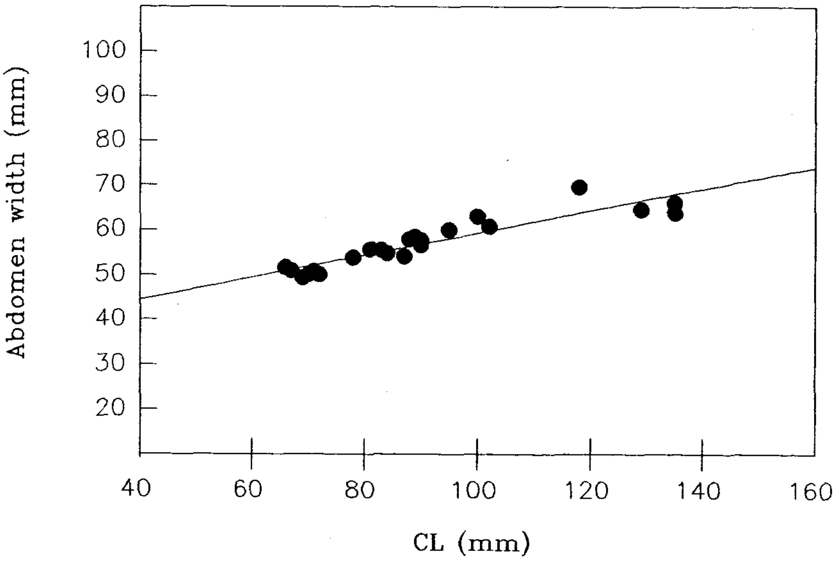


Fig. 4.42 Abdomen width (mm) plotted against CL (mm) with linear regression line for Pembrokeshire males and females, 1973

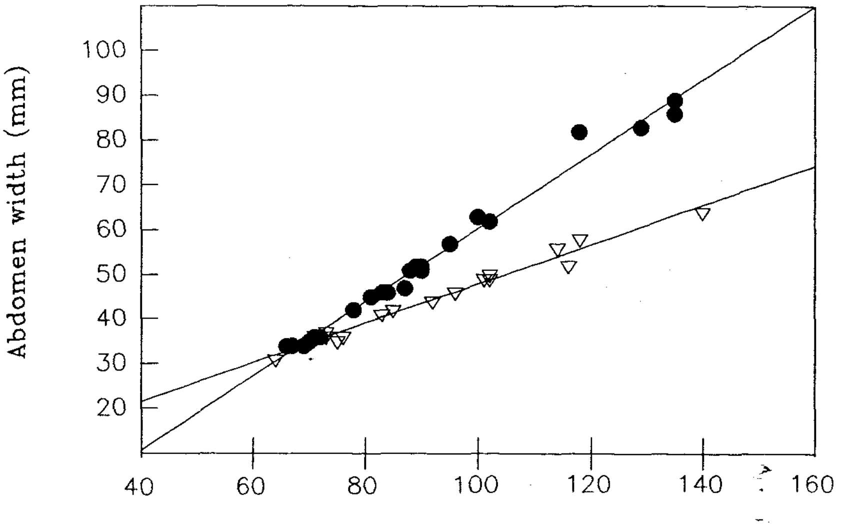


Fig. 4.43 Abdomen width (mm) plotted against CL (5 mm groups) with linear regression line for Pembrokeshire males and females, 1973

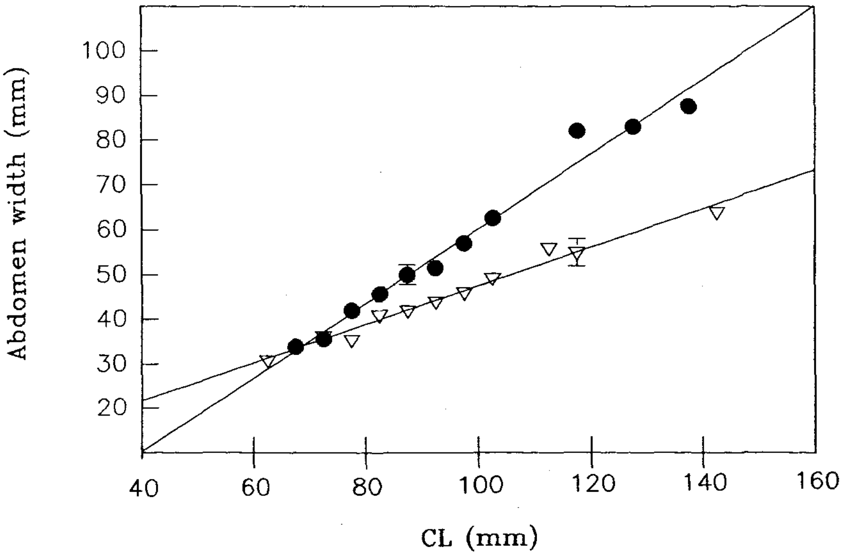


Fig. 4.44 Relative abdomen width (mm) plotted against CL (mm) with linear regression line for Pembrokeshire females, 1973

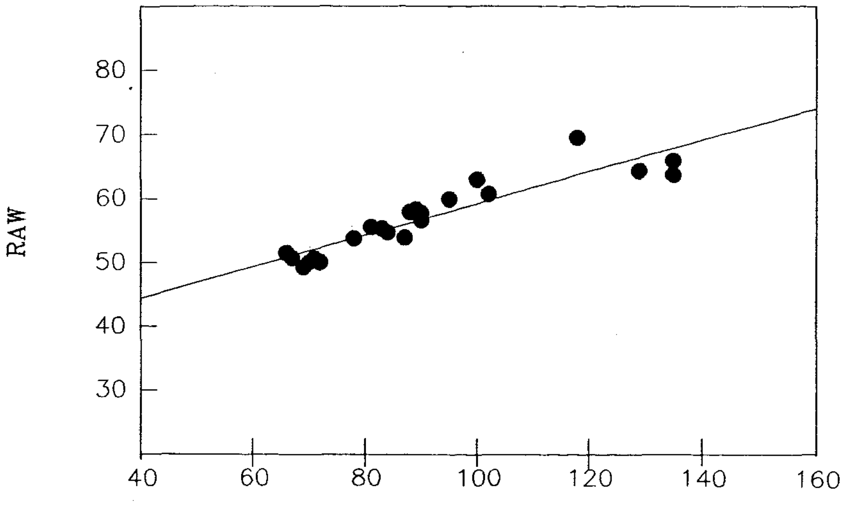


Fig. 4.45 Relative abdomen width (mm) plotted against CL (mm) with linear regression line for Pembrokeshire males and females, 1973

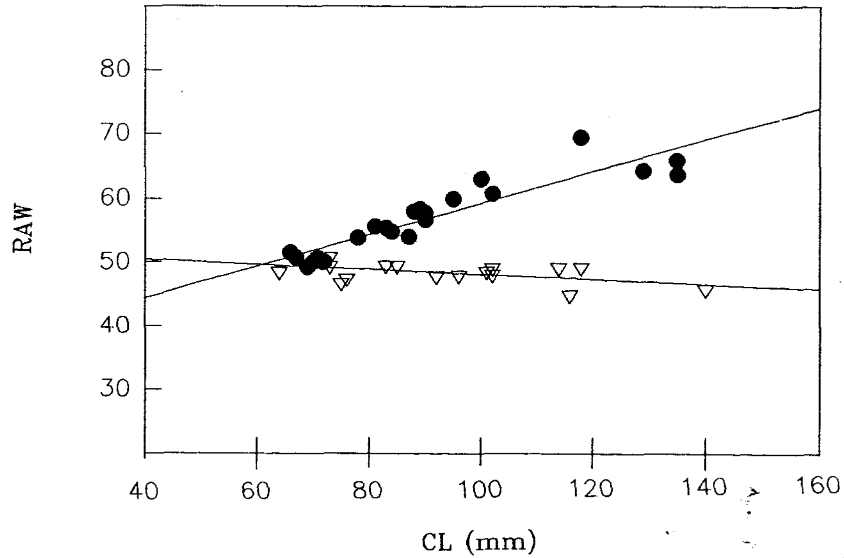


Fig. 4.46 Relative abdomen width (mm) plotted against CL (5 mm groups) with linear regression line for Pembrokeshire males and females, 1973

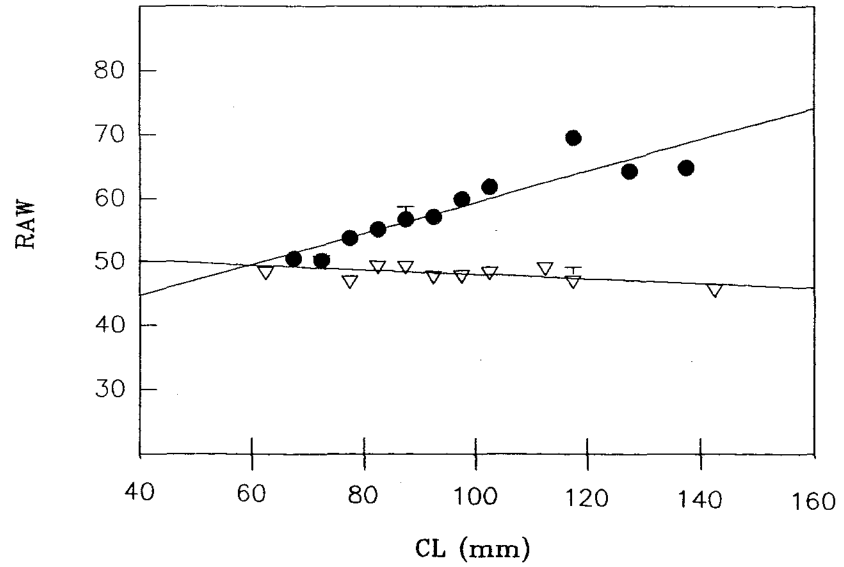


Fig. 4.47 Abdomen width (mm) plotted against CL (mm) with linear regression line for St. Davids females 1980 to 1981

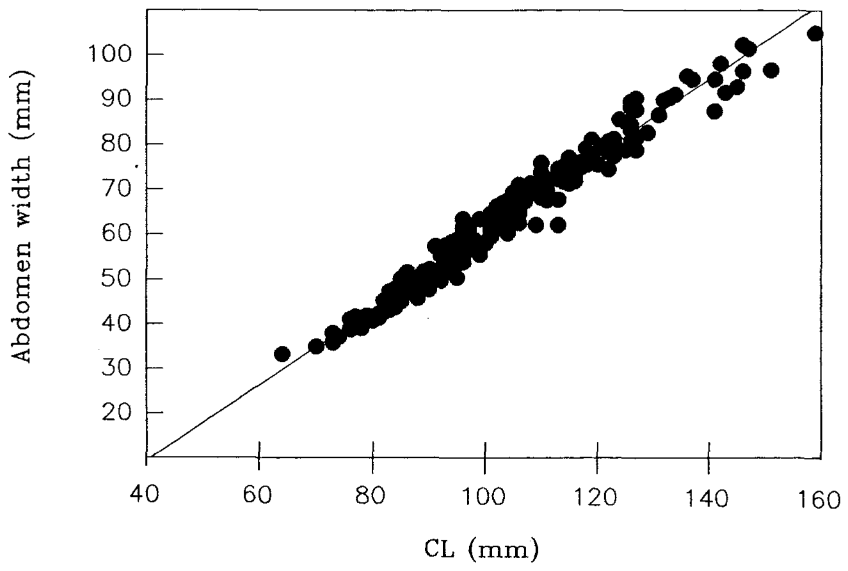


Fig. 4.48 Abdomen width (mm) plotted against CL (5 mm groups) with linear regression line for St. Davids females 1980 to 1981

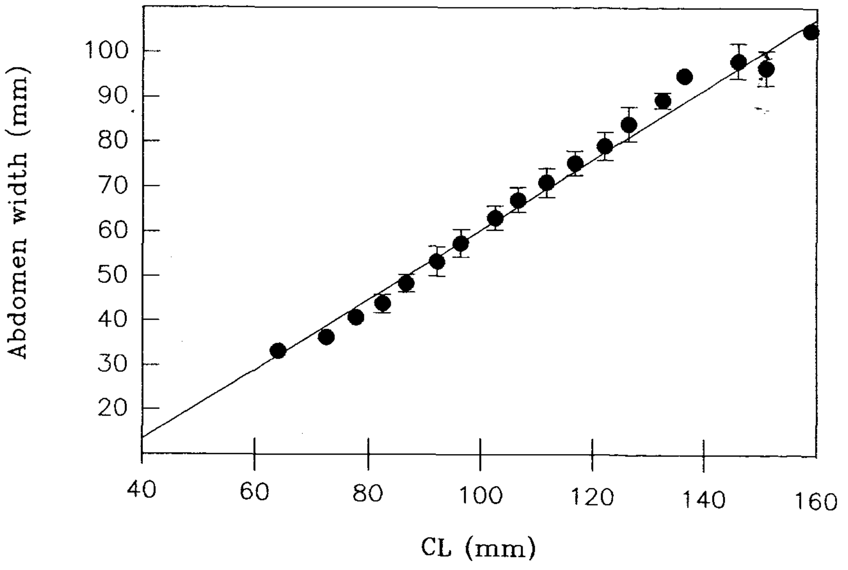


Fig. 4.49 Relative abdomen width (mm) plotted against CL (mm) with linear regression line for St. Davids females 1980 to 1981

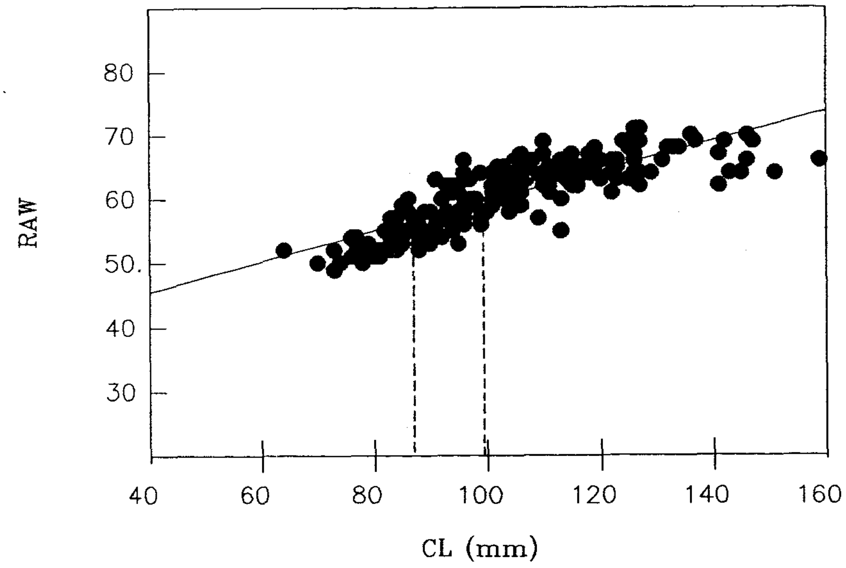


Fig. 4.50 Relative abdomen width (mm) plotted against CL (5 mm groups) with linear regression line for St. Davids females 1980 to 1981

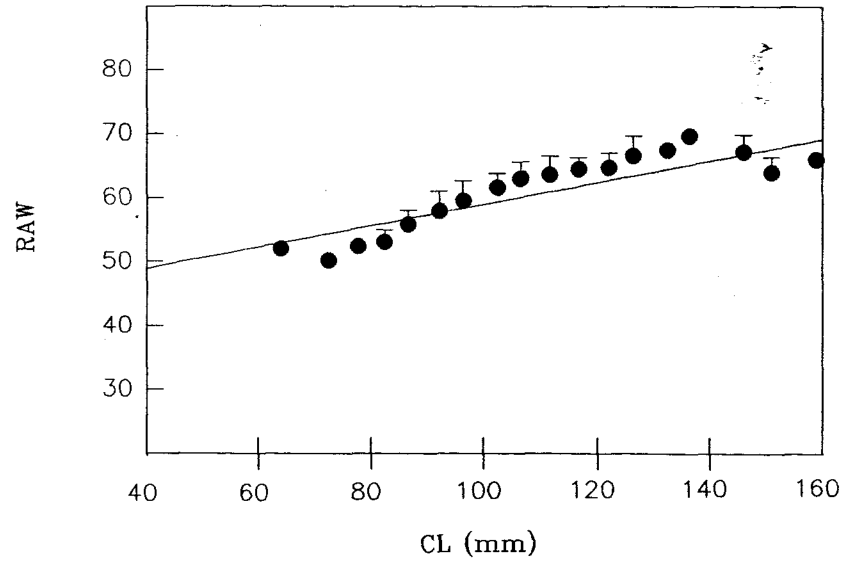


Fig. 4.51 Abdomen width (mm) plotted against CL (mm) with linear regression line for Selsey females, 1973

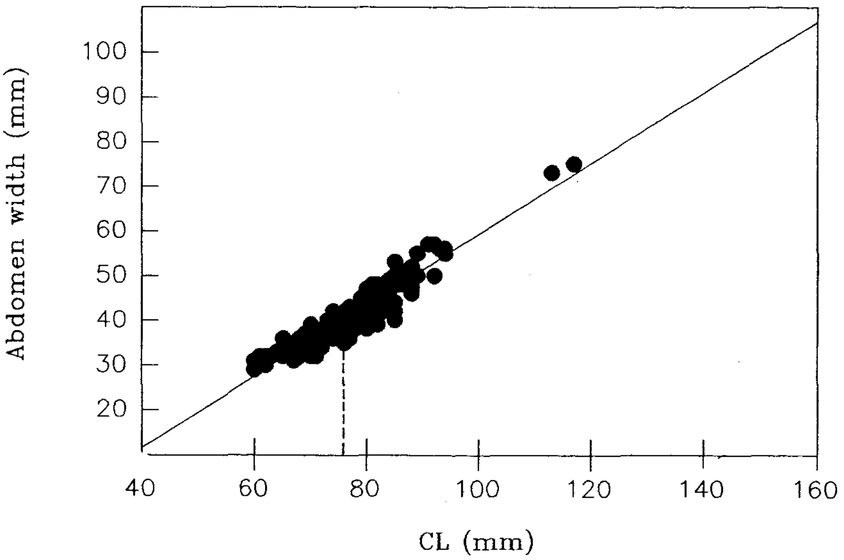


Fig. 4.52 Abdomen width (mm) plotted against CL (mm) with linear regression line for Selsey males and females, 1973

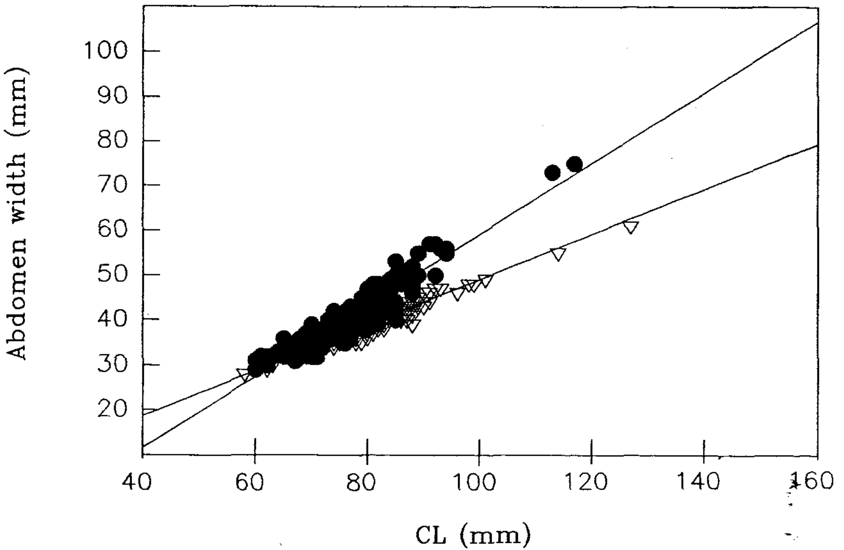


Fig. 4.53 Abdomen width (mm) plotted against CL (5 mm groups) with linear regression line for Selsey males and females, 1973

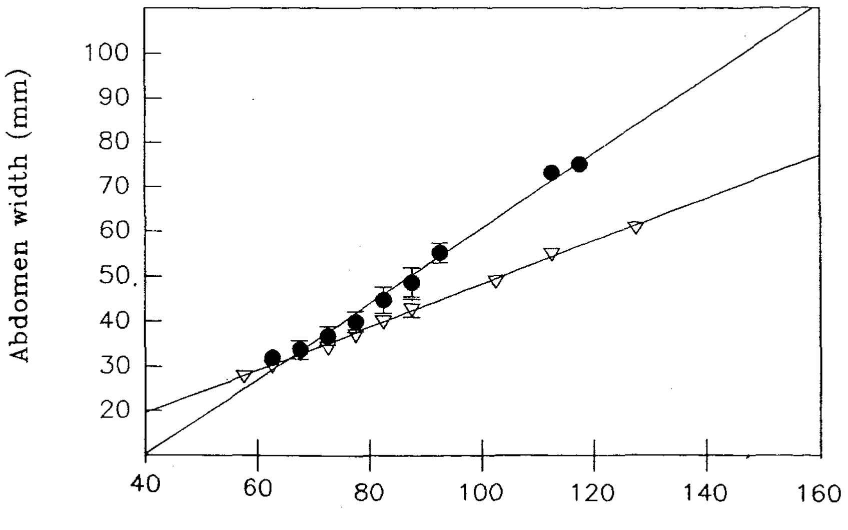


Fig. 4.54 Relative abdomen width (mm) plotted against CL (mm) with linear regression line for Selsey females, 1973

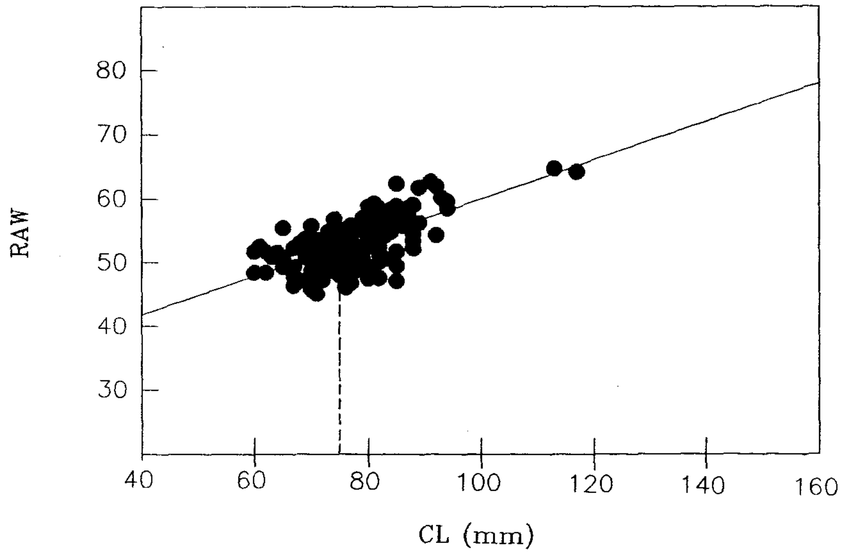


Fig. 4.55 Relative abdomen width (mm) plotted against CL (mm) with linear regression line for Selsey males and females, 1973

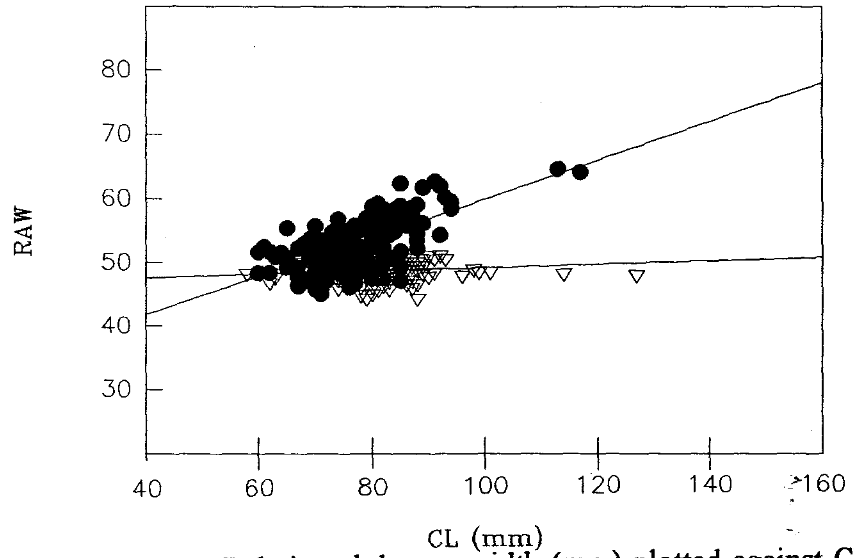
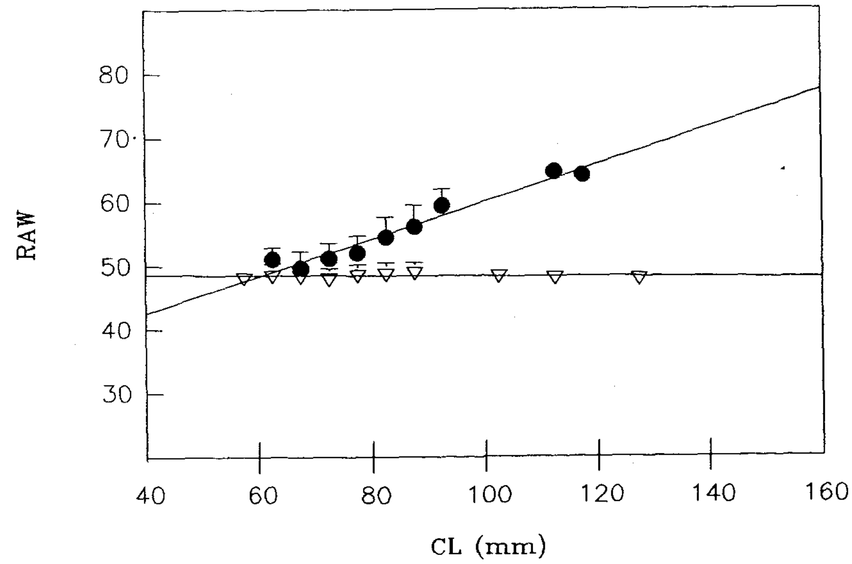


Fig. 4.56 Relative abdomen width (mm) plotted against CL (5 mm groups) with linear regression line for Selsey males and females, 1973



aggregated around the suggested intersection points. Plots of RAW against CL do suggest between-sex differences in RAW-CL, especially at larger lobster sizes (Figs. 4.5, 4.11, 4.17, 4.23, 4.29, 4.35, 4.45, 4.55). Between-year differences in RAW-CL relationships were shown for both females and males at Bridlington (1989 and 1990), Selsey (1989 and 1990) (Appendix Tables A4ii.44, A4ii.46, A4ii.54, A4ii.56), and for between-years/between-sexes at Bridlington and Selsey (Appendix Tables A4ii.52 and A4ii.62). Between-site (and year) differences for Welsh RAW-CL (Pembrokeshire 1973, St. Davids 1980 and Dale 1989) suggested a significant difference for females but not for males (Appendix Tables A4ii.76 and A4ii.78). Selsey 1973, 1989 and 1990 male and female data, and Yorkshire 1973, 1980, 1989 and 1990 female data, did not indicate significant yearly variation in RAW-CL, (c.f. Yorkshire males) (Appendix Tables A4ii.72, A4ii.74, A4ii.80, and A4ii.82). 1989 and 1990 data (Bridlington, Dale and Selsey) suggested significant differences between-years, but not between-sites for females and both between-site and between-year differences for male lobsters (Appendix Tables A4ii. 84 and A4ii.86). 1973 and 1980 (Whitby, Pembrokeshire, Selsey, Staithes and St.Davids) RAW-CL relationships did not exhibit significant differences between sites (Appendix Tables A4ii.88 and A4ii.90).

Berried females

The percentages of females berried (Figs. 4.57 to 4.4.69) (Appendix Tables A4iii.1 and A4iii.2) do not always increase by size class (e.g. Bridlington 1989; 97.5 mm CL 36.11%, 102.5 mm CL 0%); this is most probably a result of the small sample sizes of larger females. The first maturity sizes of females (smallest observed ovigerous lobsters), vary between 76 mm CL (Selsey, 1989) and 95 mm CL (Dale) (Appendix Table A4iiii.3) Using the assumption of females becoming berried every other year, 50 % maturity (i.e. 25 % observed) varies between 78 mm CL (Selsey, 1989) and 132 mm CL (Pembrokeshire, 1972), (103 mm CL, Dale 1989) (Appendix Table A4iii.4). 100 % maturity (i.e. 50 % observed), occurs between 97 mm CL (Bridlington 1990) and 131 mm CL (Selsey 1972). 66.67 % observed maturity (100 % of females breeding twice in three years) was calculated at between 100 mm CL (Bridlington 1991 and Selsey 1989) and 136 mm CL (Yorkshire 1973) but could not be determined for Dale 1989, Yorkshire 1974, Proportion of females berried, Bridlington 1989

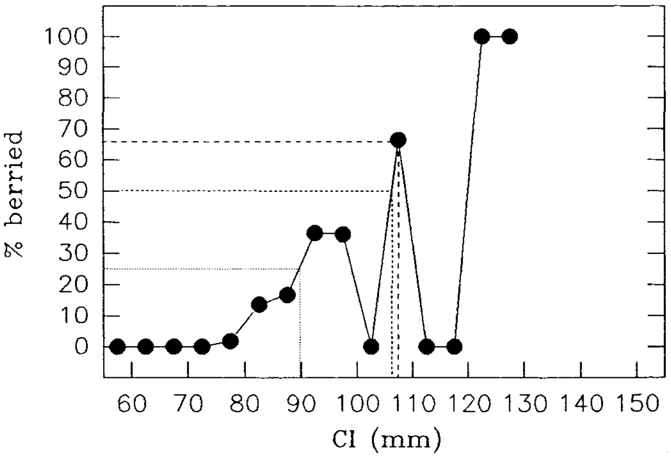


Fig.4.57

Proportion of females berried, Bridlington 1990

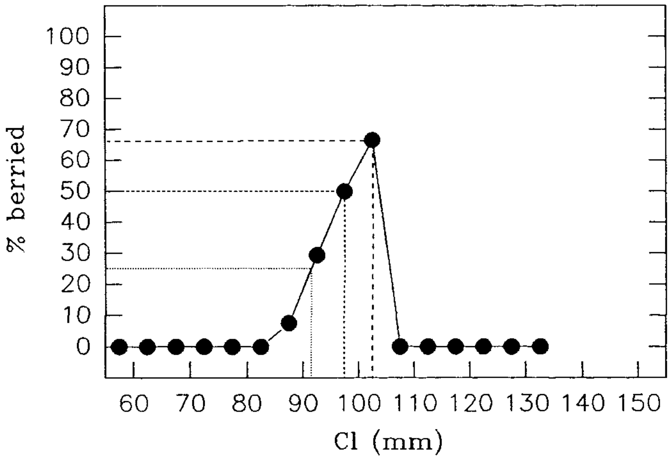


Fig.4.58

Proportion of females berried, Bridlington 1991

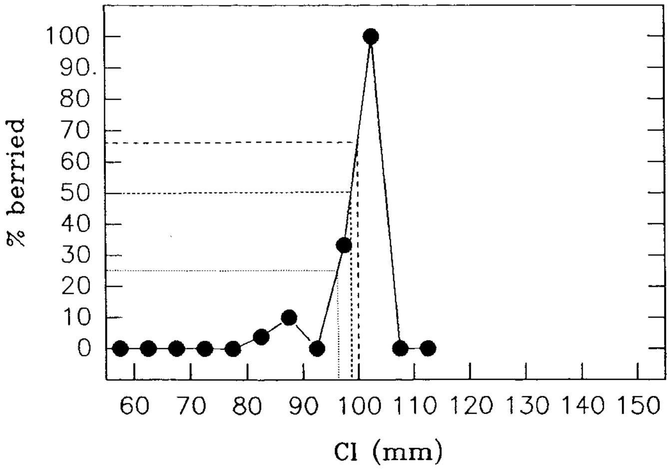
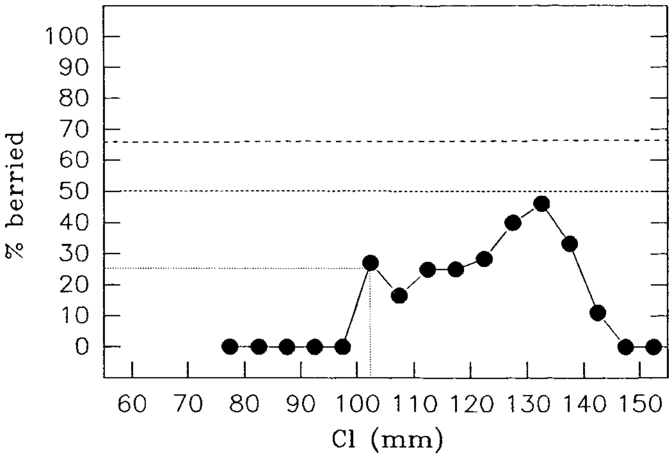
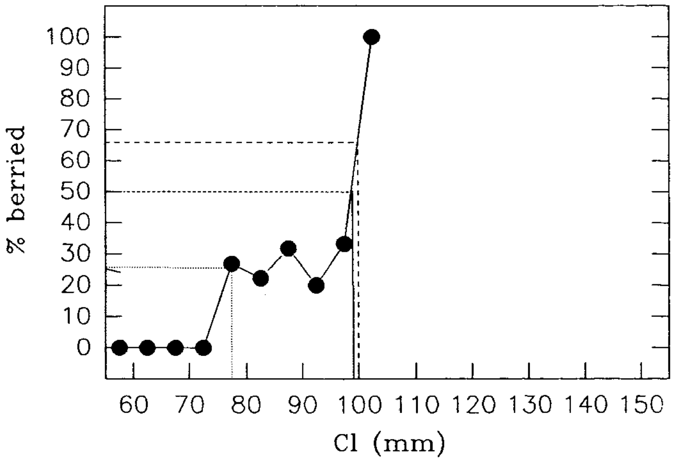


Fig.4.59



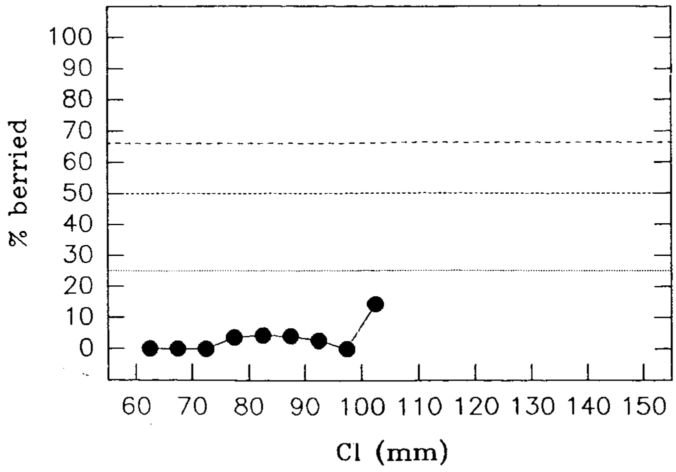
Proportion of females berried, Dale 1989

Fig.4.60



Proportion of females berried, Selsey 1989

Fig.4.61



Proportion of females berried, Selsey 1990

Fig.4.62

Proportion of females berried, Yorkshire 1972

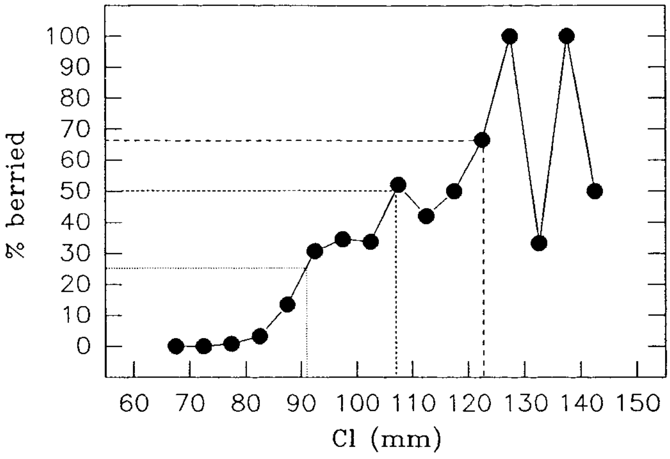


Fig.4.63

Proportion of females berried, Yorkshire 1973

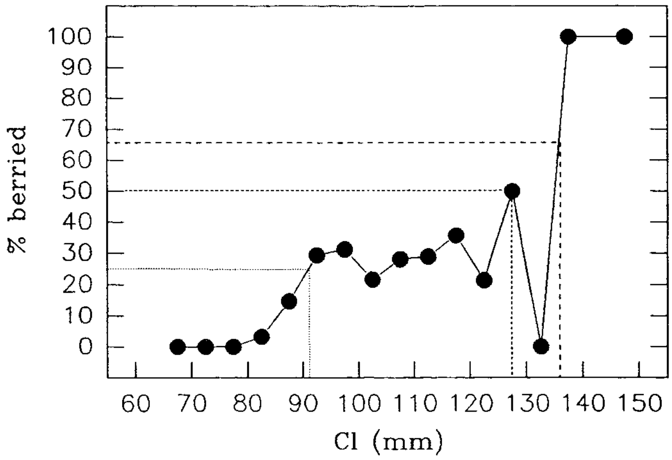


Fig.4.64

Proportion of females berried, Yorkshire 1974.

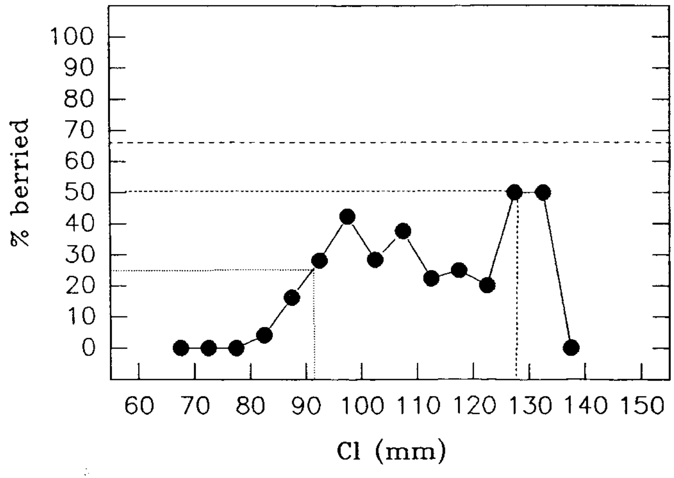


Fig.4.65

Proportion of females berried, Pembrokeshire 1972

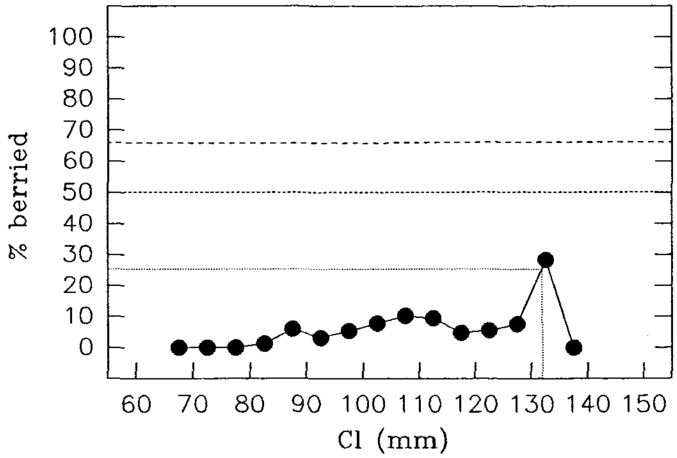


Fig.4.66

Proportion of females berried, Pembrokeshire 1973

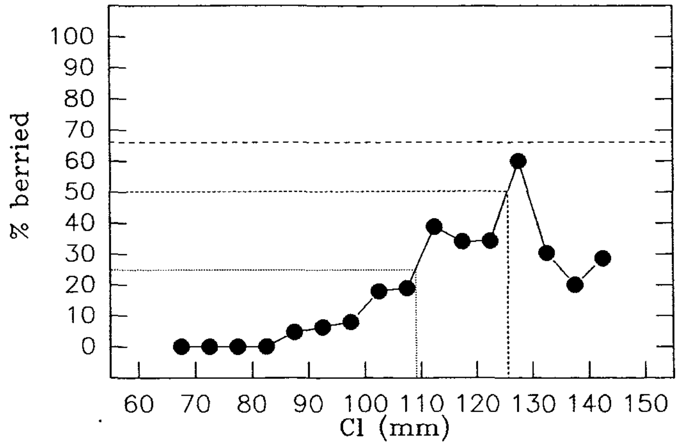


Fig.4.67

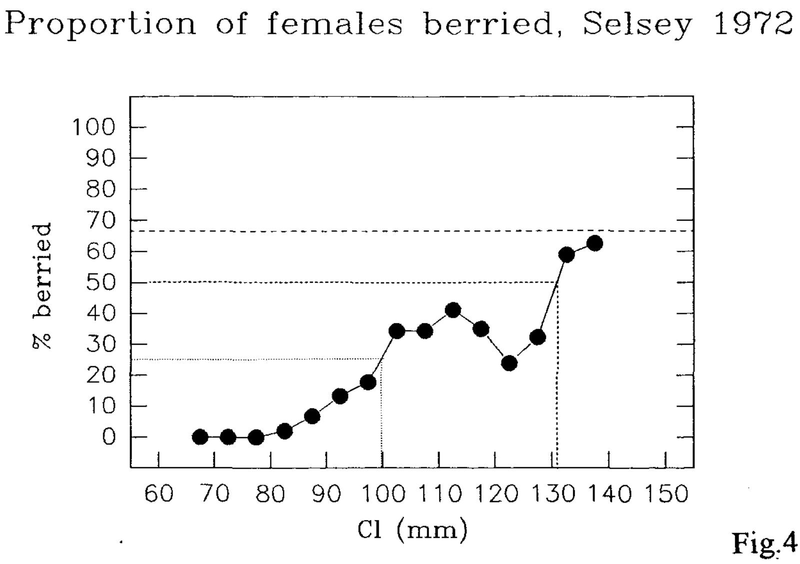


Fig.4.68

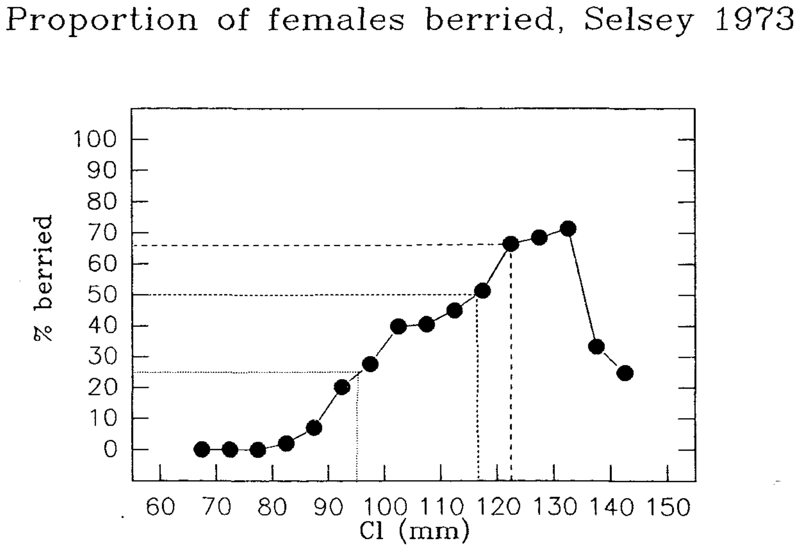


Fig.4.69

Pembrokeshire 1972 and 1973, nor Selsey 1972.

ANCOVAs between-years at Bridlington 1989 to 1991, Selsey 1989 and 1990, Yorkshire 1972 to 1974, Pembrokeshire 1972 and 1973, and Selsey 1972 and 1973 each indicate significant between-year differences in the relationship between SOM and CL (Appendix Tables A4iii.5 to A4iii.9). All-Yorkshire, all-Wales and all-Selsey data (1972 to 1991) also indicate between-year differences (Appendix Tables A4iii.10 to A4iii.12). Significant between-year and between-site and between-site/between-year differences are shown in Appendix Tables A4iii.13 and A4iii.14. Appendix Table A4iii.15 suggests that between-years differences in berry-CL relationships (significant difference) are more important than between-site differences (not significant).

Cement gland development

Cement gland development was shown to increase with ovary stage and is also incremental with Ovf (ovary factor) and ROW (relative ovary weight) (Chapter 3). Both linear and polynomial regression analyses indicate a weak correlation between CG stage and CL and a small probability of the independent variable (CL) being adequate in predicting the suggested dependent variable (CG stage), although CG stage does increase with female CL (Figs. 4.70 and 4.71). A significant difference in the covariation between the two variables can also be seen from the results of ANCOVA, as well as some between-site variation in the CG stage/CL relationships (Appendix Table A4iv.3).

Additional results

Ovigerous setae were observed on all Bridlington and Selsey females in 1990 and 1991 (no Bridlington, Dale or Selsey 1989 females were examined for this maturity criteria), except for one female of 73 mm CL from Bridlington (17/09/1990).

No Dale 1989 females were observed with green abdomens (an indication of female specific hormone). One Bridlington female (28/06/1989; 90 mm CL) and nine Selsey females (09/08/1989; 80, 80, 85, 88 mm CL: 07/09/1989; 82, 85, 87, 93 mm CL: 07/11/1990; 85 mm CL) exhibited green abdomens. The Bridlington lobster, and Selsey specimens from 09/08/1989 were dissected and shown to have ovaries of stages 5 or 6; no other individuals were seen with green abdomens.

Cement gland development stage plotted against CL (mm), Bridlington 1989 to 1991

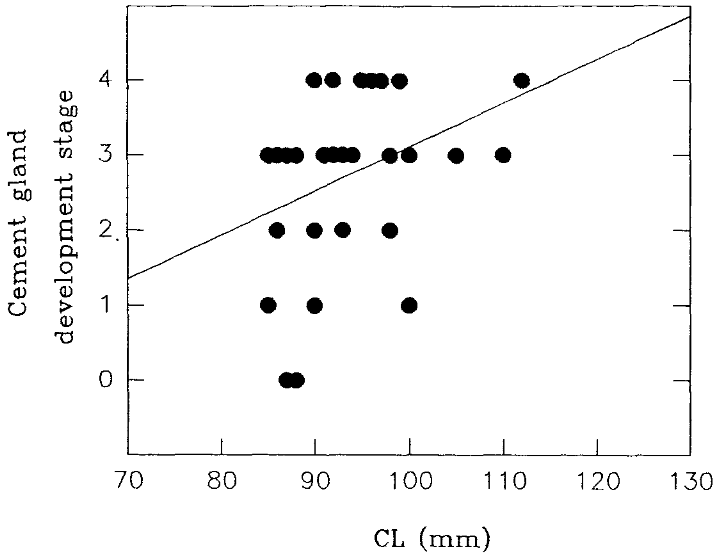


Fig. 4.70

Cement gland development stage plotted against CL (mm), Selsey 1989 to 1991

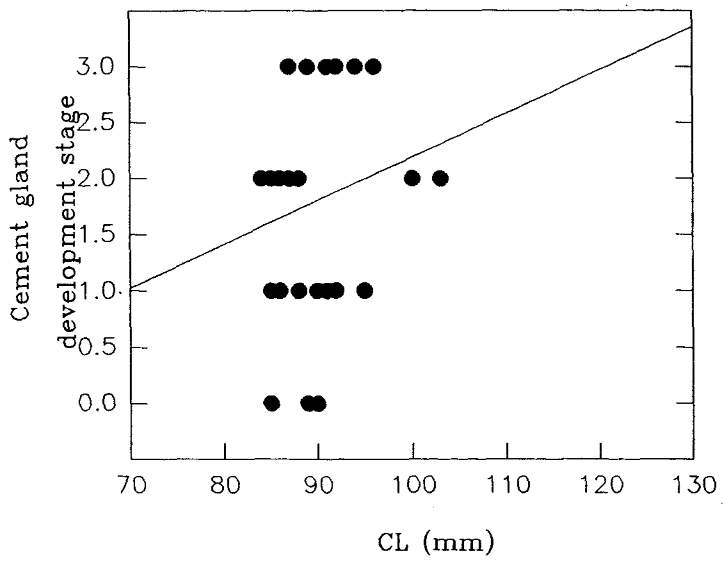


Fig.4.71

4.3.2. Internal indicators of maturity

Ovarian indicators of maturity and carapace length

Ovary wet weight, ovary factor and relative ovary weight each increase with female CL (Appendix Tables A3vi.1, Figs. 4.72 to 4.74). Figs. 4.72 to 4.74 show an increase in divergence of each of these maturity indicators with increase in female size (and therefore ovary maturity). Regression analyses results suggest a weak second order polynomial relationship between the two variables (Ovary wet weight $R^2 = 0.363$ to 0.691 c.f. 0.362 to 0.668 linear model; ROW $R^2 = 0.125$ to 0.337 c.f. 0.043 to 0.29 linear model; Ovf $R^2 = 0.159$ to 0.287 c.f. 0.046 to 0.229 linear model) (Appendix Tables A4v.1 to A4v.6), although this is best indicated by Bridlington and Selsey data-sets, rather than that for Dale, almost certainly as a result of differences in sample sizes from each of the respective sites (Bridlington, 101; Dale, 25; Selsey, 150). ANCOVAs assessing potential between-site differences in ovary maturity indicators with CL, show significant differences between-sites for all three factors with CL, being greatest for ovary weight/CL (Appendix Tables A4v.7 to A4v.9). Ovf for 5 mm CL groups of females, can be seen to increase with CL, and have greater standard deviations at larger sizes (Appendix Tables A4vi.1 to A4vi.3, Figs. 4.85, 4.87 and 4.89). ANCOVA between-sites indicates a significant difference in Ovf/CL relationships at Bridlington,. Dale and Selsey (Appendix Table A4vi.8).

Upper and lower point limit lines, drawn by eye on Figs. 4.72 to 4.74, may suggest size at onset of ovary development. One datum-point from each of the Bridlington data-sets was discounted as an outlier (possibly as a result of an erroneous recording of an ovary wet weight measurement). Ovary wet-weight/CL limit lines imply onset of ovarian development at 78 mm, 83 mm and 74 mm CL at Bridlington, Dale and Selsey respectively. Ovary factor/CL lines equally intimate that ovarian maturation begins at 75 mm CL at Bridlington, 79 mm at Dale and 73 mm at Selsey. Relative ovary weight/CL lines suggest onset of ovary development at 77 mm, 79 mm and 74 mm CL for each respective site (Bridlington, Dale and Selsey).

Hepatopancreas wet weight and RHW with CL

Hepatopancreas wet weight (HW) increases with female size (Figs 4.75 to

4.77) at all three sites. However, relative hepatopancreas weight (RHW) can be seen to decrease with female size at Selsey (c.f. Bridlington and Dale). This may be caused by the weak correlation between RHW and CL (linear regression model R^2, 0.001 to 0.012; polynomial regression model R^2, 0.009 to 0.016), compared with that for hepatopancreas weight and CL (linear regression model R^2, 0.723 to 0.897; polynomial regression model R^2, 0.0.737 to 0.0.959) (Appendix Tables A4v.10 to Av.13). ANCOVA also suggested no covariance between RHW and CL (as well as significant differences between sites) (Appendix Table A4v.15). A small between-site difference was shown in HW/CL relationships using ANCOVA, although this may be partially a result of the small Dale sample size (Appendix Table A4v.14).

Ovarian indicators of maturity and abdomen width

Ovary stage, ovary weight, relative ovary weight (ROW) and ovary factor (Ovf) each increase with AW (Figs.4.78 to 4.80). Each of these ovary maturity factors become more variable with increasing AW, and this observed variability is suggested to indicate onset of ovarian development. Ovary wet weight/AW limit lines drawn by eye imply onset of ovary development at 41 mm AW (Bridlington), 47 mm AW (Dale) and 39 mm AW (Selsey). ROW/AW lines suggest ovary maturation commences at 42 mm AW, 47 mm AW and 40mm AW, and Ovf/AW lines suggest maturation to start at 42 mm AW, 45 mm AW and 39 mm AW for each of Bridlington, Dale and Selsey respectively. The results of linear and second order polynomial regressions indicate a polynomial relationship between each ovary maturity index and AW (Appendix Tables A4v.16 to A4v.23), the highest correlation being for ovary wet weight/AW (polynomial model R^2 0.571 to 0.841; linear model R^2 0.477 to 0.755). ANCOVA results give significant between-site differences for each factor covarying with AW (Appendix Tables A4v.24 to A4v.27), although care should be taken when analysing these results because of the small Dale sample size (N=9).

Ovarian indicators of maturity and relative abdomen width

Ovary stage, ovary weight, relative ovary weight (ROW) and ovary factor (Ovf) each increase with RAW (Figs.4.81 to 4.83). Increasing RAW is reflected by an increase in each of these maturity indexes, with a greater variability in ovary maturity factor for larger RAW values. No data-point limit lines were drawn by eye, because the scatter of points was not clearly delimited. Regression analysis results give evidence for each of ovary weight, ROW and Ovf having a weak linear relationship with RAW (R^2 0.306 to 0.7, 0.025 to 0.386 and 0.022 to 0.306 respectively), and for ovary stage to have a second order polynomial relationship with RAW (R^2 0.15 to 0.447) (Appendix Tables A4v.28 to A4v.35). The weak covariance between each ovary maturity indicator and RAW is highlighted by ANCOVA results, which give a high significance to the relationships, as well as significant between-site differences (Appendix Tables A4v.36 to Av.39).

Ovary development stage 4+ and 5+ as indicators of maturity

Three parameter logistic curves fitted to the percentages of females with ovaries of stages 4+ and 5+, and therefore considered mature, are shown plotted as Figs. 4.84, 4.86 and 4.88, with the coefficients presented as Appendix Tables Avi.4 and Avi.5. The logistic curves were forced to 100% (or > 98%) maturity as a maximum. Using the resultant equations, 4+ 50 % maturities occurred at 83 mm, 87 or 97 mm, and 80 mm CL for Bridlington, Dale (two points) and Selsey respectively. 5+ 50 % maturities occurred at 92 mm, 87 or 97 mm, and 90 mm CL for the three sites. ANCOVA results suggest significant between-site differences in ovary stage/CL relationships (Appendix Tables A4vi.6 and A4vi.7).

4.3.3. Size at onset of maturity

Tables 4.1 and 4.2 summarise estimates of sizes at sexual maturity calculated using both external and internal methods respectively. Using internal ovary indices with CL limit-lines, onset of ovary development is suggested to occur at between 75 and 78 mm CL (Bridlington), 79 and 83 mm CL (Dale) and 73 or 74 mm CL (Selsey). Ovary stage logistic curves also imply differences between 50 % maturity at each of the three sites. Ovaries of stage 4+ are present in 50 % of females at 83 mm, 87 or 97 mm and 80 mm CL, and those of 5+ at 92 mm, 87 or 97 mm and 90 mm CL for Bridlington, Dale and Selsey respectively. The most obvious indication of sexual maturity is the presence of eggs, which is apparent on 50 % of females of 90 to 97 mm CL at Bridlington, 103 mm CL at Dale and 78 mm CL at Selsey in 1989.

Female internal condition indices, Bridlington, 1989 to 1991

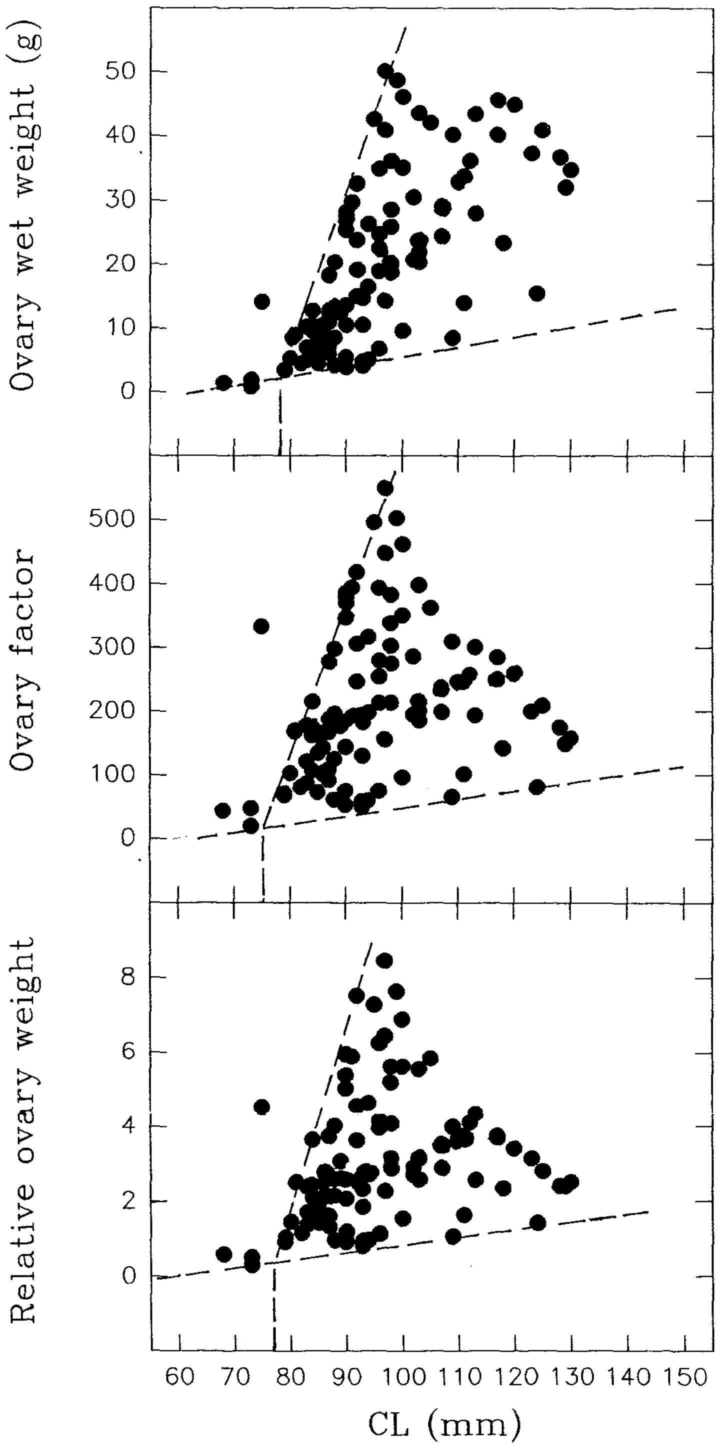


Fig.4.72

Female internal condition indices Dale, 1989

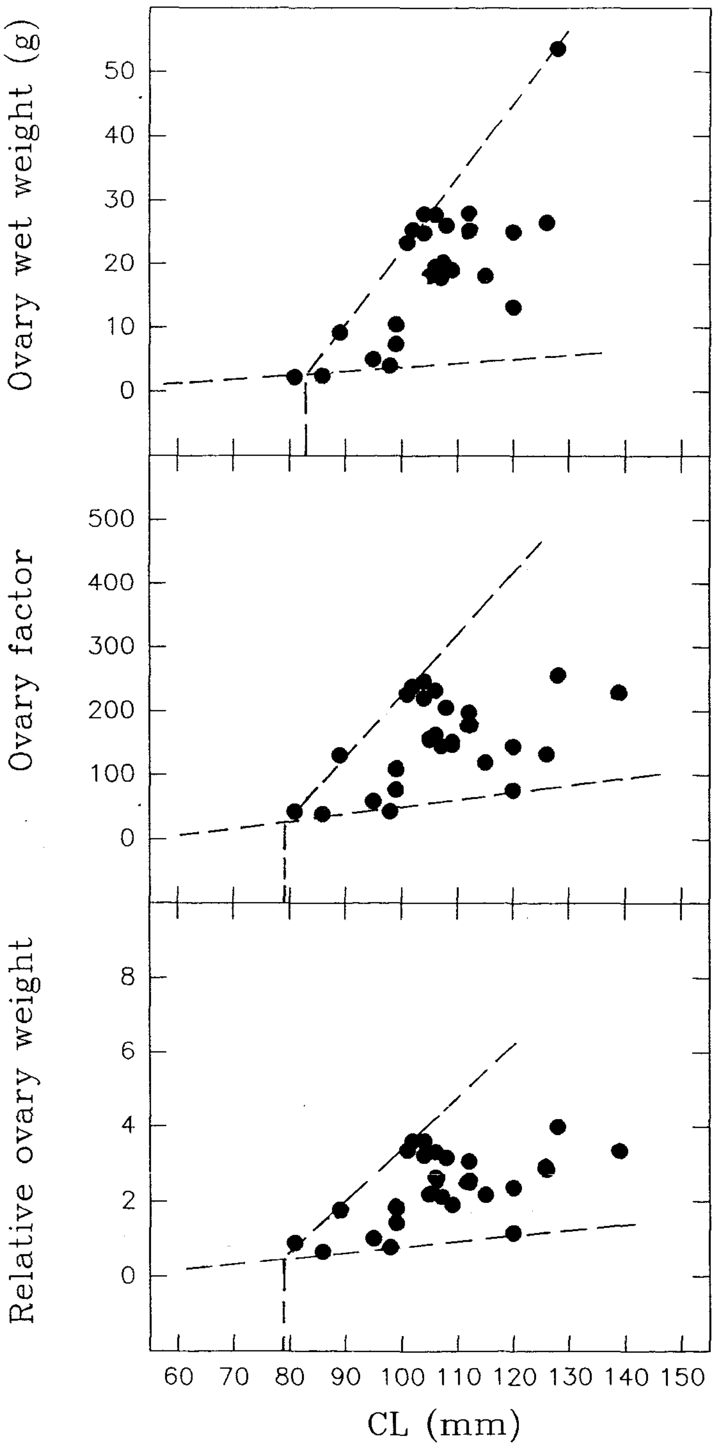


Fig.4.73

Female internal condition indices, Selsey, 1989 to 1991

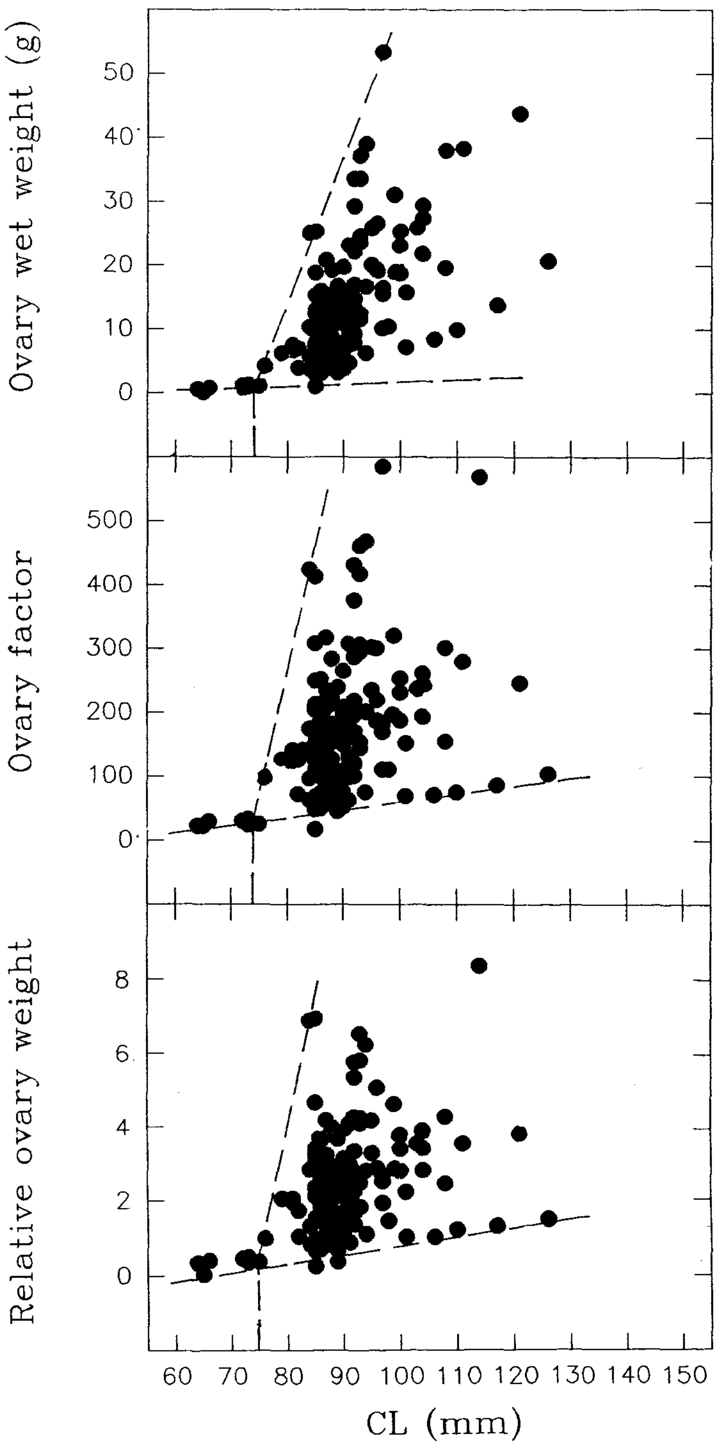


Fig.4.74

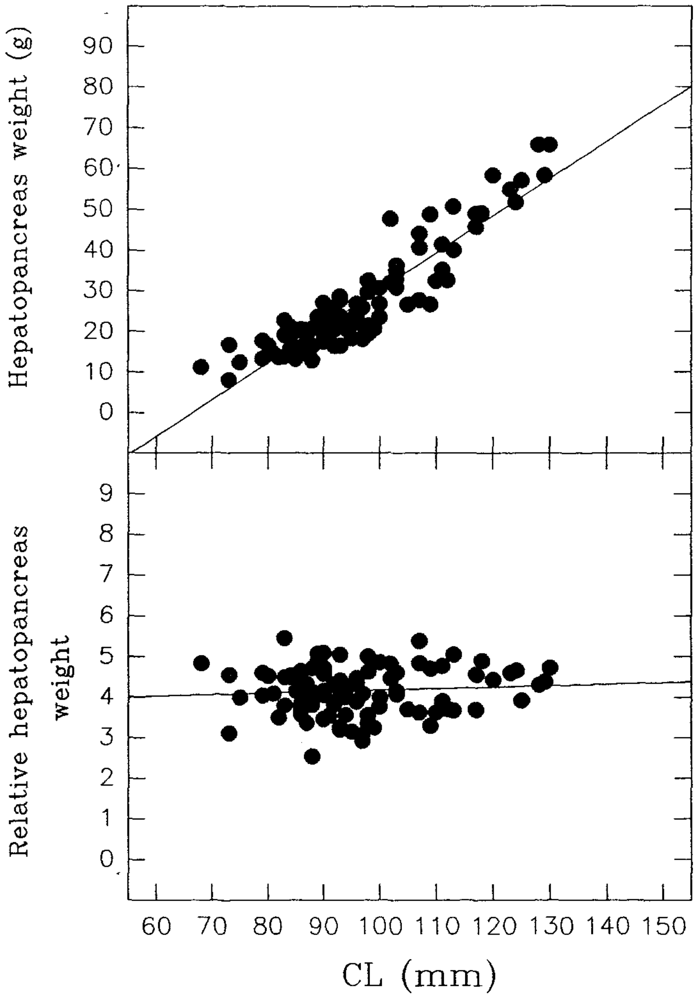

Female hepatic internal condition indices
Bridlington, 1989 to 1991

Fig.4.75

Female hepatic internal condition indices Dale, 1989

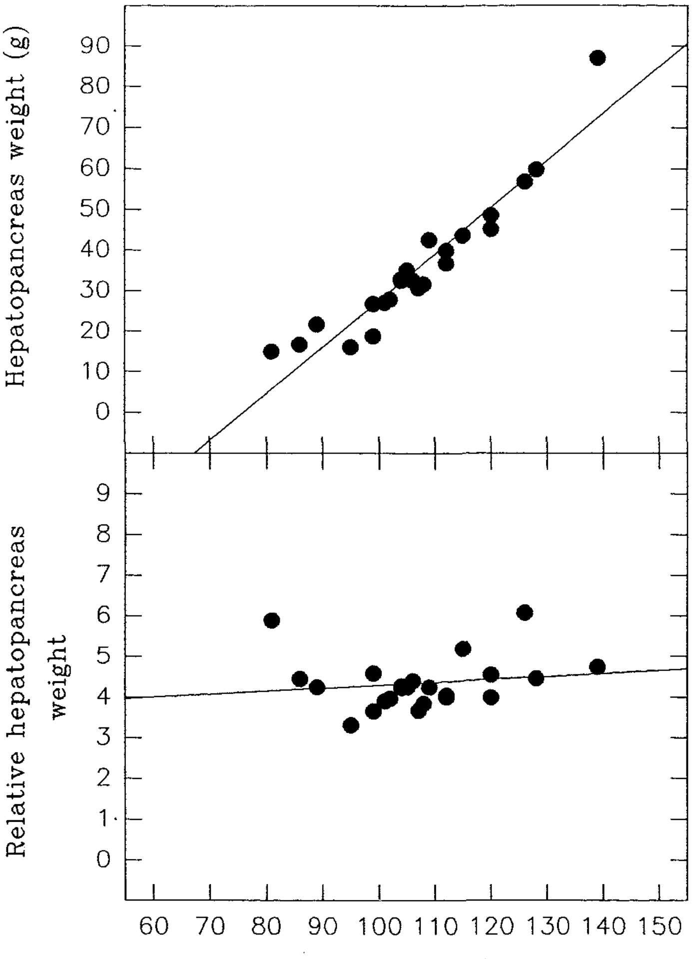


Fig.4.76

Female hepatic internal condition indices Selsey, 1989 to 1991

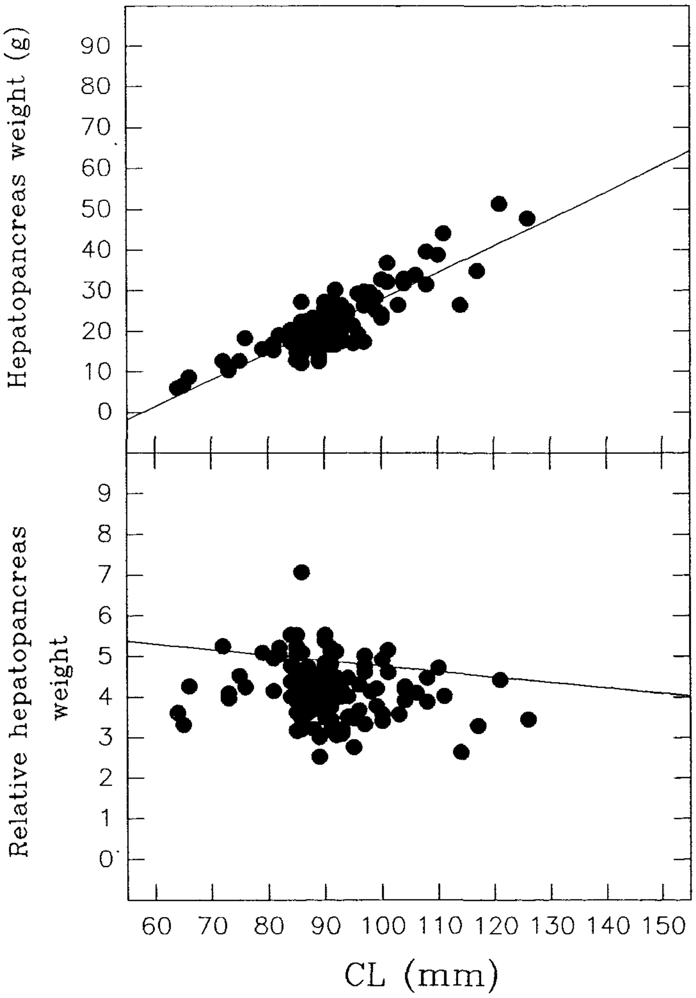


Fig.4.77

Female internal condition indices plotted against abdomen width (mm), Bridlington, 1989 to 1991

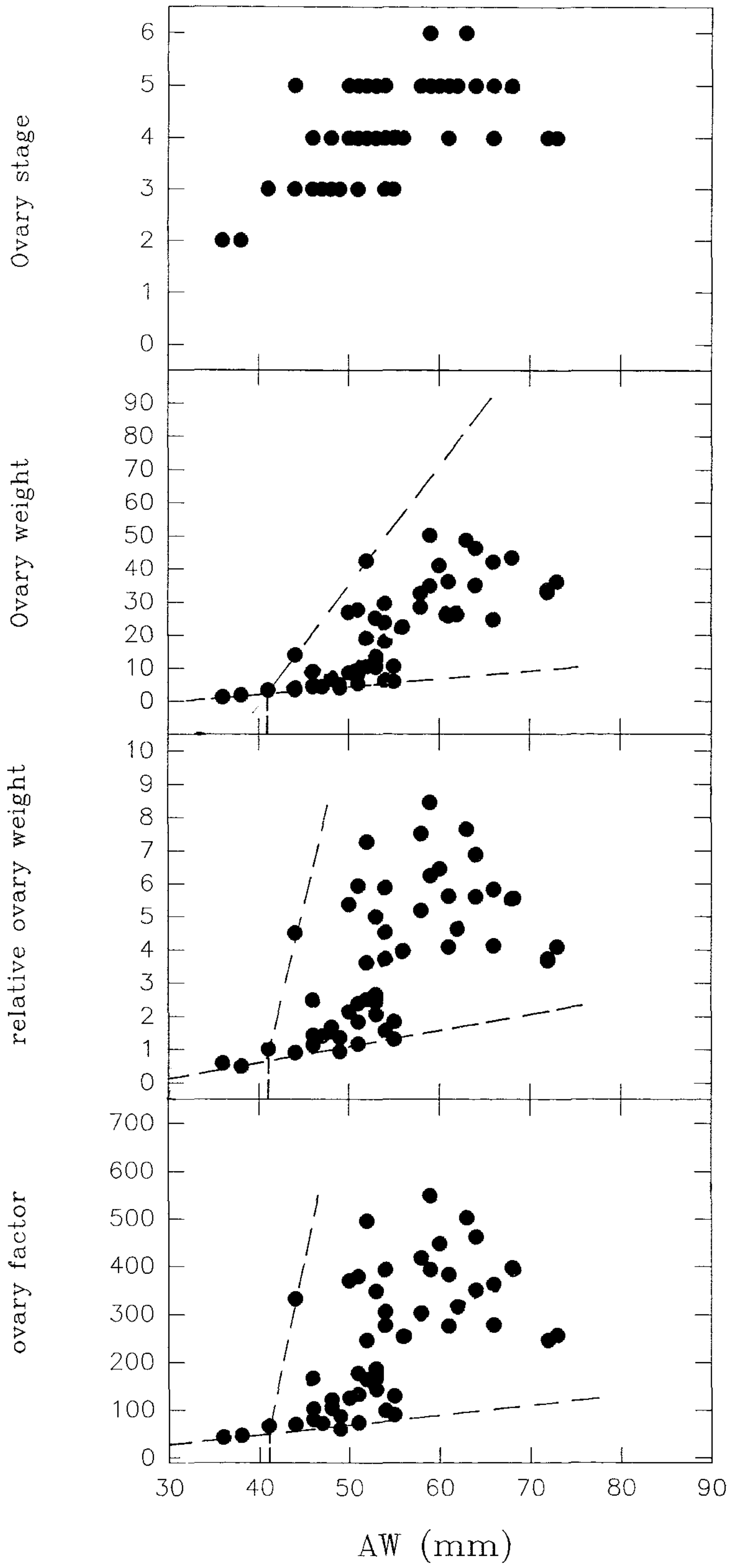


Fig.4.78

Female internal condition indices plotted against abdomen width (mm), Dale, 1989

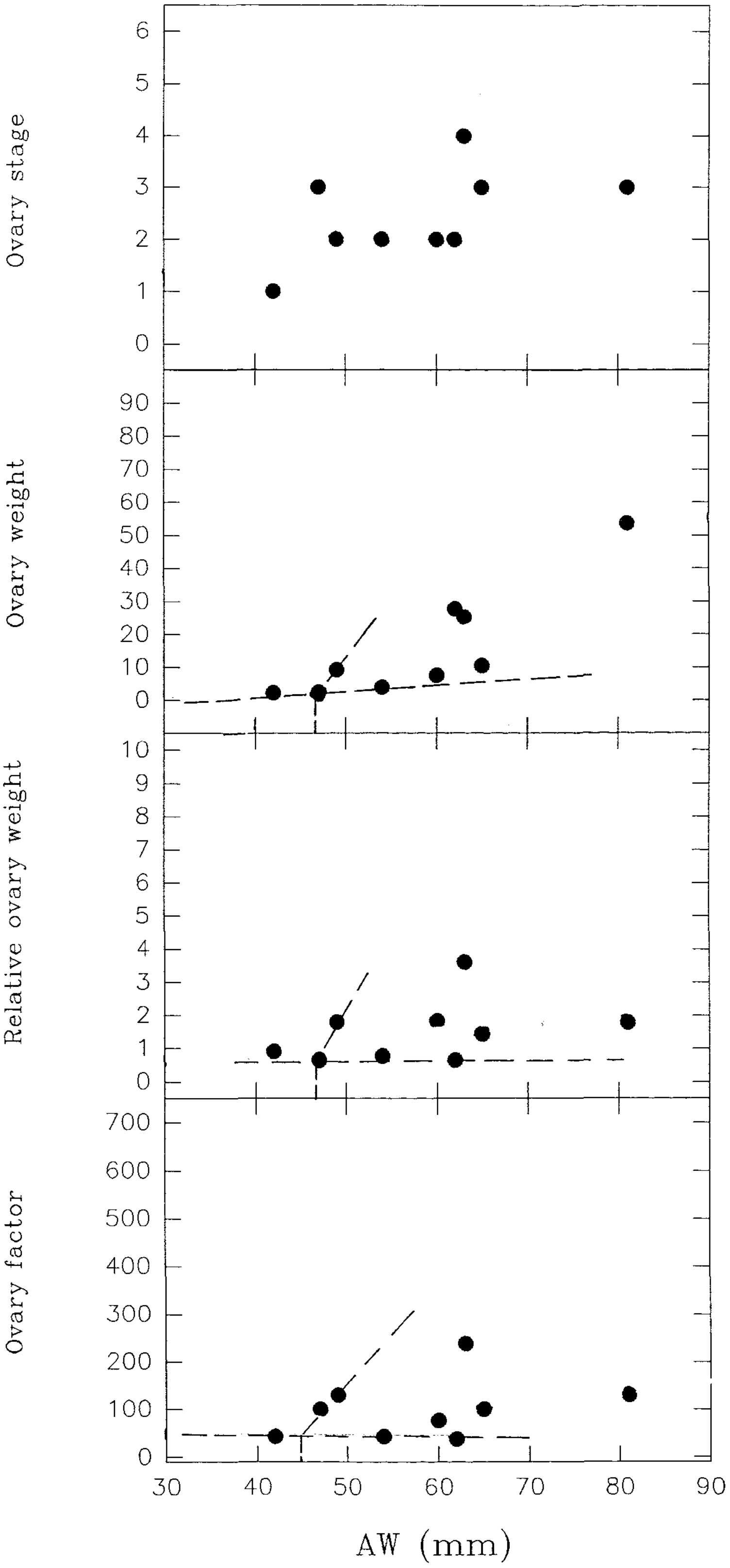


Fig.4.79

Female internal condition indices plotted against abdomen width (mm), Selsey 1989 to 1991

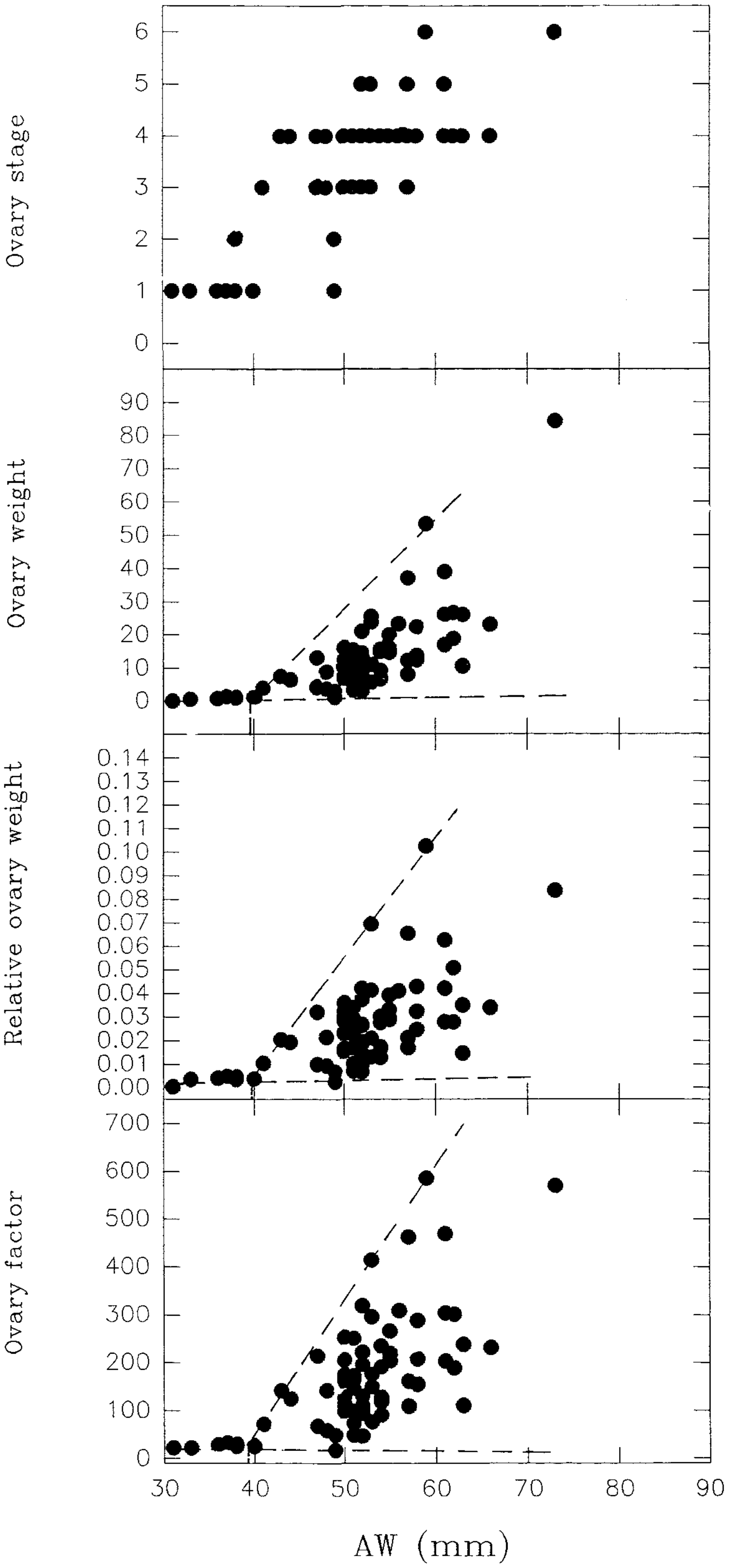


Fig.4.80

Female internal condition indices plotted against relative abdomen width (mm), Bridlington, 1989 to 1991

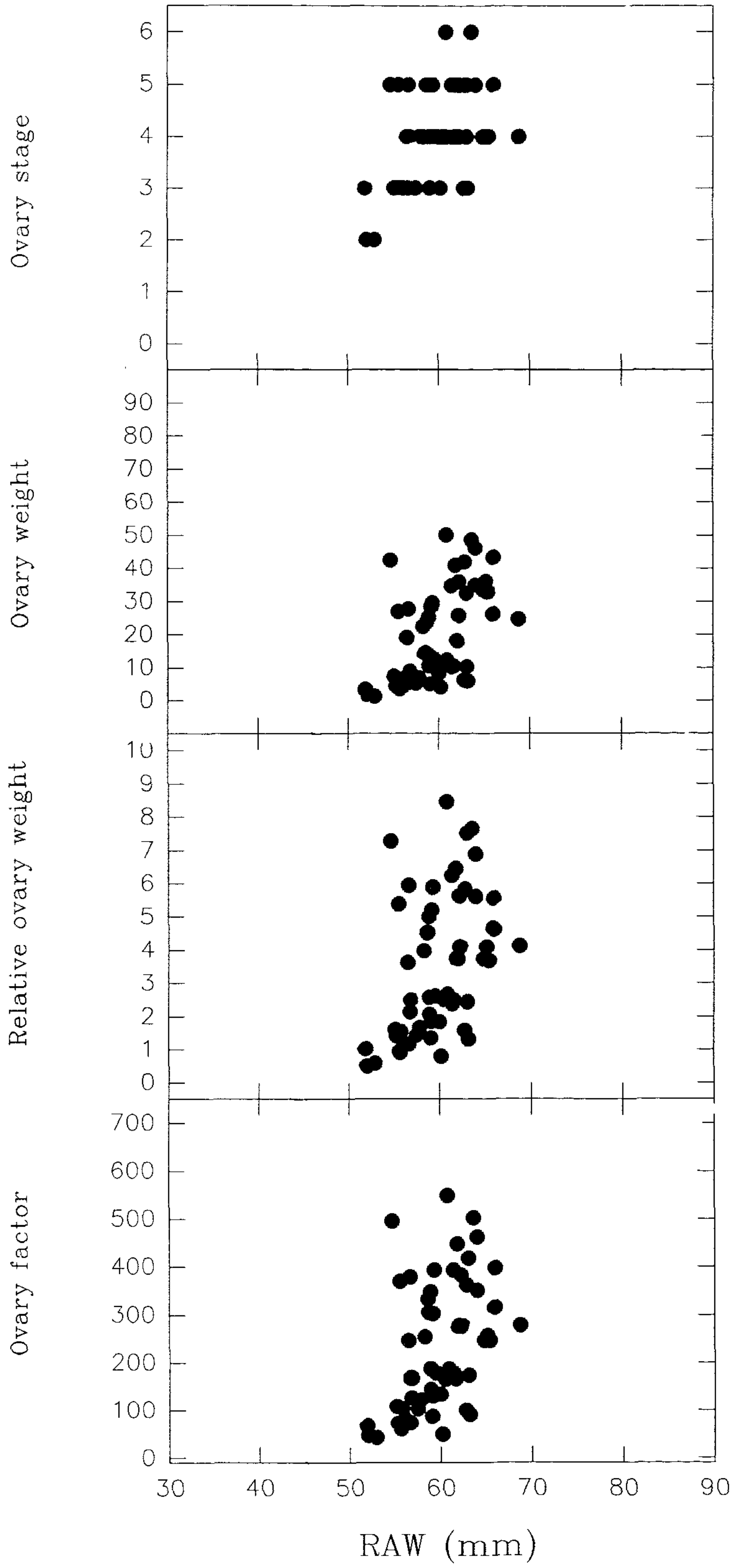


Fig.4.81

Female internal condition indices plotted against relative abdomen width (mm), Dale, 1989

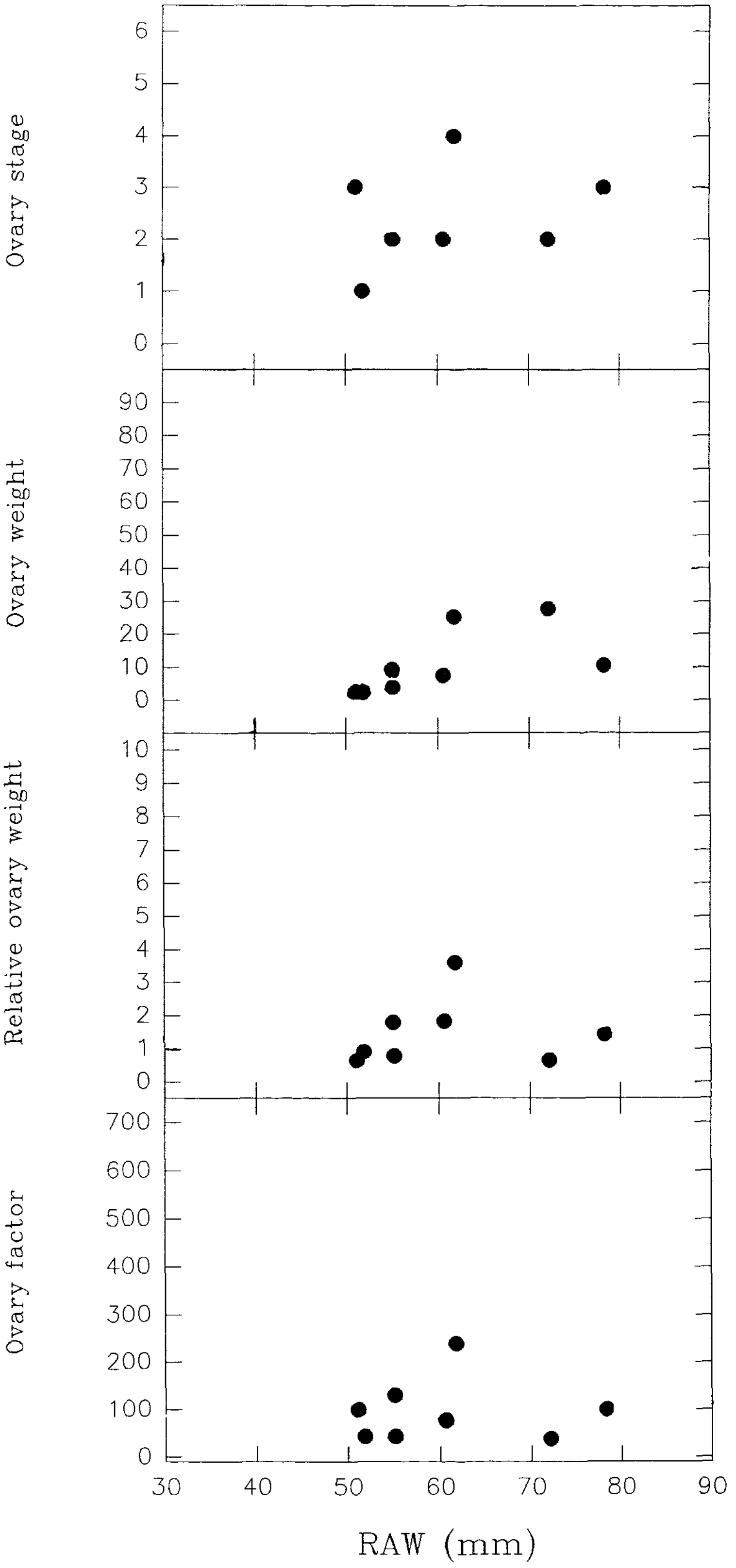


Fig.4.82

Female internal condition indices plotted against relative abdomen width (mm), Selsey 1989 to 1991

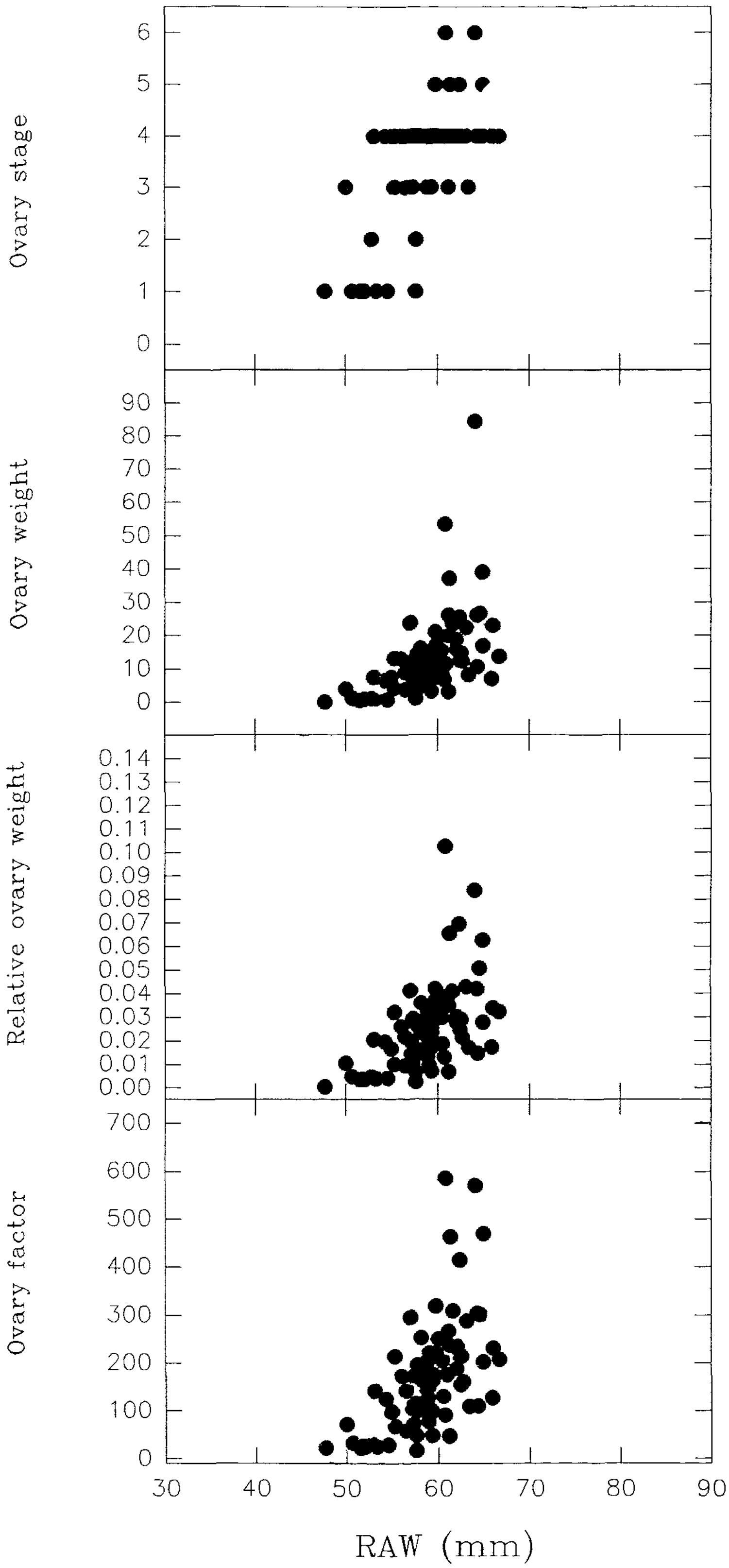


Fig.4.83

Percentage of females determined mature by ovary development stage, Bridlington 1989 to 1991

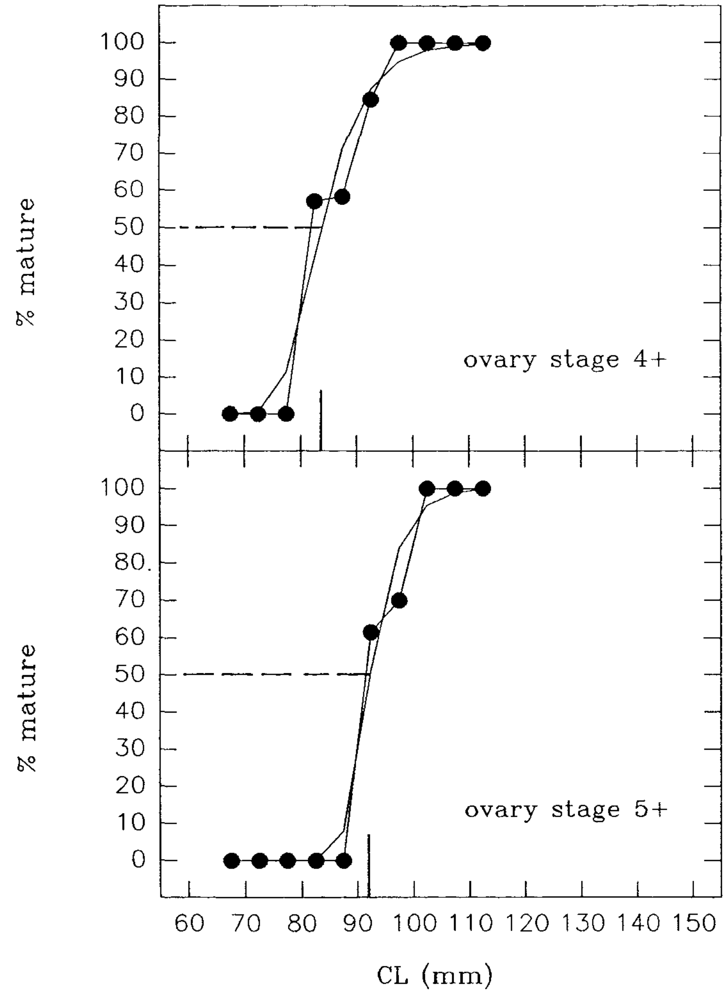


Fig.4.84

The ovary factor by 5 mm CL groups Bridlington 1989 to 1991

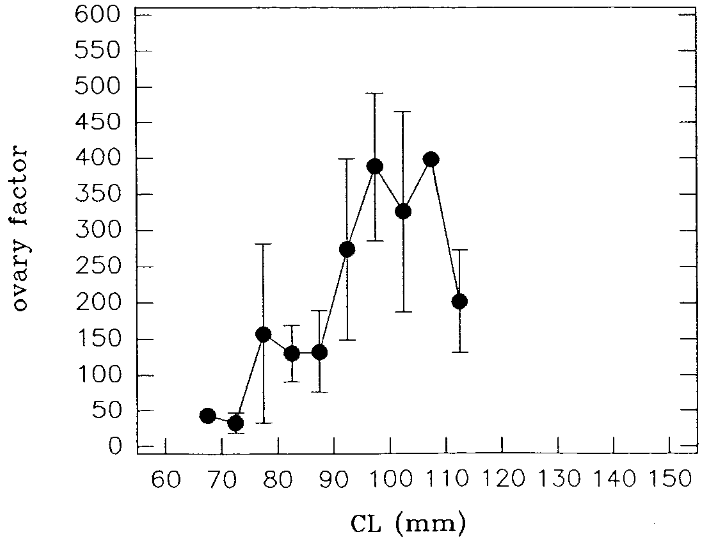


Fig.4.85

Percentage of females determined mature by ovary development stage, Dale 1989

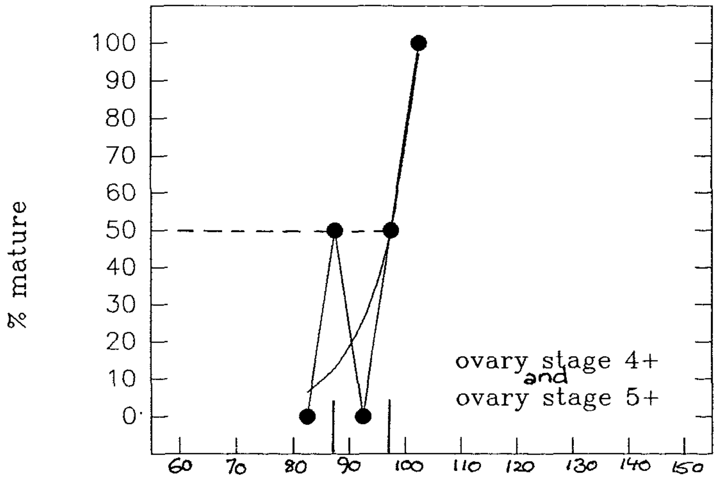


Fig.4.86

The ovary factor by 5 mm CL groups
Dale 1989

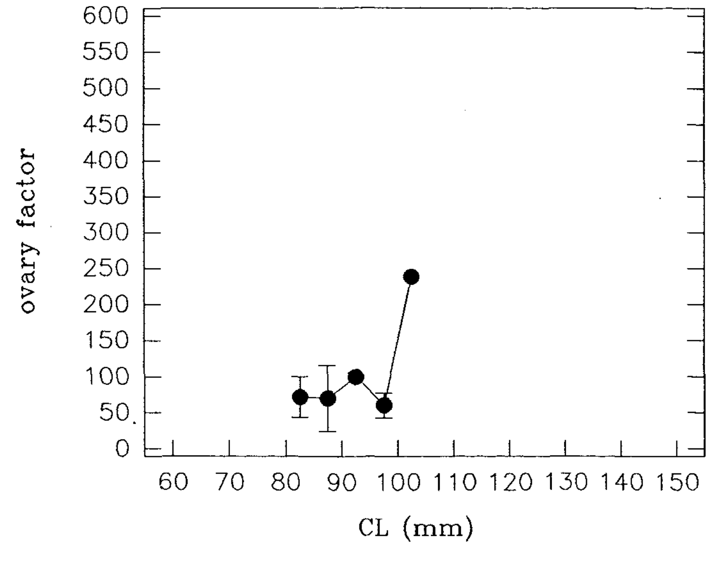


Fig.4.87

Percentage of females determined mature by ovary development stage, Selsey 1989 to 1991

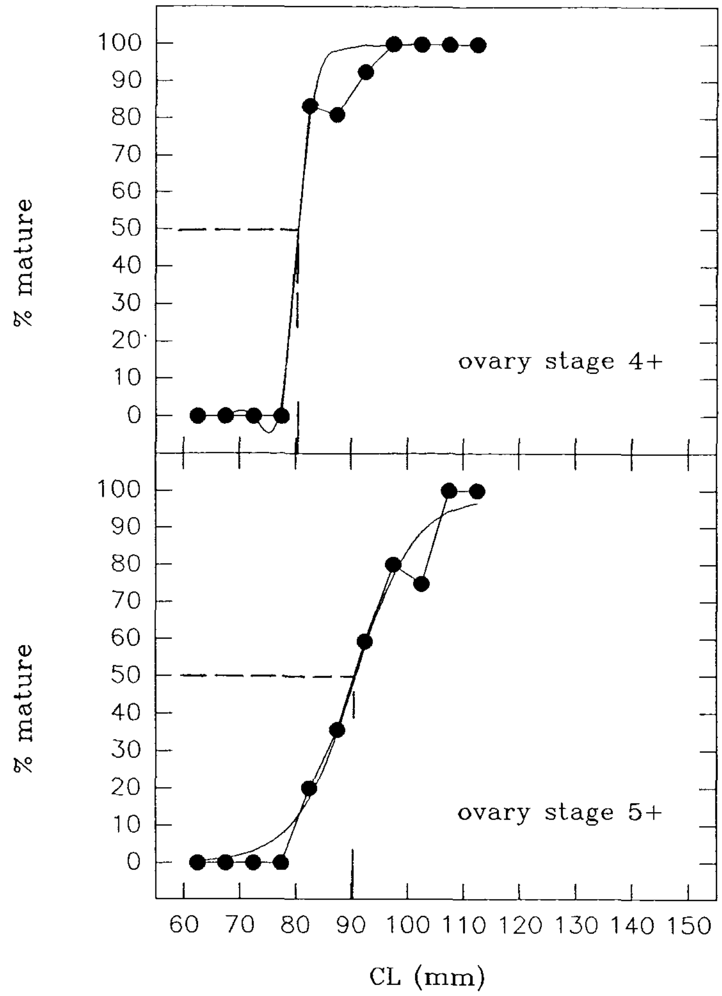


Fig.4.88

The ovary factor by 5 mm CL groups
Selsey 1989 to 1991

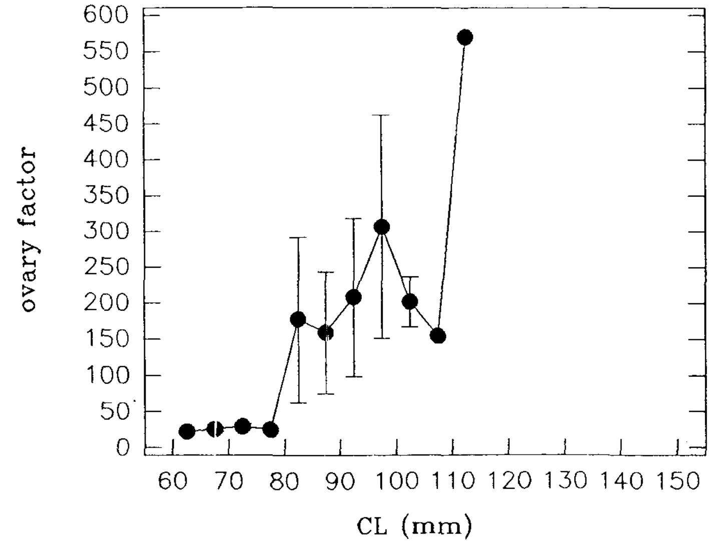


Fig.4.89

Table 4.1 Summary of female external SOM estimations

Site	year	Linear AW/CL intersections	AW/CL inflexions	2nd polynomial RAW/CL intersections	RAW/CL 1st inflexions	RAW/CL 2nd inflexions	Smallest berried	25 % berried (50% mature)
Bridlington	1989	61.2	-	61.2	79	87	78	90
Bridlington	1990	62.9	-	62	-	-	89	91
Bridlington	1991	-	-	-	-	-	82	97
Dale	1989	74.7	-	73.3	-	102	95	103
Selsey	1989	63.6	-	46.1	-	-	76	78
Selsey	1990	64.3	-	65.3	-	-	78	-
Yorkshire	1972	-	-	-	-	-	77.5	91
Yorkshire	1973	-	-	-	-	-	82.5	91
Yorkshire	1974	-	-	-	-	-	82.5	92
Whitby	1973	56.5	76.5	-	-	-	-	-
Staithes	1980	-	-	-	81.5	88	-	-
Pembrokeshire	1972	-	-	-	-	-	82.5	132
Pembrokeshire	1973	56.8	-	64.4	-	-	87.5	119
St.Davids	1980	-	-	-	86.5	99	-	-
Selsey	1973	64.6	78	56.8	-	-	82.5	95

Table 4.2 Summary of female internal SOM estimations

Site	Ovary weight/CL limit intersections	Owf/CL limit intersections	ROW/CL limit intersections	Ovary weight/AW limit intersections	Owf/AW limit intersections	ROW/AW limit intersections	50 % females ovary stage 4+	50 % females ovary stage 5+
Bridlington	78	75	77	52.08	52.857	52.857	83	92
Dale	83	79	79	62.3896	60.6756	62.38	87 or 97	87 or 97
Selsey	74	73	74	47.1885	47.1885	48.0035	80	90

4.4 Discussion

Female size at onset of maturity is an important consideration for fisheries management especially in fisheries, such as that for *H. gammarus*, which are legally governed by minimum landing size legislation (MLS). Assessment of female sexual maturity in *H. gammarus* is complex because of the length of the reproductive cycle, potential variability in the duration of the cycle with female size and geographic location (Chapter 3), and behavioural changes during the cycle (with resultant changes in female catchability) (Chapter 2). Differences between the sizes of female physiological and functional maturity may be suggested by ovarian development (assessed using ovary staging or internal indicators of maturity) and expressed maturity (i.e. ovigerous). Observed discrepancies between physiological and functional maturity may not interfere with fisheries management, as for any given year, effective reproductive stock is composed of females that will produce eggs that year (Ennis, 1980). This is confused by potential changes in catchability during the reproductive cycle (Hallback and Warren, 1972; Branford, 1976), and by difficulties in determining that a lobster will become berried in the course of a year. Cement gland development staging, used successfully by Ennis (1984) for *H. americanus*, was not found to be an adequate method of determining predisposition to becoming berried in *H. gammarus* (Chapter 3), and would require further work for comprehension of cement gland development function before its use may be substantiated for field work on *H. gammarus*.

The use of external indicators of maturity which use the allometric growth of the second abdominal segment, requires physiological validation. Results from this study suggest that the widening of the abdomen begins before size at functional maturity (possibly two moults), and also before commencement of ovary development (onset of physiological maturity) (possibly one moult). Estimations of physiological maturity using ovary staging are unfortunately destructive, and do not allow for observation of the interval before onset of functional maturity. The use of relative abdomen width as an indicator of maturity is dubious because of the lack of correlation between male RAW and CL (for intersect analysis), and statistical difficulties in determination of any suggested inflexion which might infer functional or physiological maturation for any given population. Variability in individual growth rates and individual relative growth is not adequately compensated for by size class grouping of individuals for inflexion identification; this may also be problematic for intersect analysis. Between-year differences in AW-CL relationships cannot be adequately explained and may also invalidate the use of AW-CL and RAW indices for identifying size at onset of maturity.

Internal indices of maturity (i.e. Ovf, ROW and ovary weight) are all destructive methods of maturity determination, and individual inconsistency in these factors suggests that accurate ovary stage determination, using gross morphology, may be the most useful, and simplest, method of assessing female physiological maturity. The increase in variability of these internal indices with increasing CL and AW indicated in this study also suggests preferential use of ovary development stage for determination of both physiological and functional maturity in *H. gammarus*.

Geographical variation in female size at onset of maturity has been observed using both the proportions of berried females and the proportions of females with mature ovaries (stages 4+). Both size at first maturity (smallest berried female) and size at 50 % maturity determined by ovary stage are below MILS at Selsey in 1989 and 1990 and Bridlington in 1989 and 1991. The smallest berried female and size at 50 % maturity determined by ovary stage are above the current 85 mm CL MILS at Dale. 50 % maturity of females, determined as 25 % females observed being berried (assuming equal ovigerous/ non-ovigerous catchability and females becoming berried every other year), occurs at above 85 mm CL at both Dale and Bridlington, though at 78 mm CL at Selsey. The size at occurrence of two thirds of females being berried may indicate a change in the nature of the ovarian cycle, with females breeding two years in every three, (assuming little or no change in catchability with reproductive state, and therefore equal fishing mortality for ovigerous and non-ovigerous females). Two thirds of females above 107, 103 and 100 mm CL at Bridlington (1989, 1990 and 1991) and above 100 mm CL at Selsey in 1989 were berried. Between-year differences observed for % berry/CL relationships, and the lack of between-site differences may infer a requirement for more % berry data (preferably using diver sampling) and further information on behavioural changes (and catchability changes) after oviposition.

The causes of potential geographic and temporal differences in SOM are difficult to determine and isolate. Higher temperatures, such as those observed at Selsey (Chapter 2) are thought to contribute to early maturation of *H. americanus* (Aiken and Waddy, 1986), but this may be also be caused by population density and fishing pressure (Aiken and Waddy, 1980; Cobb and Wang, 1985), or variability in growth rates. Accurate growth rate information (both moult frequency and increment) may assist in determining whether size at onset of maturity is determined by age, instar or size at any given location. Population abundance estimates may be difficult to obtain but could also assist in defining the importance of population density and therefore fishing pressure upon size at onset of maturity. The environmental factors influencing SOM need to be identified for the determination of the causes of both spatial and temporal variation in SOM, for resolution of an optimal minimum legal landing size.

CHAPTER 5 MALE SEXUAL MATURITY

5.1.Introduction

Two distinct aspects of sexual maturity have been distinguished in male lobsters (Aiken and Waddy, 1980), as well as in other decapod crustaceans (e.g. *Chionecetes opilio*, Conan and Comeau, 1986). The onset of physiological maturity occurs when the male becomes capable of producing mature spermatozoa, but it is not until the male is also functionally mature that it is capable of mating with, and successfully inseminating a female.

The size at onset of physiological maturity in *H. americanus* was investigated and found to be as small as 40-45 mm CL by Krouse (1973). Briggs and Muschake (1979) found all but one male with sperm in its testes and/or vas deferens at less than 57 mm CL (much below the size of female maturity, with 50% female maturity at 70 to 74 mm CL). Onset of physiological maturity may be determined by the presence of spermatozoa in the vas deferens, identified by histological methods. Templeman (1934) conducted mating experiments on *H. americanus* and found that males of less than 65 mm CL were too small to mate with sexually mature females, although Hughes and Mattheissen (1962) suggested that small males do try to mate with females much larger than themselves, with variable success. Male *Jasus* species apparently become functionally mature at similar sizes to females, and occasionally at a slightly smaller size (Heydorn, 1965; MacDiarmid, 1989). Since the presence of spermatozoa in the vas deferens of male homarid lobsters is not a valid indication of functional maturity (Briggs, 1976; Van Engel, 1980; Aiken and Waddy, 1980), and the size at which the ability to mate is developed is impractical to assess, other methods have been devised for use in the field.

Templeman (1935) first described changes in the cheliped size of *H. americanus* and used chela propodite length (which he suggested increases rapidly in relation to total body length after male functional maturity) as an indicator of sexual maturity. Templeman (1935) used cheliped propodite length relative to total body length and plotted against total length with some success (especially when compared to female relative claw/body lengths against total length). Aiken and Waddy (1980) suggested that this method was invalid as an indicator of male functional maturity when CL was used instead of total length; and that cheliped propodite length directly plotted against CL did not indicate a clear inflection point for the onset of maturity. Squires (1970) and Ennis (1971; 1980) observed a stronger inflection of maturity caused by the positive allometric increment of crusher claw weight when compared against carapace length. This method, however, is also difficult to use in the field. Aiken and Waddy (1980) devised the "Anderson cheliped index" (AI)(Appendix A5i.1) to take crusher claw volume into account without having to measure claw weight. Ennis (1980) investigated the use of the AI in *H. americanus*, but discovered no distinct inflection, when it was plotted against carapace length, that might indicate the onset of functional maturity. Aiken and Waddy (1989) then developed an alternative method, using the crusher propodite index (CPI)(Appendix A5i.1), which gave a direct indication of the size at onset of functional maturity, without the need for logarithmic transformations to demonstrate a distinct point of inflection. The CPI, when plotted against CL intersected on the female regression line of CPI at the point of male functional maturity. Conan *et al* (1985) refuted the idea of determination of male *H. americanus* onset of maturity using claw morphometry (after attempting the process using log-linear transformations, bivariate allometric plots and principal components analysis), and suggested that the sexual differentiation of claw size is initiated from early juvenile stages. However, principal components analysis has since been used successfully to ascertain size at functional maturity in both *Chionoecetes opilio* (Conan and Comeau, 1986) and *Necora puber* (Freire and Gonzalez-Gurriaran, 1992).

MacDiarmid (1989)(working on *Jasus edwardsii*) noted that internal criteria should be used when no external indicators of maturity are available because of the problem of differentiating functional and physiological maturity in male lobsters. Aiken and Waddy (1980) observed a relationship between vas deferens weight and the onset of functional sexual maturity in *H. americanus* and developed a vas deferens factor (VDF) to exploit this (Appendix A5i.1). This factor includes the use of the cube of the individual's carapace length to facilitate its use as an indicator of maturity, by compensating for different sample size distributions. As Aiken and Waddy (1980) commented; because the rate of increase in vas deferens weight becomes faster than the corresponding increase in CL^3, the factor may only be used in samples with a comparatively small size range. Aiken and Waddy (1980) suggested that there is a uniform size of vas deferens at maturity in *H. americanus*, irrespective of male size, thereby reinforcing the potential use of vas deferens weight, in some format, for estimating male size at onset of maturity. MacDiarmid (1989) demonstrated highly variable vas deferens wet weights in male *J. edwardsii* of a given size and suggested that the males must have been caught at varying intervals after mating, thereby implying the requirement of a recovery time before males could successfully fertilise eggs again. This is also suggested by Aiken and Waddy (1991) for *H. americanus*, with lobsters exhibiting considerable variation in potency and enthusiasm to re-mate both within and between individuals.

Heydorn (1964) developed an index of abundance of spermatozoa in *J. lalandii*, and showed a seasonal cycle of spermatozoa number. Total male gonad weight was shown to increase steadily with size, although this increase tended towards an asymptote at the largest lobster sizes.

Regional variation in male size at onset of maturity has been identified using the Anderson cheliped index by Aiken and Waddy (1980), with both the immature male AIs and the mature AIs from different regions showing similar regression slopes. Aiken and Waddy (1989) also showed regional variation in the onset of maturity using their CPI on *H. americanus* from different areas in Canada. Templeman (1935) had also shown spatial variation in the sizes at male maturity of *H. americanus* using his claw length index method.

5.2 Methods and statistical analysis

5.2.1. External indicators of male sexual maturity

External indicators of male maturity, using crusher propodite dimensions (Appendix A5i.1) were calculated for both male and females collected from Bridlington (1989 to 1990), Dale (1989), and Selsey (1989 to 1990). In addition, data collected from male lobsters from Staithes, Yorkshire (1980 to 1981), and St. Davids, West Wales, (1980 to 1981) were also used to assess the practicality of the Anderson Index for use in male maturity assessments.

5.2.2. Internal indicators of male sexual maturity

Dissections of male lobsters from Bridlington, Dale and Selsey, were used to investigate the relationships between hepatopancreas wet weight, lobster size and reproductive potential and relative hepatopancreas weight (RHW; Appendix A5i.1). The vas deferens of a number of lobsters were removed, wet weighed and used for the calculation of potential internal maturity indices (vas deferens weight against CL, relative vas deferens weight (RVDW) and vas deferens factor; Appendix A5i.1). The vas deferens of twelve lobsters from Selsey (75 to 95 mm CL) were examined for the presence of spermatozoa using a microscope (x400). Crusher claw wet weights, (and claw weight relative to total body weight; RCPW), vas deferens wet weights and vas deferens factors (Vdf), calculated for male lobsters from Staithes and St. Davids (1980 to 1981), were also used in this study for analysis of their potential as indicators of maturity.

5.2.3. Data Analyses

Internal and external criteria data from each site, were used for analysis both in 5 mm CL groups, and for individual lobsters. 5 mm CL group summary statistics (mean and standard deviation) were calculated for each mensuration.

Crusher propodite lengths (CPL), Anderson indices (AI), and crusher propodite indices (CPI) were each plotted against CL, with linear regression lines, for males from Bridlington, Dale and Selsey, by year groups (and for Anderson Indices for males from Staithes and St. Davids, 1980 to 1981). Male and female measurements were also shown together on graphs with linear regression lines for each criteria, for Bridlington, Dale and Selsey for each year of sampling. Figures were also produced for males, and males and females in 5 mm CL classes.

Normality and homoscedacity tests were carried out on external morphometric data before regression analysis proceeded. Linear regression results are presented with estimates of r (correlation coefficient) and R^2 (coefficient of determination) and Sx/y (standard error of estimation) as a measure of variability about the regression line. Regression coefficients, (according to the equation $y = a+bx$), their standard error of estimation, and t-statistics are also presented. Additionally, the coefficient's probability (P) of their use in predicting the dependent variable using the independent variable is shown. P(F), the probability of association between the independent and dependent variables, was calculated using Analysis of variance (ANOVA), and has been given in linear regression tables. Polynomial regression results (according to the equation, $y = a+bx+cx^2$), have been presented with their estimates of r, R^2, coefficients and their P-values. Linear regression results were also produced from natural log-transformed data. Analysis of covariance (ANCOVA) were performed to compare the covariance of external maturity criteria with CL, between-sites, between-years, and between-sexes.

The point of intersection between male and female regression lines, for each maturity criteria were calculated (using linear, natural log and polynomial regression coefficients) using the method of simultaneous equations.

Potential inflection points (ascertained by eye) on male Anderson Index plots were identified whenever possible for AI-CL, CPL-CL and CPI-CL data.

Internal maturity criteria (RHW, VDW, RVDW and Vdf) were also plotted against CL, with linear, log and polynomial regression lines, for individual males and males in 5 mm CL groups. Linear, polynomial and natural log regression analyses and ANCOVA were also performed for these criteria and their relationships with CL. The relationship between vas deferens factor and relative hepatopancreas weight was investigated using regression analysis for Bridlington, Selsey and Dale; as have those of vas deferens factor with crusher claw weight and vas deferens weight with claw weight for Staithes and St. Davids.

Potential inflection points on CPW, RCPW and vas deferens weight (VDW) against CL plots were determined by eye.

One way ANOVA was used to compare estimates of SOM according to method of calculation, and according to sample site and year.

5.3 Results

5.3.1.External indicators of maturity

Male crusher propodite length (CPL), Anderson Index (AI) and crusher propodite index (CPI) each increase with carapace length (CL)(Appendix Tables A5ii.1 to A5ii.12) (Figs. 5.1 to 5.19). Female crusher claw indices show a lesser increase with increase in CL, and may therefore produce an intersection point, which has been investigated for its use as an indication of size at onset of male maturity (SOM). Additionally the Anderson Index, when plotted against CL, may infer an inflection point (indicating allometric growth of the crusher claw), which has been investigated regarding its relevance to male SOM.

Crusher propodite length

Regression equations, produced to assess the relationship between CPL and CL indicate a strong linear relationship between the two variables (R^2, 0.829 to 0.965); preferable to a polynomial model (R^2, 0.842 to 0.963) because of the mathematical preference for the use of the simplest model in cases with two models showing similar degrees of variable association (Appendix Tables A5iii.1 to A5iii.3). 5 mm CL class regression results (Appendix Tables A5iii.10 to A5iii.11) indicate an increase in R^2 from those of individual regressions, although many cases indicate an increase in P (thus reducing the probability of using the 5 mm CL group regression coefficients in predicting the dependent variable); therefore implying that the linear, individual model is the most useful for describing the relationship between CPL and CL.

Male and female CPL indices intersect at between 83 and 109 mm CPL (between 65 and 86 mm CL) (linear model), 78 and 104 mm CPL (between 59 and 84 mm CL)(natural log linear model) and 75 to 118 mm CPL (between 59 and 96 mm CL)(polynomial model)(Appendix Tables A5iii.45, A5iii.48 and A5iii.51). No inflections could be determined in either the individual, or 5 mm CL class graphs (Figs.5.1 to 5.17). The preference for the linear regression model for CPL and CL suggest that the calculated linear male female intersections are the most accurate (Appendix Table A5iii.45).

ANCOVAs comparing sexual differences between the CPL and CL relationship (Appendix Tables A5iii.30, A5iii.33, A5iii.36, A5iii.39 and A5iii.42) suggest no significant differences between males and females at each site (per year) except for Selsey, 1990. The lack of significant between-sex differences may be caused by the spread of the data-sets, with most data points occuring near to potential intersections. However, sexual differences in CPL-CL relationships are apparenent from graphs, and the use of this indicator of maturity for sexual discrimination is therefore considered valid. Between-year ANCOVAs for

Bridlington and Selsey (Appendix Tables A5iii.16 and A5iii.19, respectively) suggest temporal variation in the CPL/CL relationship. Yearly variations and site and year interactions have been shown to be significant by ANCOVAs for both males from all three sites and females from the three sites (Appendix Tables A5iii.22 and A5iii.27 respectively).

Anderson Index

The Anderson Index (AI) indicates a 2nd order polynomial relationship with CL (R^2, 0.648 to 0.931; excepting Selsey males 1989)(Appendix Tables A5iii.4 to A5iii.6). 5 mm CL regression results also indicate a preference towards a polynomial relationship between AI and CL (R^2, 0.878 to 0.99); suggesting a curvilinear relationship between the two variables (Appendix Tables A5iii.12 to A5iii.13).

Male and female AI indices intersect at between AI 52 and 134 (between 60 and 89 mm CL)(linear model), and AI 52 and 111 (between 58 and 80 mm CL)(natural log model). AI intersections could not always be determined for the polynomial model in those instances where male and female regression lines did not meet within a probable range (40 to 120 mm CL)(Appendix Tables A5iii.46, A5iii.49 and A5iii.52).

Inflection points (Appendix Table A5iii.54) were apparent by eye for the AI when plotted against CL (Figs. 5.1 to 5.19) (except for Selsey 1990); these occurred at between 77.5 and 102 mm CL.

ANCOVAs comparing sexual differences between the AI and CL relationship (Appendix Tables A5iii.31, A5iii.34, A5iii.37, A5iii.40 and A5iii.43) suggest no significant differences between males and females at each site (per year). Between-year ANCOVAs suggest a highly significant difference between-years for the Selsey data, and a marginally significant difference in the AI/CL relationship between-years at Bridlington (Appendix Tables A5iii.17 and A5iii.20). No significant differences are apparent in the male AI/CL relationship between-sites (including Staithes and St.Davids), nor between sample years (Appendix Tables A5iii.25 to A5iii.26). However, significant differences between-sample-years were indicated for all sites for both males (excluding Staithes and St. Davids) and females (Appendix Tables A5iii.23 and A5iii.28).

Crusher propodite index

Linear, natural log and polynomial regression equations indicate a lack of correlation between CPI and CL (R^2 0.004 to 0.688, 0.003 to 0.631 and 0.028 to 0.688 respectively) (Appendix Tables A5iii.7 to A5iii.9) (Figs. 5.1 to 5.17). 5 mm CL class regression results indicate a higher association between the two variables (R^2 0.151 to 0.947, and 0.178 to 0.947 for linear and polynomial models respectively) (Appendix Tables A5iii.14 and A5iii.15).

Male and female CPI indices intersect at between CPI 16 and 23 (linear regression model), and CPI 15 and 21 (natural log regression model)(Appendix Tables A5iii.47 and A5iii.50). No intersections could be calculated for male and female lobster CPI/CL polynomial regression lines (Appendix Tables A5iii.53).

ANCOVAs to investigate male and female variability between CPI/CL regressions (Appendix Tables A5iii.32, A5iii.35, A5iii.38, A5iii.41 and A5iii.44) do not indicate significant sexual differences for each site, per year. However, Appendix Table A5iii.44, for Selsey 1990 suggests a significant lack of covariance between the two variables. This apparent lack of covariance for CPI/CL can be seen in the results of between-year ANCOVA for Selsey 1989 and 1990 (Appendix Table A5iii.21), which also shows significant temporal differences in the CPI/CL relationship. Bridlington 1989, 1990 comparisons using ANCOVA also indicate variations in the covariates relationship between-years (Appendix Tables A5iii.18). Yearly differences in CPL/CL relationships were found to be significant both all-males and all-females ANCOVAs (Appendix Tables A5iii.29 and A5iii.24); site and year interactions apparently being the main significant effect for male CPL/CL variations.

Comparisons of methods

ANOVA (analysis of variance) results comparing size at onset of maturity (SOM) estimates from all sites, between-external indicator methods (using CPL, AI and CPI male-female regression line intersections and AI inflexion points) (Appendix Table A5iv.1) do not suggest significant differences between estimates calculated using each of the techniques (P=0.164). However, summary statistics of the results (presented in Table 5.1) show larger estimates of SOM using the AI inflexion method, than either polynomial, linear, or natural log regression intersects

Fig. 5.1 External indicators of maturity, with linear regression lines
Bridlington males 1989

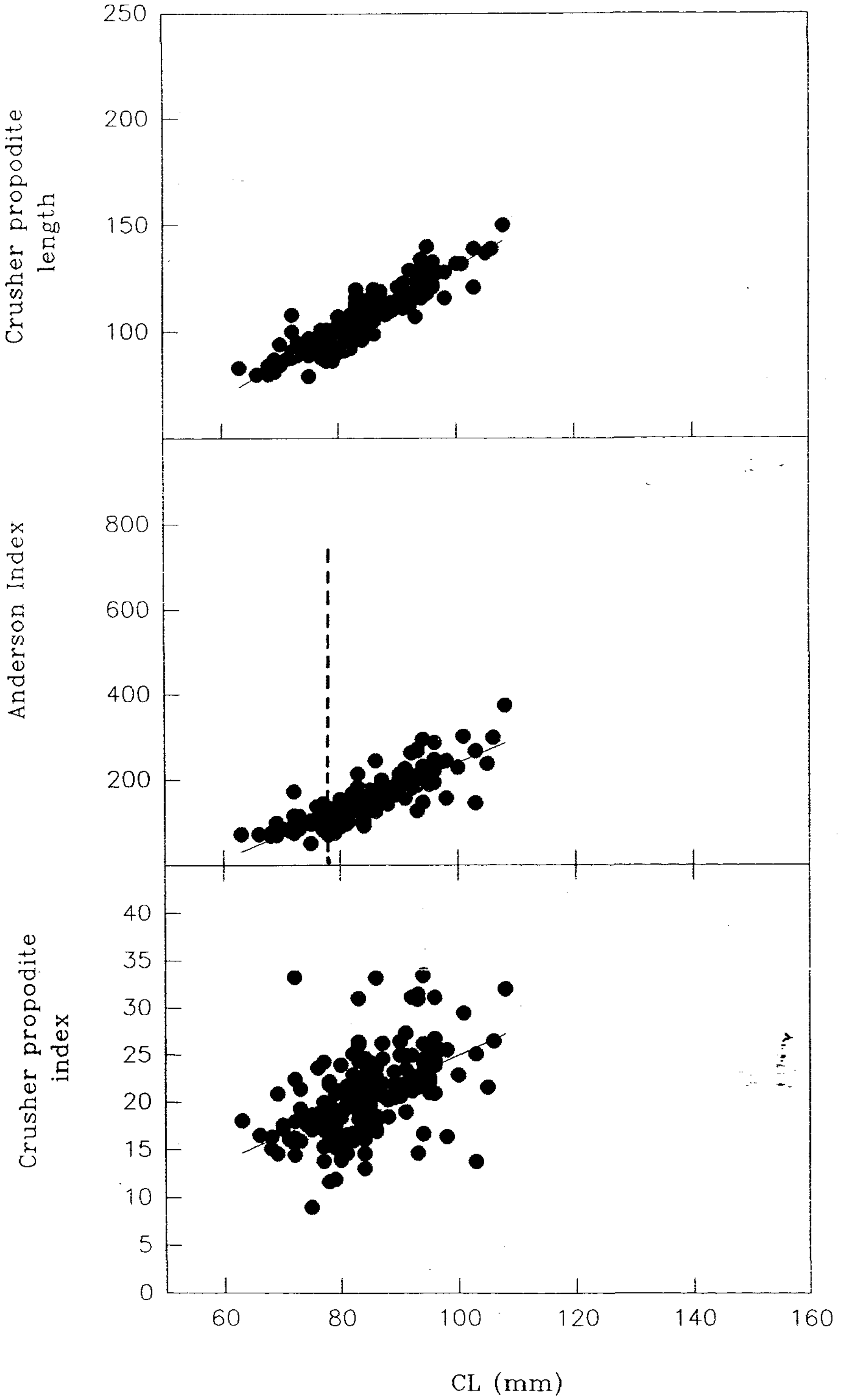


Fig. 5.2 External indicators of maturity, with linear regression lines Bridlington males and females, 1989

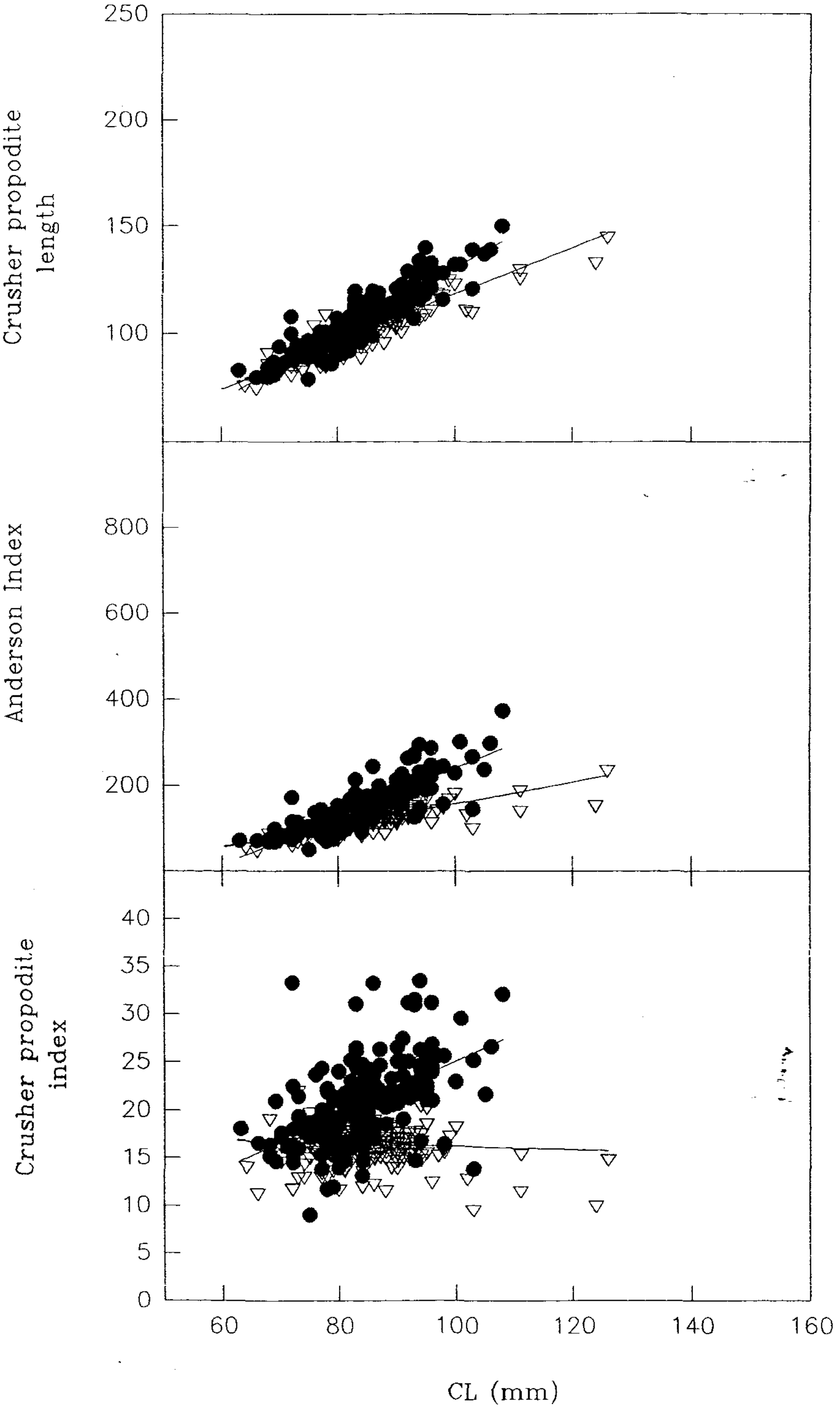
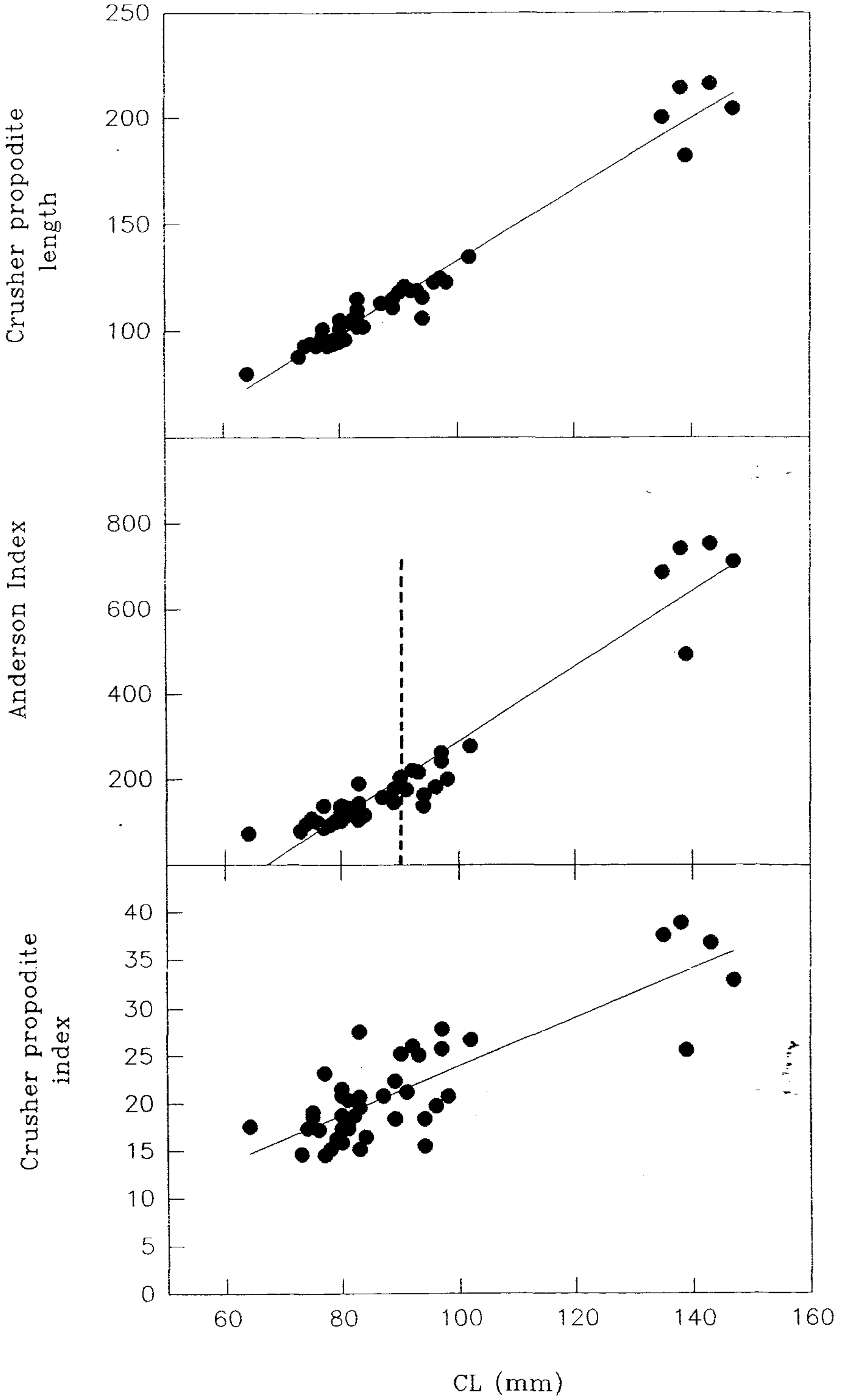


Fig. 5.3 External indicators of maturity, with linear regression lines
Bridlington males 1990



<u>Fig. 5.4 External indicators of maturity, with linear regression lines</u>
<u>Bridlington males and females, 1990</u>

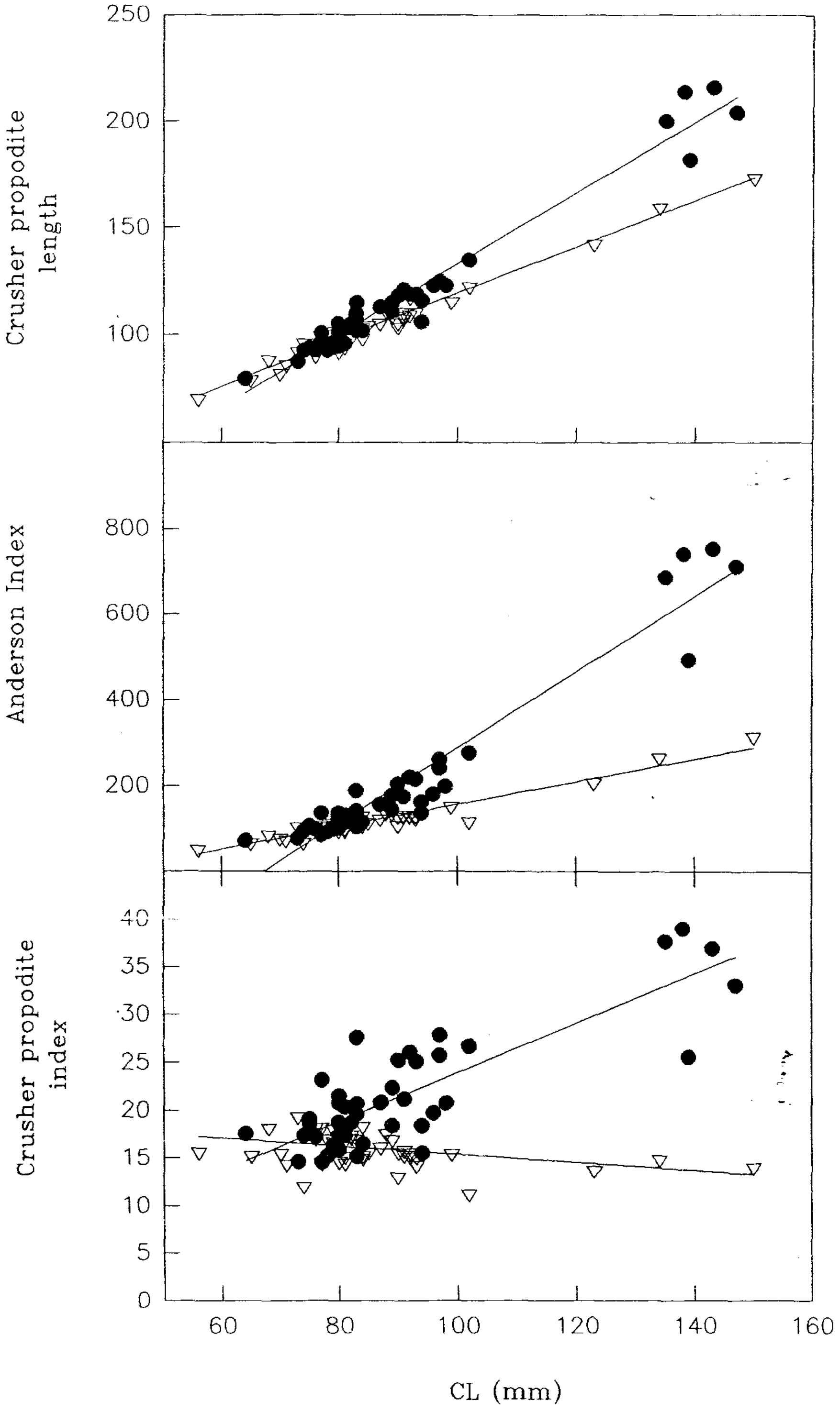


Fig. 5.5 External indicators of maturity, with linear regression lines Dale males 1989

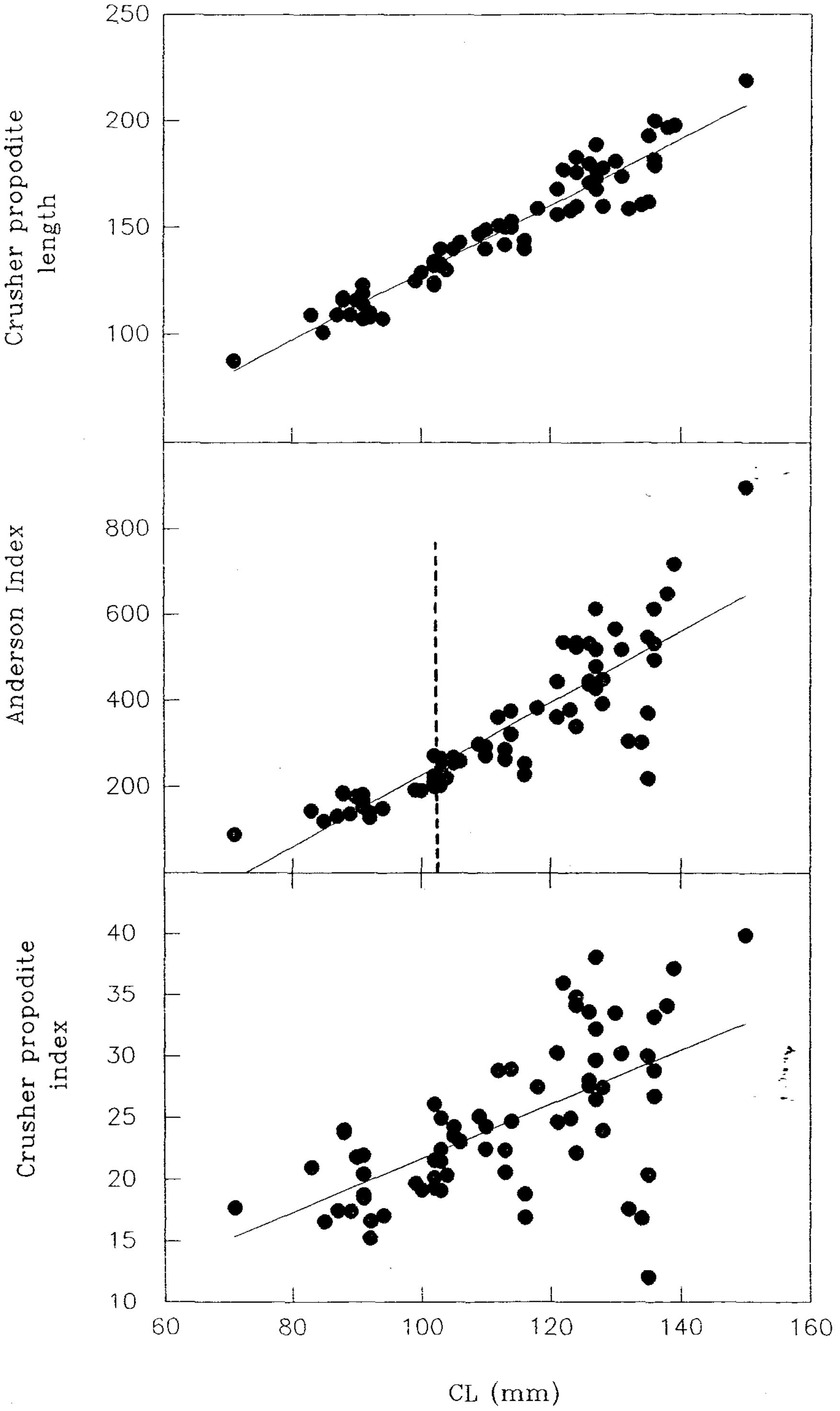


Fig. 5.6 External indicators of maturity, with linear regression lines Dale males and females, 1989

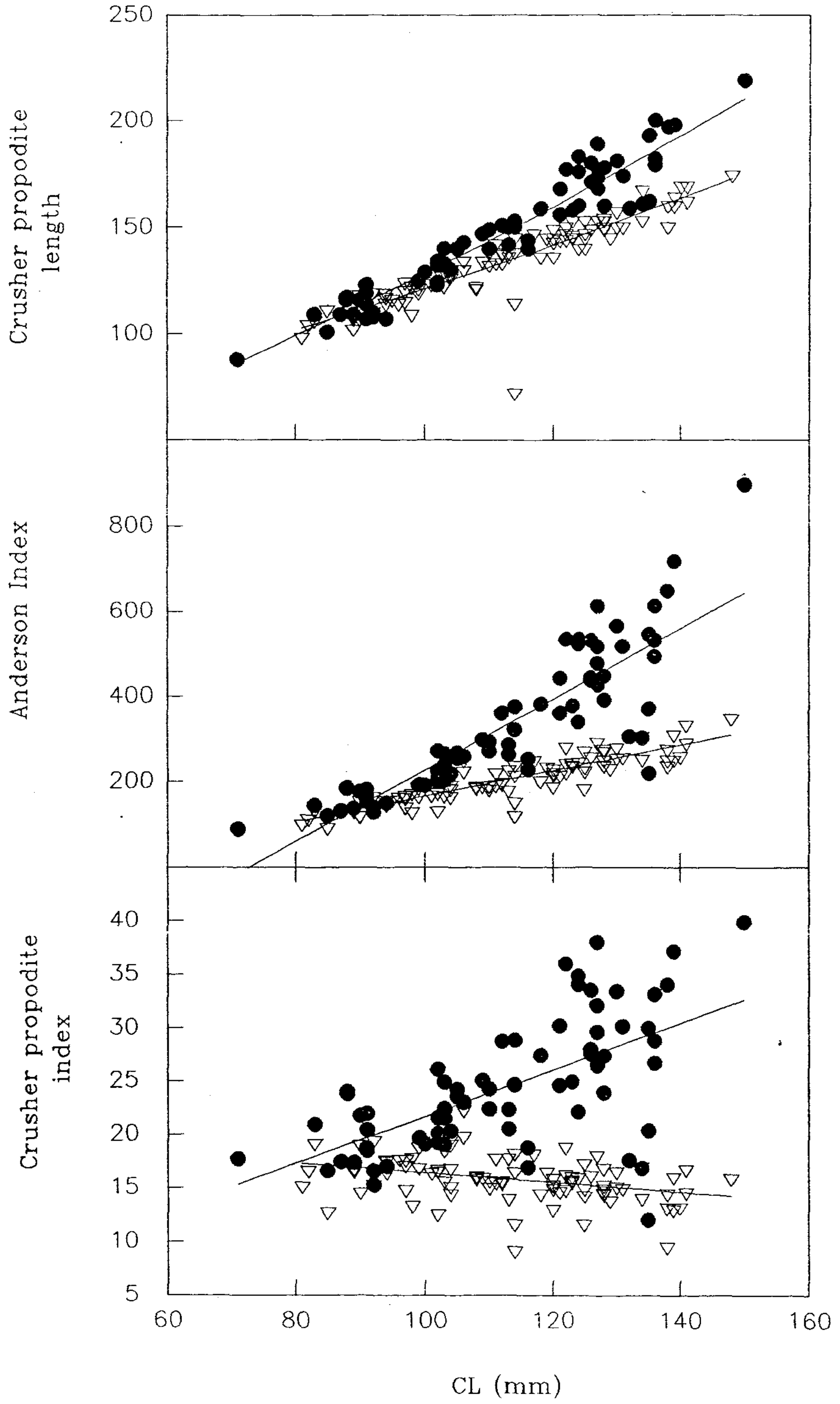


Fig. 5.7 External indicators of maturity, with linear regression lines Selsey males 1989

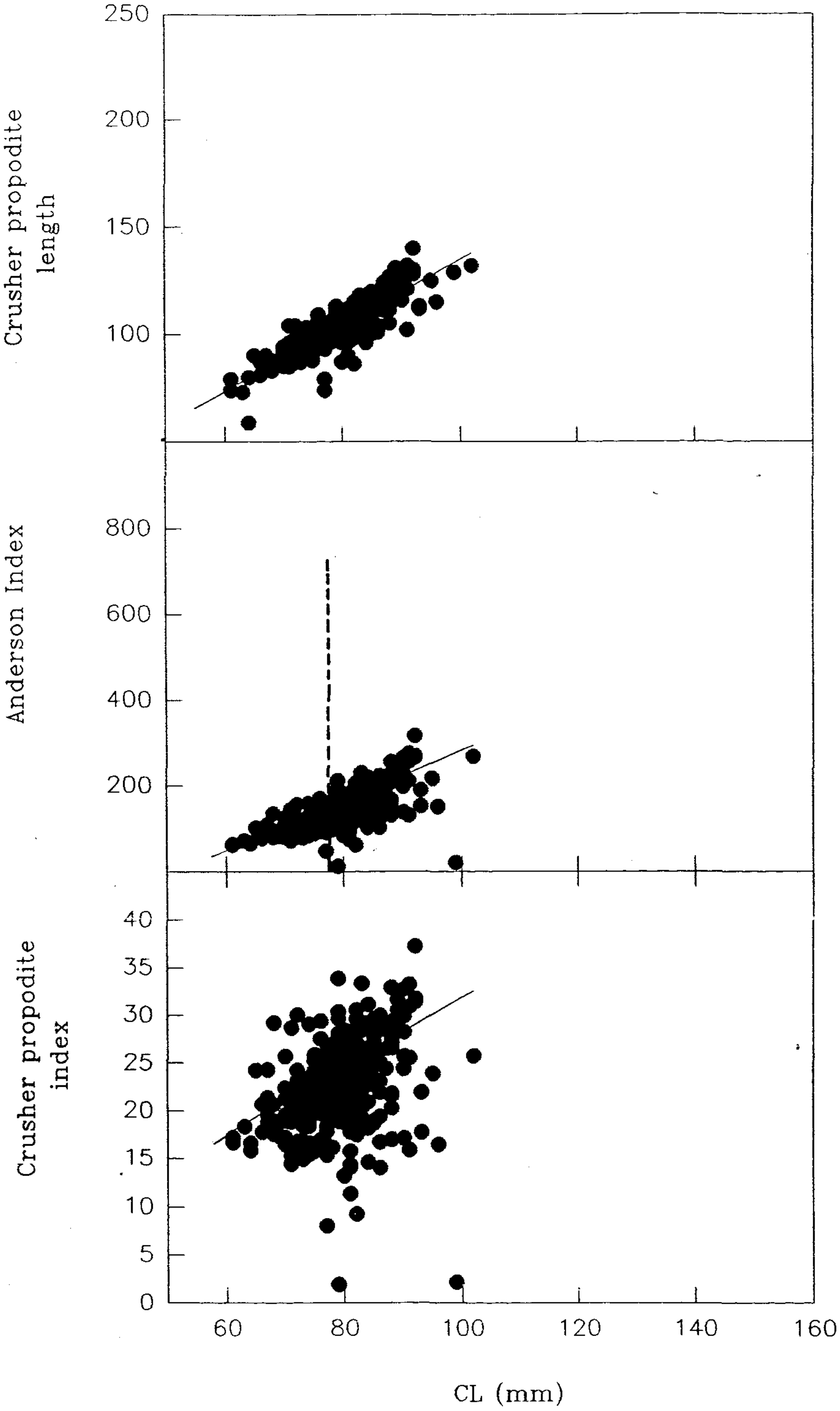


Fig. 5.8 External indicators of maturity, with linear regression lines Selsey males and females, 1989

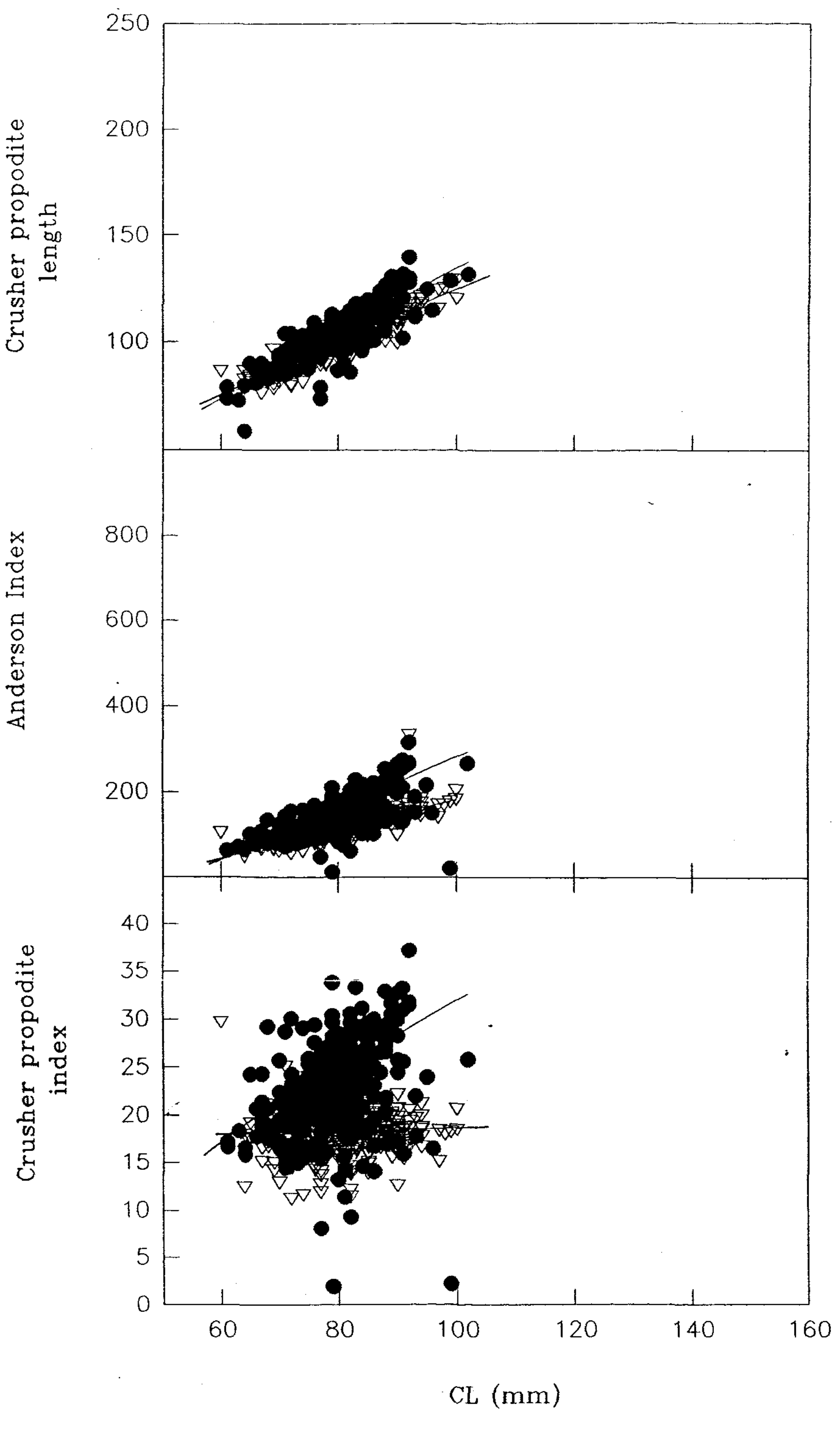


Fig. 5.9 External indicators of maturity, with linear regression lines Selsey males 1990

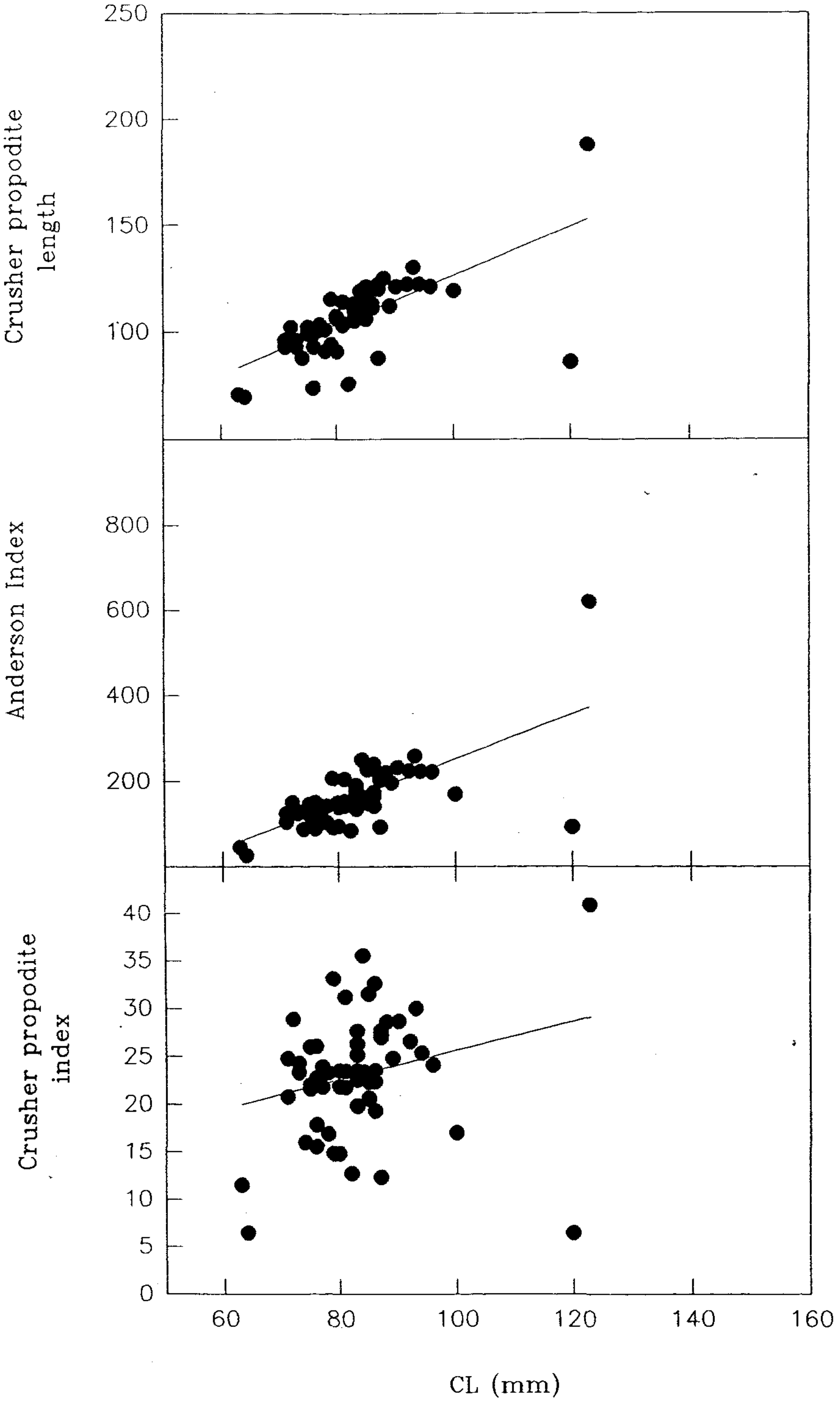


Fig. 5.10 External indicators of maturity, with linear regression lines Selsey males and females, 1990

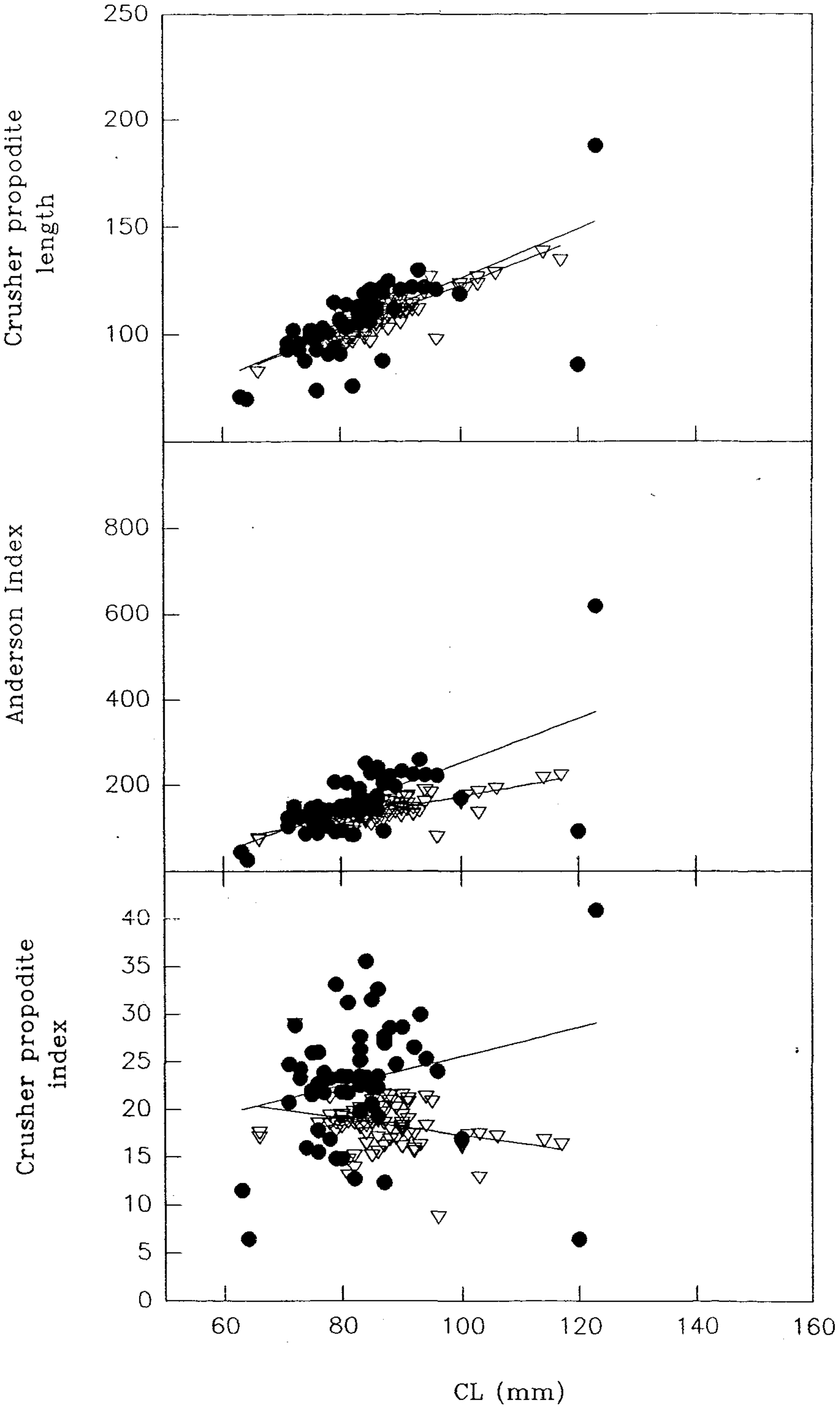


Fig. 5.11 Anderson index, with linear regression lines for Staithes males, 1980 to 1981

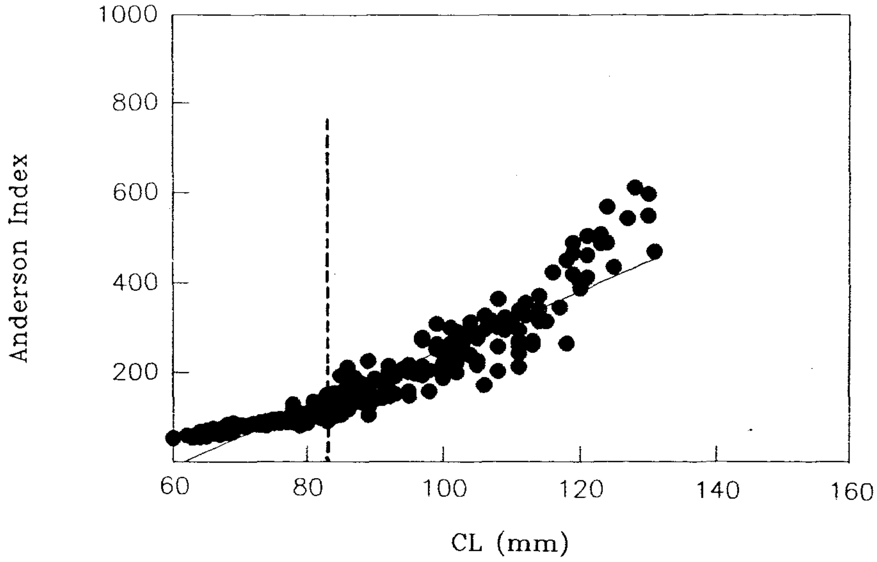


Fig. 5.12 Anderson index, with linear regression lines for St. Davids males, 1980 to 1981

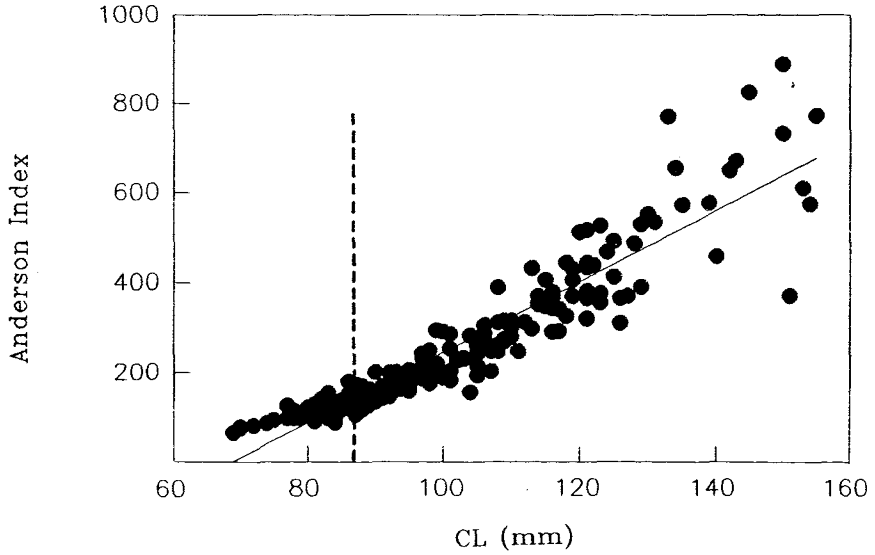


Fig. 5.13 External indicators of maturity, with linear regression lines Bridlington males and females (5 mm CL groups), 1989

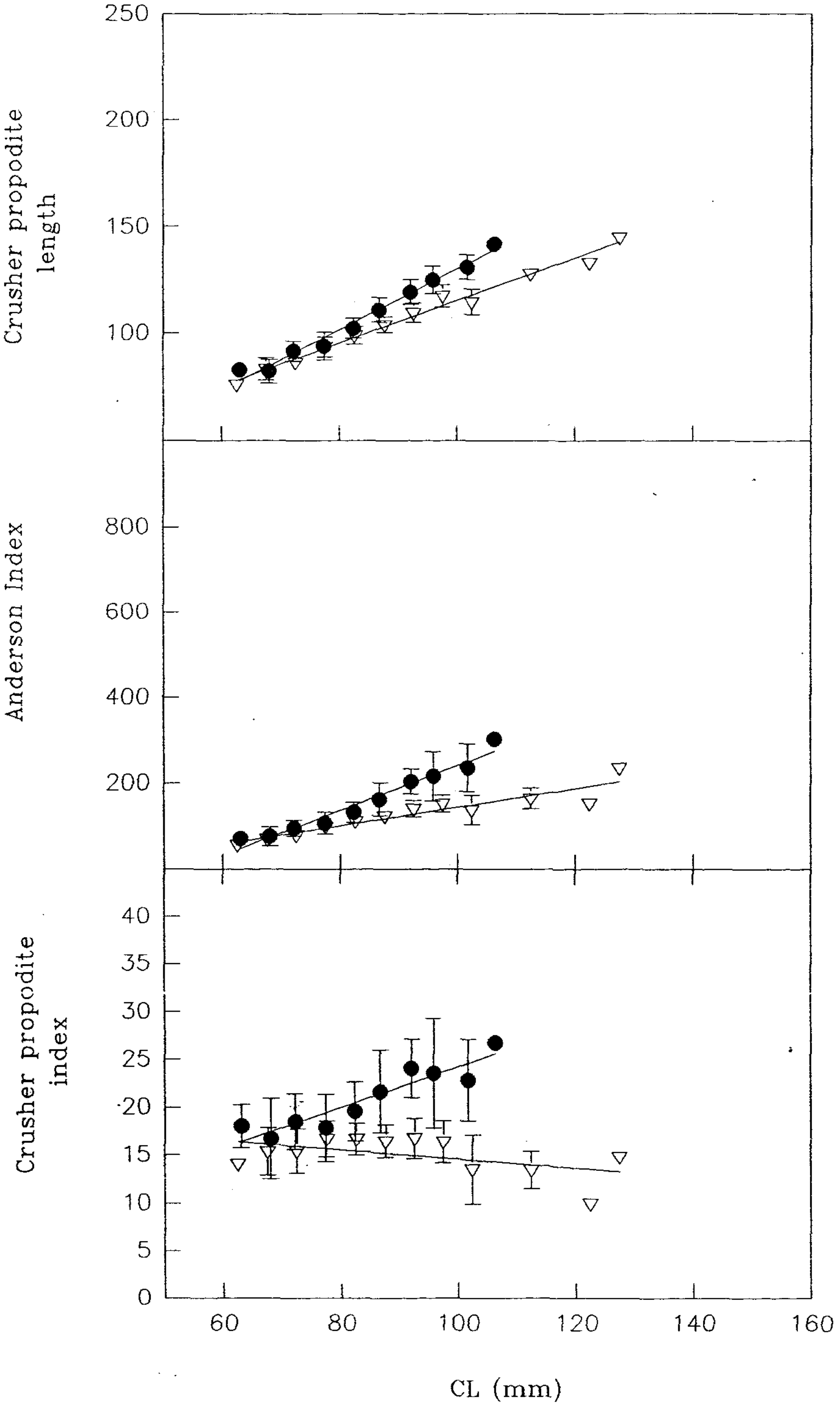


Fig. 5.14 External indicators of maturity, with linear regression lines Bridlington males and females, (5 mm CL groups) 1990

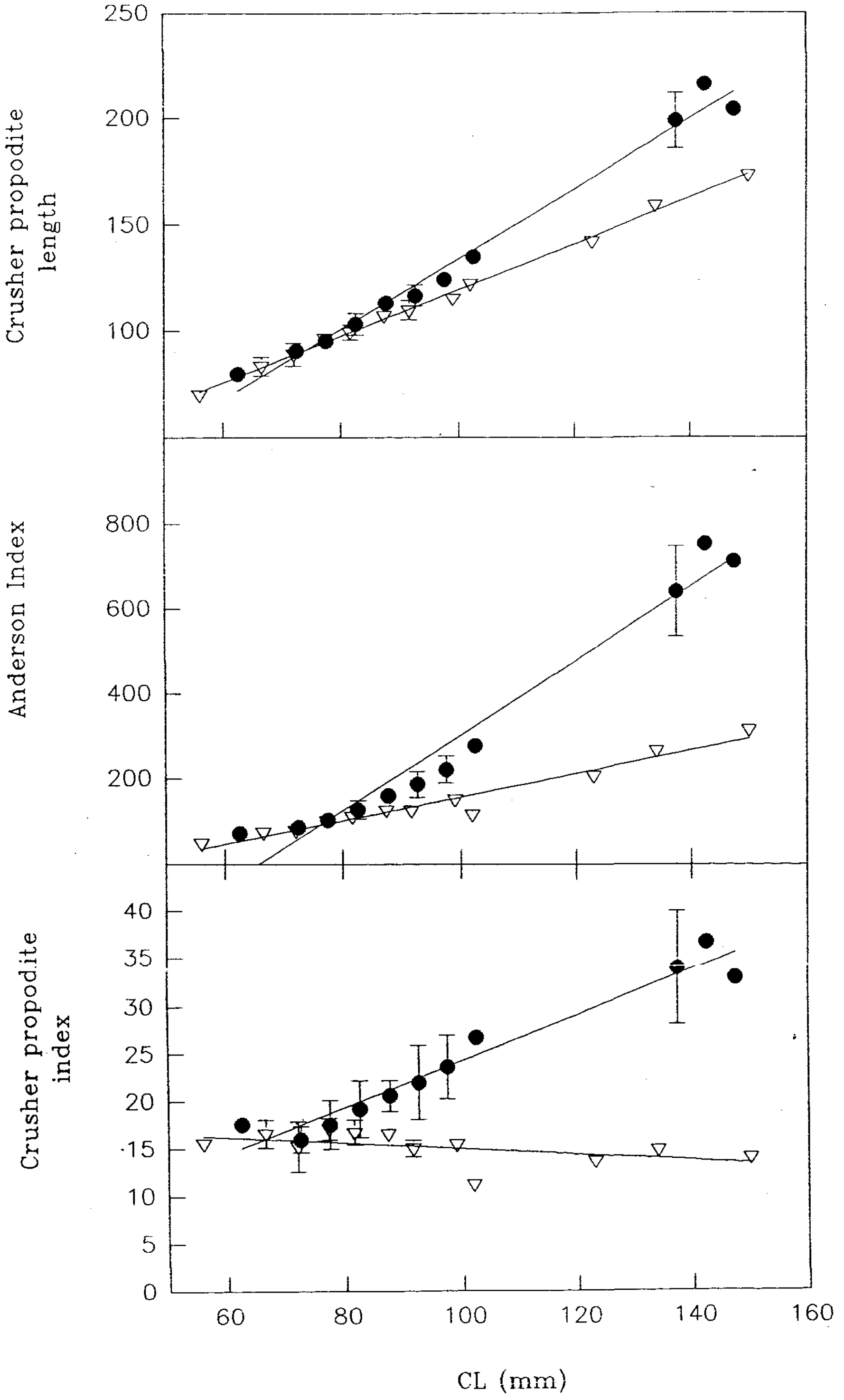


Fig. 5.15 External indicators of maturity, with linear regression lines Dale males and females, (5 mm CL groups) 1989

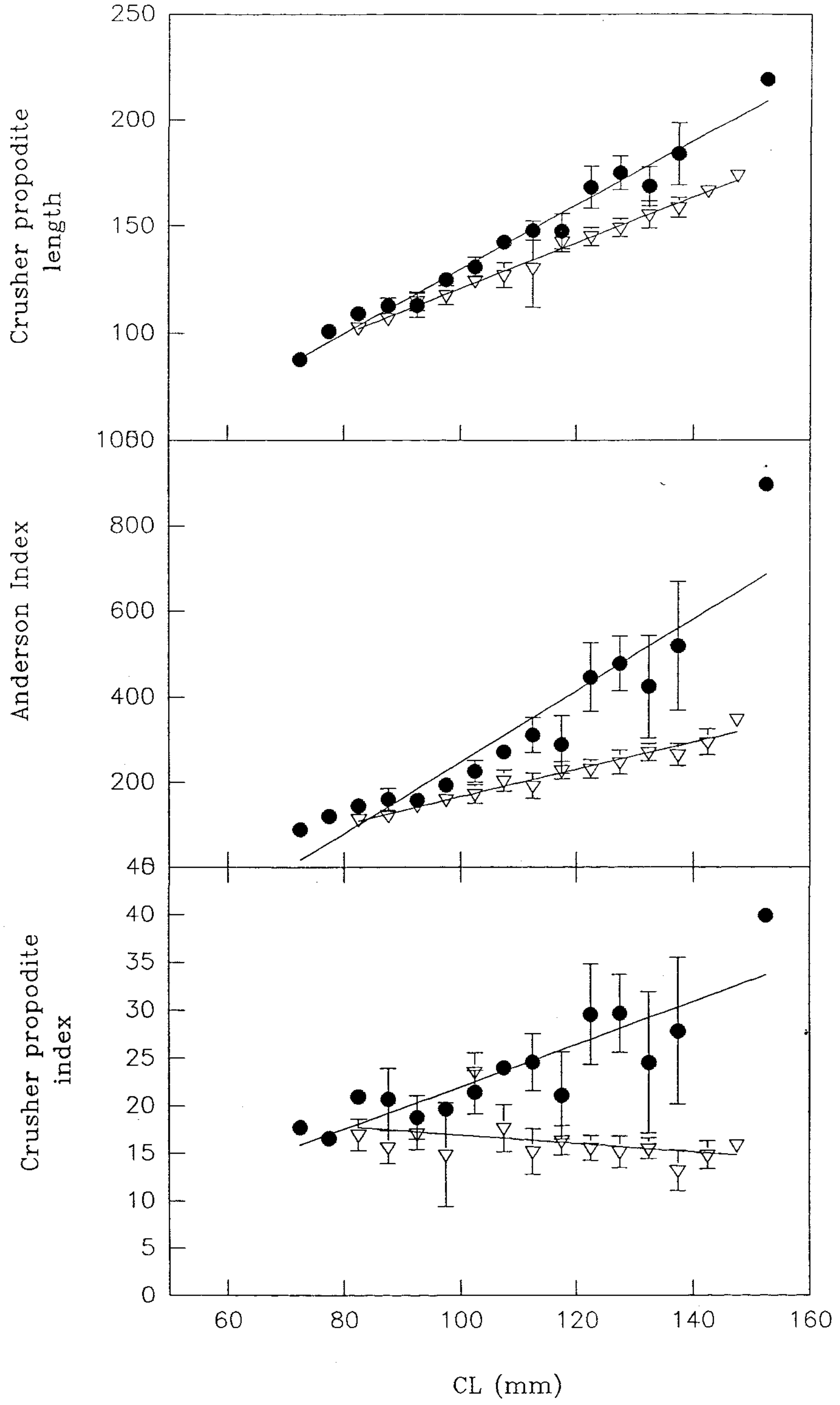


Fig. 5.16 External indicators of maturity, with linear regression lines Selsey males and females, (5 mm CL groups) 1989

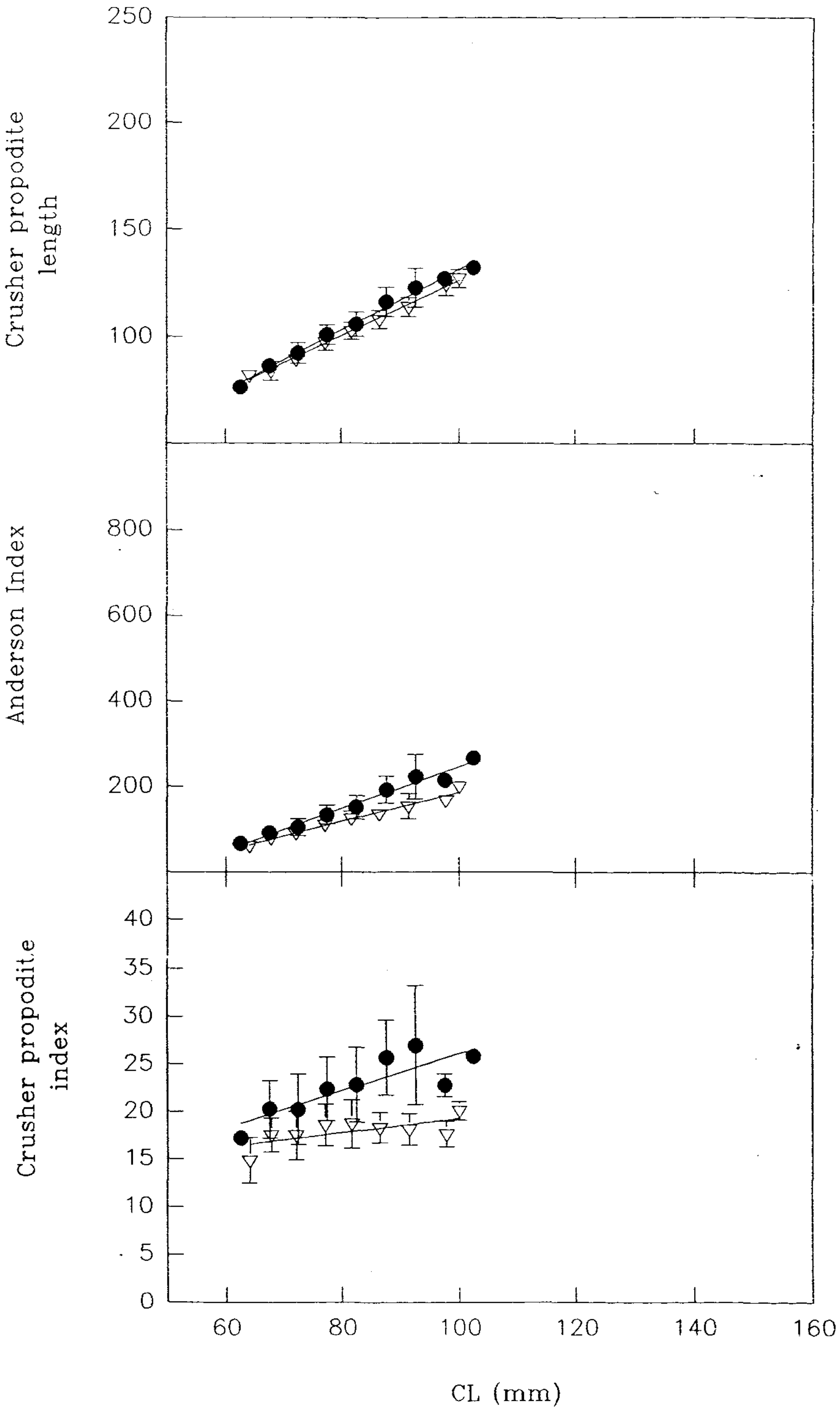


Fig. 5.17 External indicators of maturity, with linear regression lines Selsey males and females, (5 mm CL groups) 1990

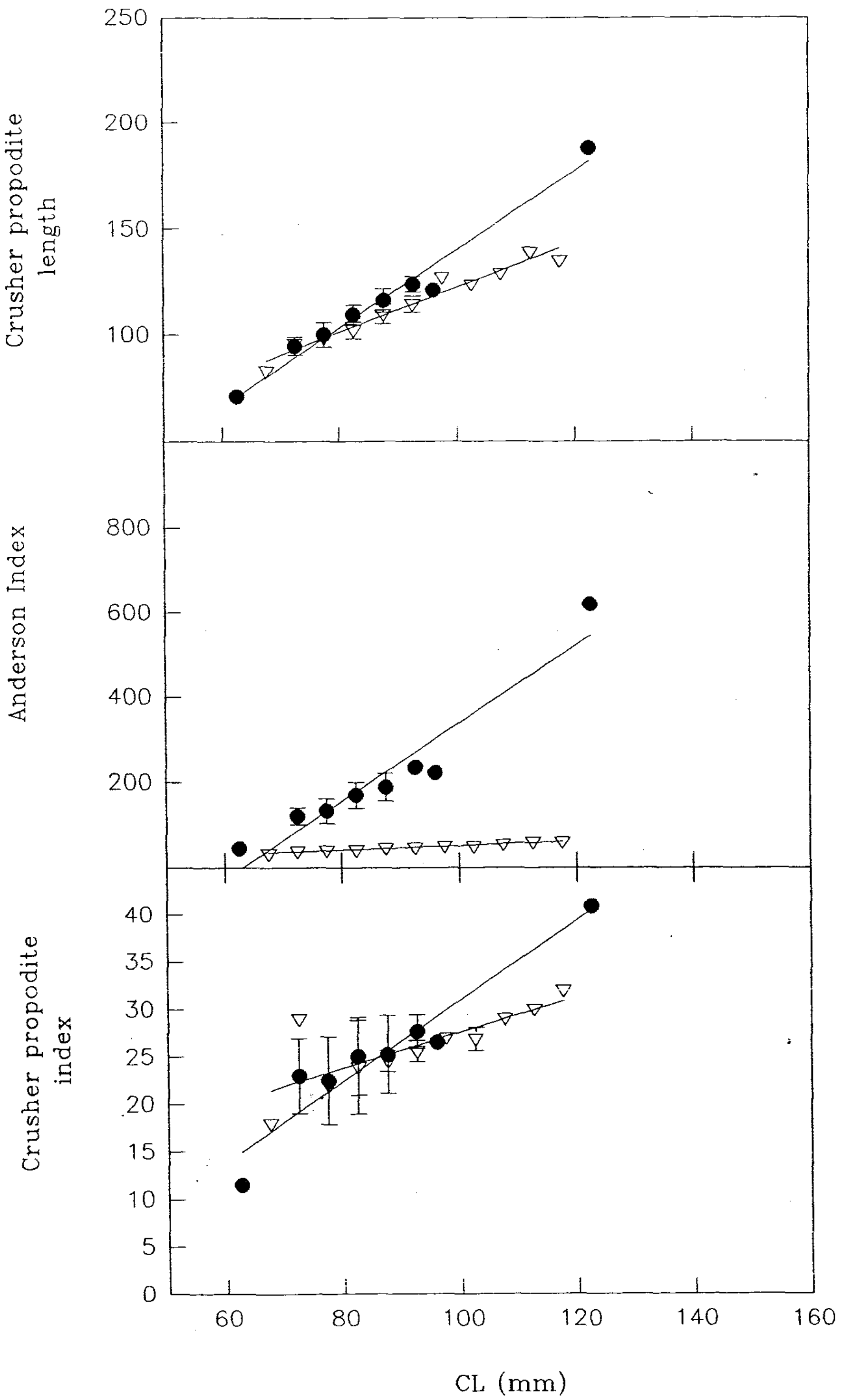


Fig. 5.18 Anderson index, with linear regression lines for Staithes males (5 mm CL groups), 1980 to 1981

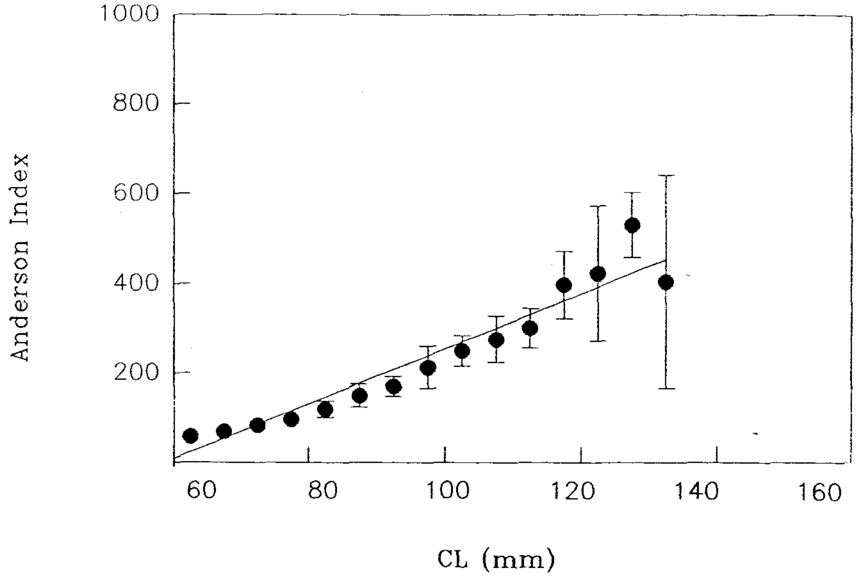
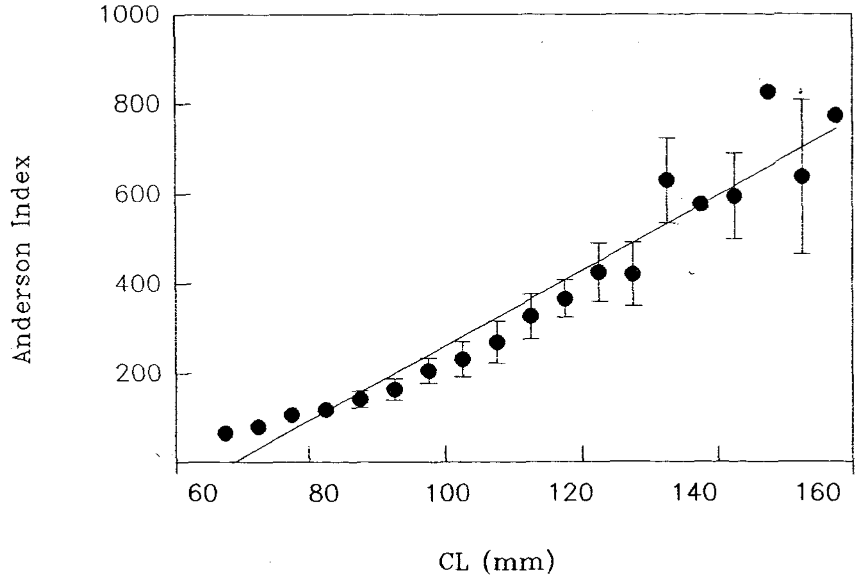


Fig. 5.19 Anderson index, with linear regression lines for St. Davids males (5 mm CL groups), 1980 to 1981



as indications of SOM.

5.3.2. Internal indicators of maturity

Relative hepatopancreas weight

Hepatopancreas weight for Bridlington, Dale and Selsey appears to increase with CL, although RHW may be considered constant with size (Appendix Tables A5ii.13 to A5ii.15)(Figs. 5.25 to 5.27). Individual male measurements of RHW do not show a strong correlation between the two variables ($R^2$0.001 to 0.221, linear regression model; 0.101 to 0.934 polynomial model; 0.001 to 0.128, natural log model)(Appendix Tables A5ii.55 to A5ii.57). Correlation is increased for 5 mm CL class regressions (Appendix Tables A5ii.70 to A5ii.73), being higher for hepatopancreas weight/CL relationship than for RHW/CL relationship (0.72 to 0.959 linear, 0.956 to 0.995 polynomial for HWT and 0.035 to 0.328, linear; 0.582 to 0.991, polynomial for RHW). ANCOVA for the three sites indicates a significant difference between-sites for hepatopancreas weight covarying with CL (Appendix Table A5ii.105), and a significant lack of covariance with CL for RHW (Appendix Table A5ii.106).

Crusher propodite weight

Crusher propodite weight (CPW) and relative crusher propodite weight (RCPW), measured for Staithes and St. Davids (1980 to 1981), both increase with CL (Figs. 5.28 and 5.29)(Appendix Tables A5ii.16 to A5ii.17). CPW regressions indicate a polynomial relationship with CL (Appendix Tables A5iii.79 to A5iii.81)(R^2 0.911 and 0.945). RCPW can be seen to have a natural log relationship with CL (R^2 0.886 and 0.947), although a polynomial model is also satisfactory (R^2 0.862 and 0.925)(Appendix A5iii.82 to A5iii.84). ANCOVAs between sites for both CPW and RCPW do not indicate a strong site effect ($P = 0.0054$ and $P = 0.0005$ respectively)(Appendix Tables A5iii.115 and A5iii.116).

Figs. 5.28 and 5.29 demonstrate an inflection point, by eye, for both CPW and RCPW when plotted against CL. These are both suggested to be at 90 mm CL for Staithes, and at 86.5 and 84.5 mm CL for CPW and RCPW respectively for St. Davids (Appendix Table A5iii.119).

Vas deferens weight

Vas deferens weight generally increases with an increase in CL (Figs. 5.24 to 5.29)(Appendix Tables A5ii.13 to A5ii.17), and appears to become asymptotic therefore indicating a potential inflexion point.

Bridlington, Dale and Selsey vas deferens weight measurements suggest that a polynomial regression model is the most appropriate for describing the relationship between VDW and CL (R^2 0.388 to 0.991)(Appendix Tables A5iii.58 to A5iii.60). 5 mm class regression results are presented in Appendix Tables A5iii.74 and A5iii.75, but are not considered valid because of the very high standard error of estimation. ANCOVA results for individual and 5 mm CL classes suggest significant differences in the covariance of VDW and CL between Bridlington, Dale and Selsey ($P = 0.488$ and $P = 0.2412$ respectively)(Appendix Tables A5iii.104 and A5iii.110)

Analyses of Staithes and St. Davids data suggest that the polynomial regression model gives the best fit for the relationship between VDW and CL (R^2 0.807 and 0.876 respectively), with a slightly lower standard error of estimation than for the natural log model (Appendix Tables A5iii.85 to Aiii.87). 5 mm CL class results indicate an improvement in R^2 for the polynomial regression for Staithes but not for St. Davids (0.911 and 0.782 respectively). ANCOVA does not indicate a highly significant difference in VDW covarying with CL for these two sites ($P = 0.0015$)(Appendix Table A5ii.117). The significance of the ANCOVA between all five sites ($P = 0.2591$) may be caused by differences in the sample numbers and sample size distributions of the 1980 to 1981 and 1989 to 1990 data sets.

Figs. 5.28 and 5.29 indicate potential inflection points for VDW when plotted against CL, which was determined by eye. These are suggested to be at 90 mm CL for Staithes, and at 85.5 CL for St. Davids (Appendix Table A5iii.119).

Relative vas deferens weight

Relative vas deferens weight (Figs. 5.24 to 5.27)(Appendix Tables A5ii.13 to A5ii.15) increases with CL. Selsey data shows a wide variation in RVDW for individuals of a similar size; although this may be caused by the small size range of males from Selsey used in this study. Linear, polynomial and natural log regression models demonstrate this poor correlation for Selsey data (Appendix Tables A5iii.61 to A5iii.63), whilst also suggesting the inadequacies of linear, polynomial and natural log models for Bridlington and Dale data (despite polynomial R^2 of 1 for both sites, as Sy/x is exceptionally large). ANCOVA results (Appendix Table A5iii.111) for 5 mm CL classes (to try and reduce the effect of individual variation) also suggests significantly poor covariance between RVDW and CL, and a significant difference between the three sites (Appendix Table A5iii.111).

Vas deferens factor

The vas deferens factor (Vdf) can be seen to increase with CL, but varies considerably between males of similar sizes (Appendix Tables A5ii.13 to A5ii.17; Figs. 5.24 to 5.29). Regression analysis of Bridlington, Dale and Selsey data (Appendix Tables A5iii.64 to A5iii.66 and A5iii.78) does not suggest a satisfactory model for describing the relationship between Vdf and CL, because of the high calculated P values for each model. Staithes and St. Davids Vdf/CL data (with larger sample size distributions), have been shown to be best represented by a natural log or polynomial model (R^2 0.375 and 0.461 or 0.287 and 0.451 respectively)(Appendix Tables A5iii.88 to A5iii.90). This correlation is increased by sorting the data into 5 mm CL classes (R^2 0.894 and 0.98 for the polynomial model)(Appendix Tables A5iii.101 and A5iii.102).

ANCOVA between Bridlington, Selsey and Dale Vdf/CL data (both of individuals and males in 5 mm CL classes) suggest significant differences between the sites, and a poor covariance of the two variables (Appendix Table A5iii104 and A5iii.112). A slight site effect may be observed between the Staithes and St. Davids Vdf/CL relationships in ANCOVA Appendix Table A5iii.118 ($P = 0.0051$). 5 mm CL class ANCOVA between all five sites also suggests differences between the sites (Appendix Table A5iii.113).

Additional analysis

Vas deferens factor covariance with CPW was analyzed for Staithes and St. Davids data (Appendix Tables A5iii.91 and A5iii.92), indicating a polynomial relationship between the two variables (R^2 0.31 and 0.471 for Staithes and St. Davids respectively). Vas deferens weight was shown to have a high linear

Fig. 5.20 Male internal condition indices (with linear regression lines), Bridlington 1989 to 1990

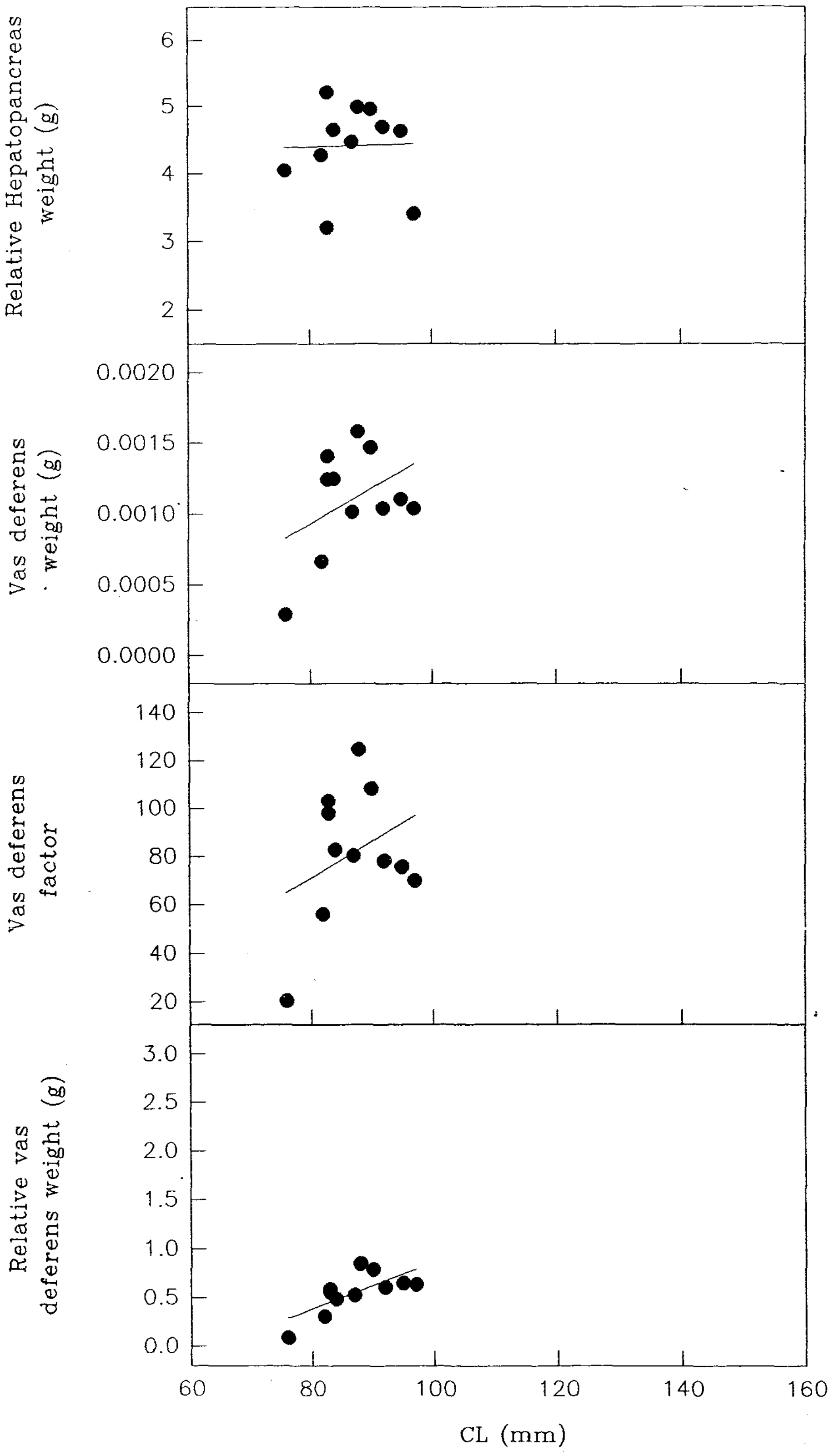


Fig. 5.21 Male internal condition indices (with linear regression lines), Dale 1989

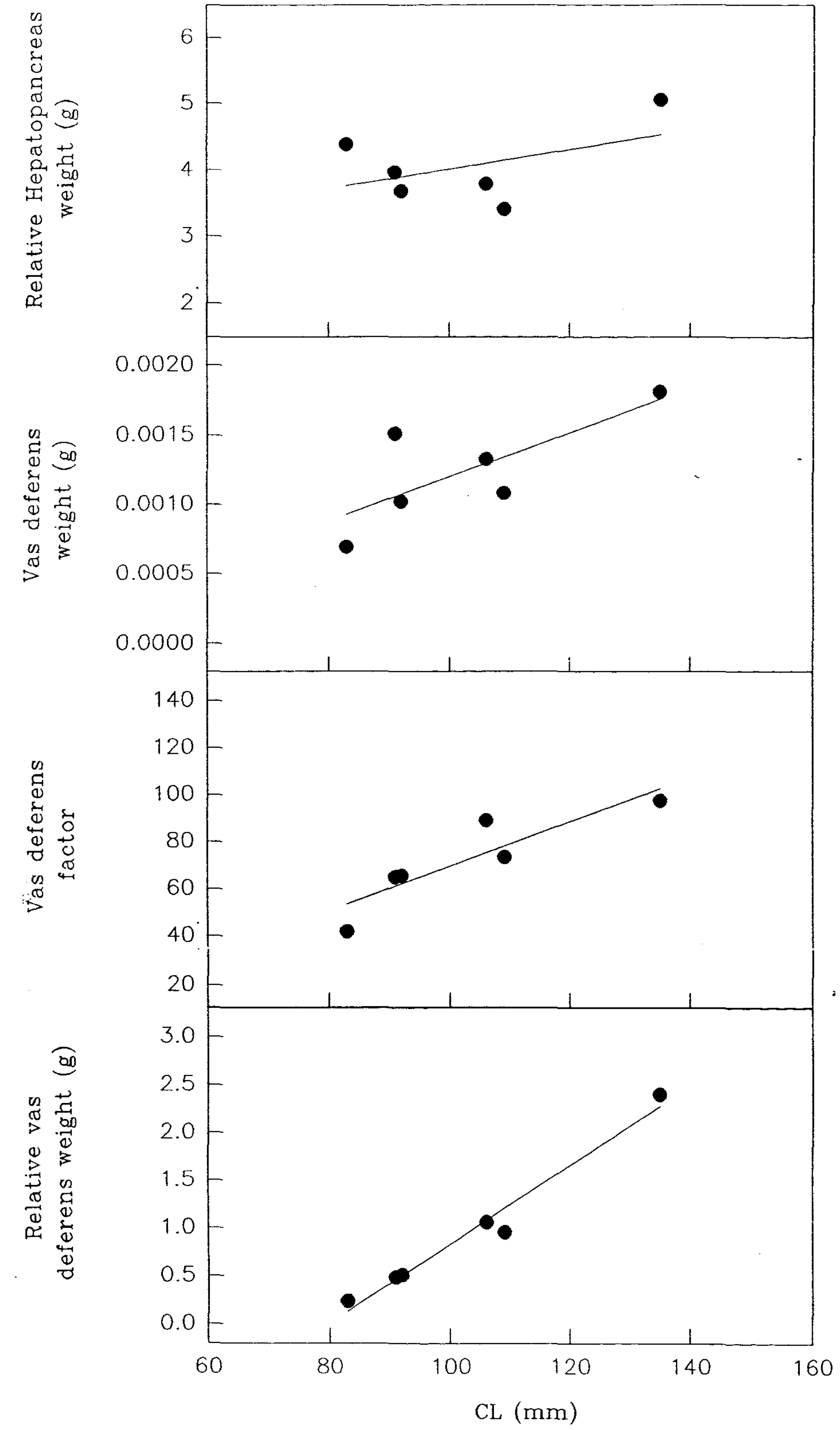


Fig. 5.22 Male internal condition indices (with linear regression lines), Selsey 1989 to 1991

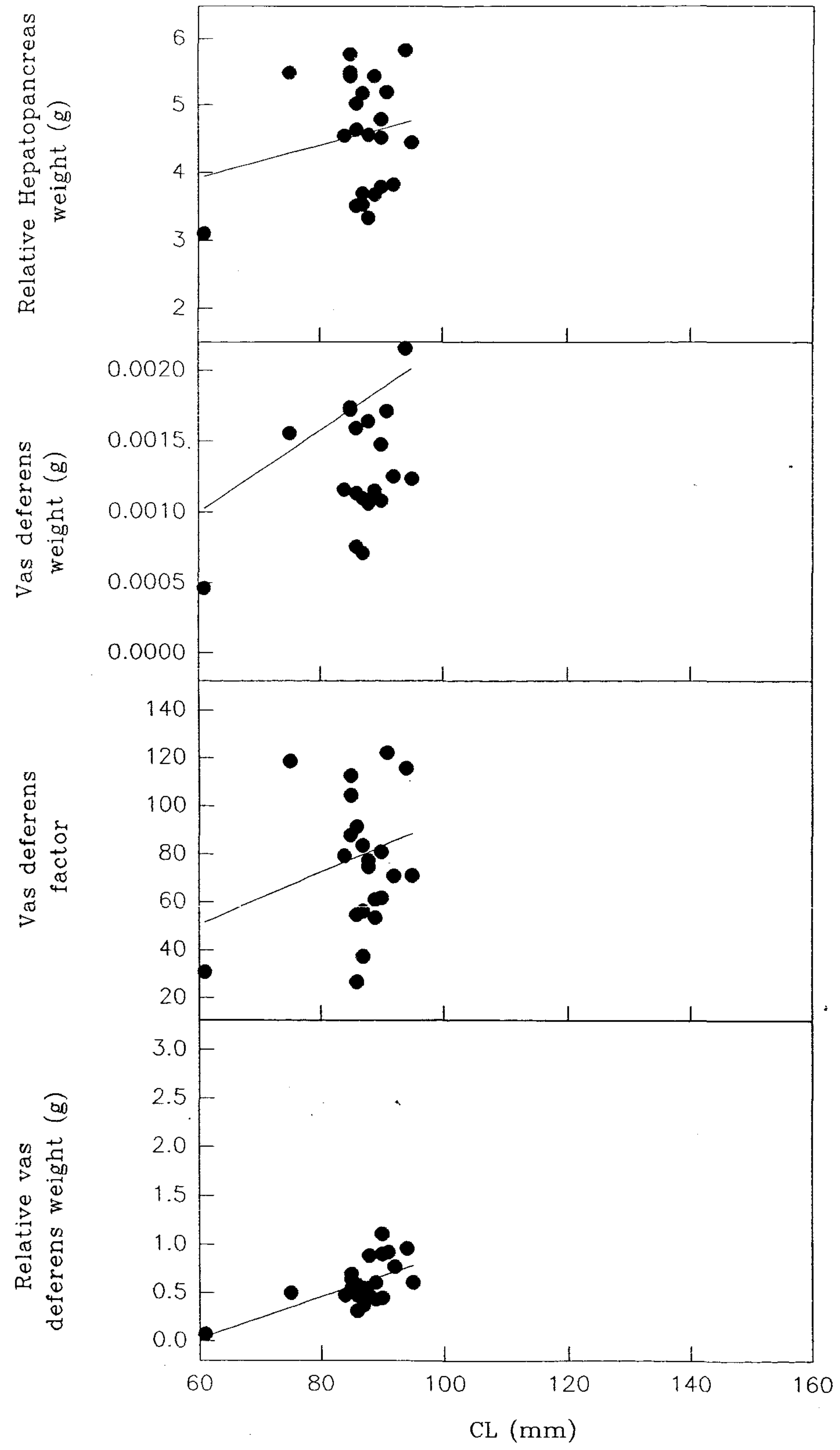


Fig. 5.23 Male internal condition indices (with linear regression lines). Staithes 1980 to 1981

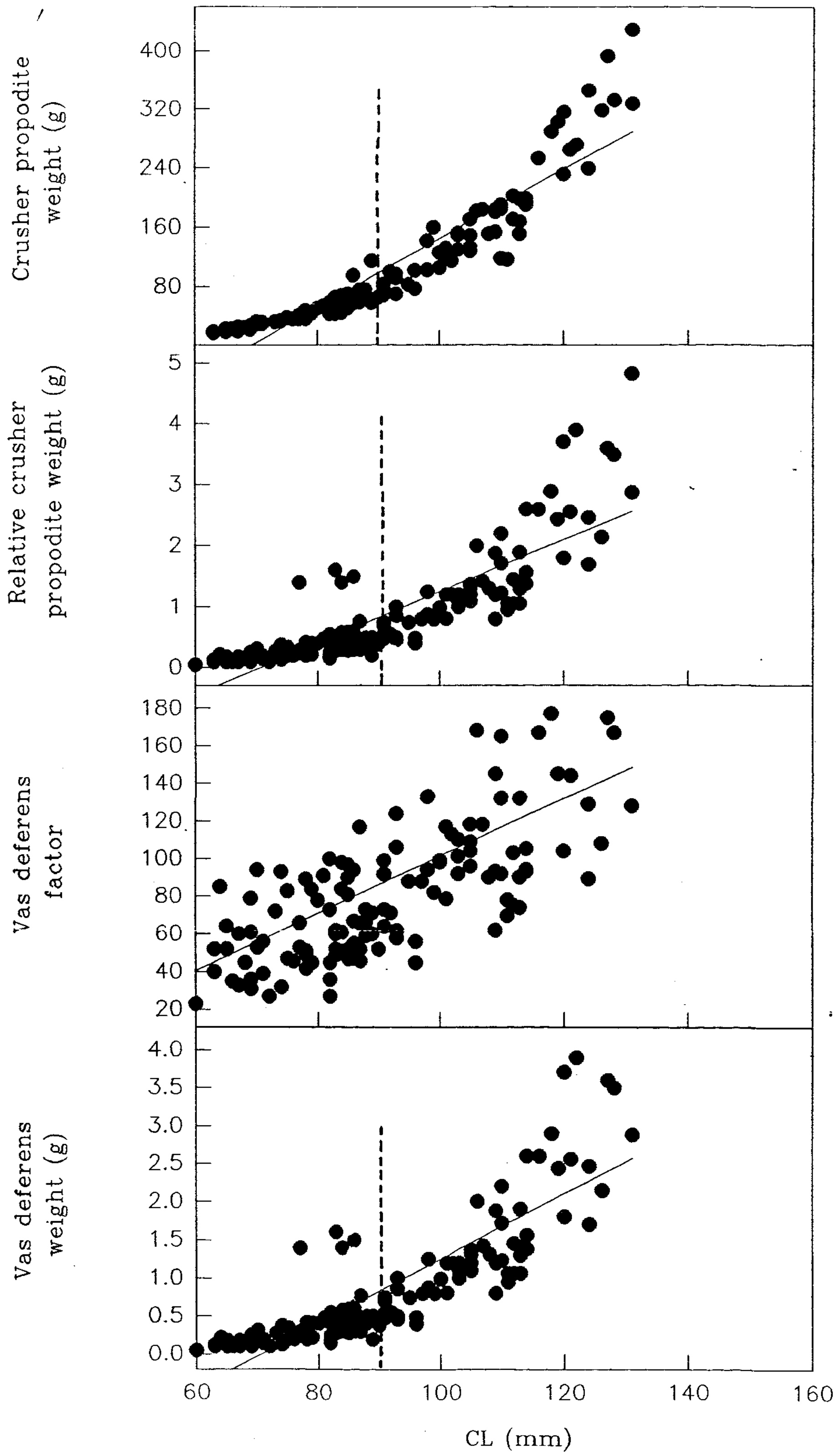
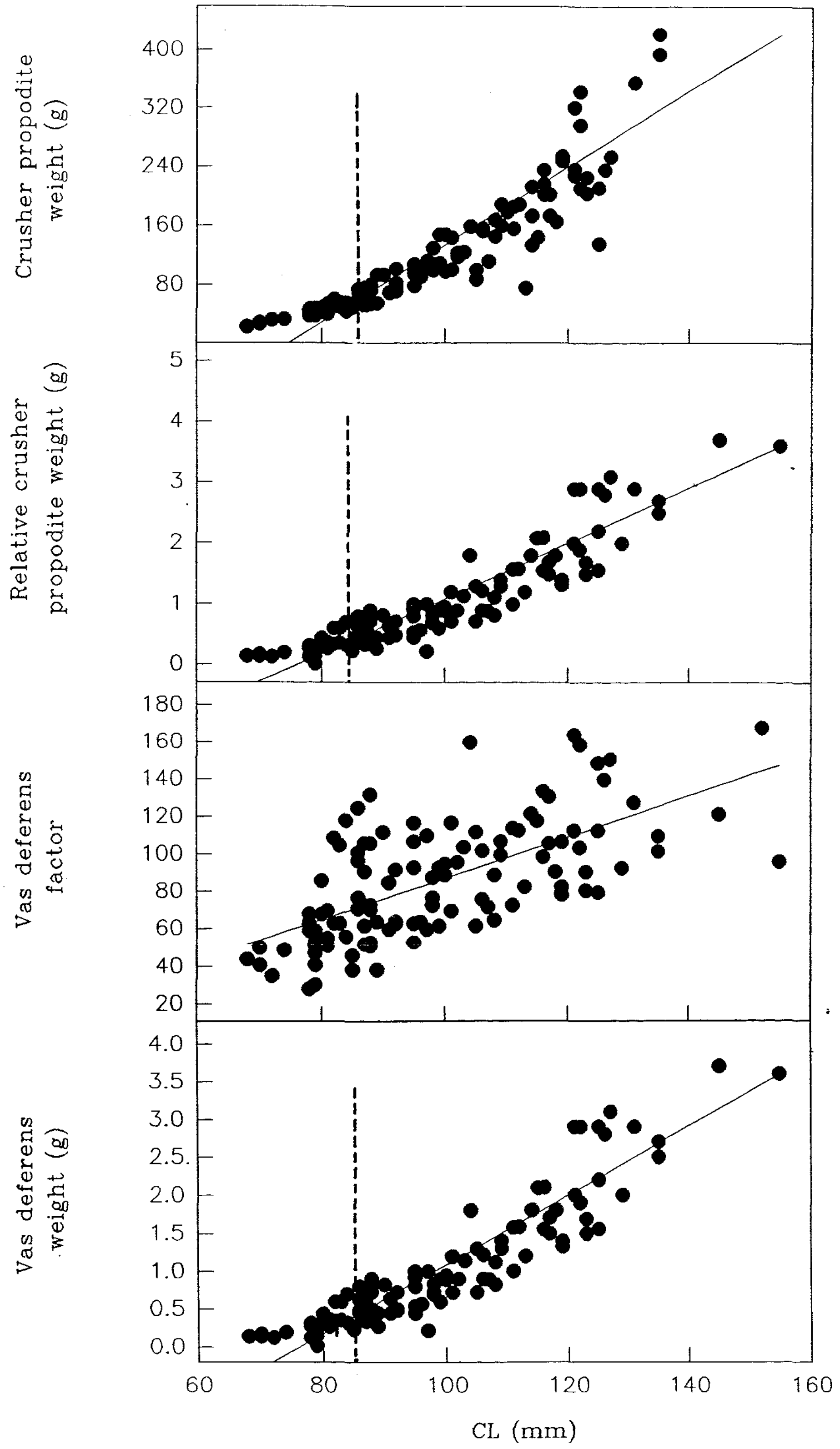


Fig. 5.24 Male internal condition indices (with linear regression lines), St. Davids 1980 to 1981



correlation with CPW (R^2 0.849 and 0.877)(Appendix Tables A5iii.93 to A5iii.94). Appendix Tables A5iii.67 to A5iii.69 suggest that a natural logarithmic model adequately describes the relationship between RHW and Vdf at Bridlington, Selsey and Dale (R^2 0.569 to 0.932).

Each of the twelve vas deferens dissected from Selsey males, between 75 and 95 mm CL, were found to contain live spermatozoa when examined microscopically.

5.3.3. Size at onset of maturity

Bridlington

Bridlington 1989 male maturity estimates range from 69.8 to 77.5 mm CL, averaging 72.2 mm (Tables 5.1 and 5.2). CPL-CL linear regression lines for males and females intersect at 72.7 mm CL. Anderson index plot male and female linear regression lines intersect at 74.2 mm CL, lower than the observed 77.5 mm CL Anderson index inflexion point. Bridlington 1990 results suggest a larger SOM than for 1989 data, averaging 75.2 mm CL, with estimates ranging from 69.2 to 90 mm CL (Tables 5.1 and 5.2). CPL-CL male and female linear regression lines for 1990 intersect at 76.9 mm CL. The 1990 Anderson index male-female linear regression line intersects at 78.7 mm CL.

Dale

Dale 1989 male SOM estimates average 87.174 mm CL, ranging from 79.53 to 102.5 mm CL. CPL-CL male and female linear regression lines intersect at 86.9 mm CL.The Anderson index male-female linear regression lines intersect at 88.717 mm CL (Tables 5.1 and 5.2).

Selsey

Selsey 1989 estimates of the size at male onset of maturity range from 58.653 to 77.5 mm CL, averaging 64.071 mm CL. CPL-CL and Anderson index linear regression lines for males and females intersect at 65.9 mm CL and 60.178 mm CL respectively (Tables 5.1 and 5.2). Selsey 1990 data exhibits a higher mean SOM estimate of 69.124 mm CL, ranging from 59.921 to 76.846 mm CL (no Anderson index inflexion point could be determined for Selsey 1990 males)(Tables 5.1 and 5.2). CPL-CL and Anderson index male and female linear regression lines

Table 5 .1 Summary of estimates of SOM calculated by regression line intersections and observed plot inflexions

Site and year	CPL intersections			AI intersections			CPI intersections			AI inflections
	linear	polynomial	ln	linear	polynomial	ln	linear	polynomial	ln	
Bridlington, 1989	72.731	-	71.179	74.159	-	70.149	69.821	-	70.15	77.5
Bridlington, 1990	76.897	69.059	73.95	78.682	73.393	71.707	71.415	-	71.76	90
Dale, 1989	86.92	95.45	83.59	88.717	-	79.53	80.636	-	80.05	102.5
Selsey, 1989	65.912	59.776	68.395	60.178	67.669	58.653	58.93	-	59.62	77.5
Selsey, 1990	73.745	-	59.921	65.088	-	69.59	76.846	-	69.55	-
Staithes, 1980 to 1981	-	-	-	-	-	-	-	-	-	83.5
St. Davids, 1980 to 1981	-	-	-	-	-	-	-	-	-	86.5

Table 5.2 Average and standard deviations of male SOM estimates using external indicators

Site and year	Mean	Std. Dev.
Bridlington, 1989	72.241	2.80881
Bridlington, 1990	75.207	6.2743
Dale, 1989	87.174	8.1989
Selsey, 1989	64.071	6.396
Selsey, 1990	69.124	6.0393
Staithes, 1980 to 1981	83.5	0
St. Davids, 1980 to 1981	86.5	0

intersect at 73.8 mm CL and 65.088 mm CL respectively.

Staithes

As no female crusher propodite dimensions were available for Staithes and St. Davids data, the AI inflexion point method was the only one available for use on these data. The AI inflexion occurred at 83.5 mm CL for Staithes males, 1980 to 1981 (Tables 5.1 and 5.2). This is lower than the inflexion point for CPW, RCPW and VDW plot observed inflexion points, all of which were at 90 mm CL (Appendix Table A5iii.119).

St. Davids

The AI inflexion point occurred at 86.5 mm CL for St. Davids males (1980 to 1981) (Tables 5.1 and 5.2). CPW, RCPW and VDW plots revealed inflexion points of between 84.5 and 86.5 mm CL (Appendix Table A5iii.119).

Between all sites

Estimates of male SOM from all sample sites for each sample year, calculated using external indicators of maturity intersections and inflexions, were compared using ANOVA. Appendix Table A5iv.2, showing the results of the ANOVA, suggests significant differences between the sample site and year estimates of SOM ($P< 0.001$). A Student-Newmann-Keuls test (for pairwise comparisons)(Appendix Table A5iv.3) showed that the Selsey 1989 estimates of SOM were significantly different from those of all other sites but Selsey 1990. The Dale 1989 SOM estimates were also found to be different from those of other sample areas, except for Staithes and St. Davids (1980 to 1981). No other pairwise comparisons were shown to be significantly different from each other at the 5% level.

5.4. Discussion

The validity of external male maturity indicators for *H. gammarus*, using crusher propodite dimensions, is of considerable importance to fisheries management. The success of fisheries management based upon minimum legal landing size legislation (MLS), is undoubtedly reliant on MLS being above the size at maturity of an adequate proportion of individuals in order to avoid recruitment failure. The difference, however, between size at onset of male lobster maturity and

MLS may not be as critical as female maturity from a management perspective, assuming that some lobsters will always avoid capture and the potential for multiple insemination by individual males.

This study has investigated the use of crusher propodite length (CPL), the Anderson index (AI) and crusher propodite index (CPI) as external indicators of male maturity for *H. gammarus*.

The Anderson index, plotted against CL, appears to exhibit an inflexion for male lobsters which may be conceived to represent male functional maturity. The use of the Anderson index was disputed for *H. americanus* by Ennis (1980), who did not observe such an inflexion point. The poor clarity of this point (e.g. Selsey 1990) and its accurate determination by eye are two inhibiting factors against the use of this index. Statistical calculation of inflexion points is a potentially difficult procedure, complicated by individual variability within a population data set such as those interrogated during lobster size at onset of maturity (SOM) investigations.

The use of male and female regression line intersection points is a more practical method of determining male SOM. The use of CPL or AI and CPI intersection methodology depends upon the nature of the allometric growth of male crusher claws; CPL intersections assume a linear relative growth of the claw in relation to CL, compared to AI and CPI indices which assume that lobster claw volume is the parameter displaying positive allometric growth to growth in CL. The methods of calculating both AI and CPI involve the use of the dependent variable (CL)(Appendix 5i.1), and are therefore not as statistically valid as CPL which is independent of CL. The linear nature of CPL-CL regression lines shown during this investigation (and therefore the lack of a defined inflexion point, as suggested for *H. americanus* by Aiken and Waddy, 1980: c.f. Templeman, 1935 CPL-TL) also facilitates the use of CPL as an indicator of sexual maturity.

CPI has not been shown as a good indicator of male sexual maturity for *H. gammarus*, because of poor correlation with CL, and the probability of higher individual variability in the CPI-CL relationship, compared to AI and CPL. Confirmation of CPL, or AI male and female regression line intersections as valid indicators of male sexual maturity, is complicated by the difference between size at physiological and size at functional maturities. AI male and female plots against

CL are best described by a second order polynomial model, with regression lines that do not always intersect; the adequacy of using the linear model regression line intersection is dubious and the AI intersection method as an indication of sexual maturity is therefore doubtful.

Crusher propodite weight and relative crusher propodite weight both suggested inflexion points when plotted against CL for Staithes and St. Davids data, 1980 to 1981 (as suggested for *H. americanus* by Squires, 1970 and Ennis, 1971; 1980). Vas deferens weight has been shown to be highly correlated (linear model) to crusher propodite weight, and CPW may therefore be a good indication of male internal condition. The use of these potential indicators of maturity is made difficult in field work at sea, and also by the cost of claw removal. It is worth noting, however, that the suggested AI inflexion point is at a higher CL for St. Davids than for Staithes, and that RCPW and CPW inflexion points are at a lower CL for St. Davids than for Staithes. The reason for this is uncertain, but may be important in the consideration of the validity of the Anderson index as a representation of claw volume and therefore as an external indicator of male maturity.

The sizes at which each of the above suggested inflexion points and intersections of female and male regression lines occur do require validation in relation to size at maturity. The observed change from isometric to allometric growth of the crusher propodite relative to the growth of CL may occur at the moult prior to the functional maturity moult, although it is most probable that this is not the case and that the rapid change in claw growth rate occurs at the maturity moult itself. In this study the use of external maturity indicators is based upon population data, not individual growth patterns, and is therefore complex; individual variability in size at moult and maturity may confuse analyses to find population trends. The concept of a local population of lobsters becoming sexually mature at approximately the same size is acceptable, but analysis of data collected from a large number of individuals may encompass data from more than one population (stock), because of fishing area boundaries, and the problem of delimiting the natural, local, population. However, this study suggests that comparisons between SOM at different locations (sufficient for fisheries management purposes) are possible using the CPL-CL linear regression line intersections between male and female lobsters (c.f. Conan and Comeau, 1985).

Unfortunately, as a result of the destructive and expensive methods of lobster dissection examination, no investigation into seasonal or annual variation in male internal condition indices has been undertaken during this study (concentrating more on female internal indicators of maturity because of the potentially greater relevance of female SOM for fisheries management purposes; Chapter 4). The differentiation between physiological and functional maturity (Ennis, 1980) in male *H. gammarus* was also not fully explored during this study, because of the practicalities of the required increase in the size range of individuals studied. Physiological maturity in *H. americanus* may occur at less than 57 mm CL (Krouse, 1973; Briggs and Mushacke, 1979) and the cost and effort of studying animals smaller than those captured by fishing was considered prohibitive. The difference between male size at physiological and functional maturity has still therefore to be investigated fully for *H. gammarus*. Size at functional maturity is more important than that at physiological maturity for fisheries management, although the determination of functional maturity using internal condition indices may be complicated by the earlier onset of physiological maturity (MacDiarmid, 1989).

For Staithes and St. Davids data, the vas deferens factor did not show any distinct inflexion points when plotted against CL; Vdf also showed a high degree of individual variability. Staithes and St. Davids vas deferens weight plotted against CL did produce an inflexion point that may be considered as an indication of SOM, with an increase in individual variation after the inferred SOM, suggesting variability in recovery time after mating (MacDiarmid, 1989; Aiken and Waddy, 1991).

Selsey 1989 SOM estimates were shown overall to be significantly lower than estimates from all other sample sites by year, except for Selsey 1990 data. The Dale SOM also differed significantly from all but the Staithes and St. Davids SOM, being at a larger size than for the other study areas (Appendix Table A5iv.3). ANCOVA showed some temporal variation in external index-CL regressions within sites, indicating the potential for annual variation in the external indicator intersection values. However, no differences in the size at onset of maturity were shown to be significant at any one site between years, therefore suggesting spatial but no short-term temporal variation in SOM of male lobsters at the sites studied during this project.

CHAPTER 6 FECUNDITY AND EGG DEVELOPMENT

6.1 Introduction

Fecundity estimates are an important consideration for fisheries management, as they are important in estimating spawning stock biomass and thus egg production. Comprehension of fecundity/size-relationships may lead to management legislation for the protection of certain size ranges of broodstock, in order to maintain the highest theoretical levels of recruitment.

Management legislation involving a ban of the fishing of ovigerous females exists in most north American *Homarus* fisheries, but only in Spain and Portugal for two months a year, and Limfjord in Denmark for the European lobster (Bennett, 1980; 1981). The Maine lobster fishery successfully uses a ban on the landing of v-notched females, which are voluntarily marked by fishermen when the females are ovigerous (Daniel *et al*, 1989).

English and Welsh byelaws banning the landing of berried hens were converted into national law in 1951. This law was repealed in 1966 because of difficulties in enforcement and a lack of knowledge of the relationship between stock and recruitment relationships (Thomas, 1965; Bennett, 1980). The protection of the breeding stock of *H. gammarus* has therefore centred on legislation based solely on raising the minimum legal landing size to above the size at onset of maturity, to avoid recruitment failure. Although large increases in egg production would occur with a ban on the landing of berried females (Bennett, 1981), any management options which increase stock biomass (particularly of females) would also increase egg production and therefore reduce the risk of recruitment failure.

Oviposition takes place between 1 month and 2 years after mating (Bumpus, 1894; Byard, 1975) in *H. americanus*, but can also occur without successful fertilization (Aiken and Waddy, 1980). The timing of both moult and egg extrusion has been shown to vary throughout the lifespan of the female *H. americanus* (Aiken and Waddy, 1976); with larger females extruding eggs later in the season. This may be a response to optimise energy partitioning at different stages of an individual's life history (Attard and Hudon, 1987). Larger female American lobsters in the Iles de la Madeleine (Quebec) were shown to carry more developed eggs than smaller individuals (Attard and Hudon, 1987) and this phenomena may be related to differing times of egg extrusion and/or local temperature regimes during egg development.

The spawning period of *Homarus gammarus* populations have been reported by Branford (1978) to begin in July and finish in September. *Homarus americanus* females have been reported to spawn any time between May and October, but most commonly between June and September (Bumpus, 1894; Herrick, 1894; Templeman, 1940; McLeese and Wilder, 1964; Ennis, 1971; Thomas, 1973, Aiken and Waddy, 1980). Templeman (1940) suggested that the timing of spawning in populations was variable between locations, with lobsters from warmer waters starting egg incubation later than individuals from cool water areas. Aiken and Waddy (1990) suggested that lobster spawning of inshore stocks may be regulated reliably by significant seasonal temperature changes. Maturation, vitellogenesis and spawning in areas without temperature variation required photoperiod cues as exogenous control (Aiken and Waddy, 1990).

Templeman (1937) made two laboratory observations of female American lobsters spawning, and reported an egg laying position with the females forming a brood chamber with their abdomen tucked and the ventral side uppermost (cf. Knight (1918) who reported the dorsal side to be uppermost). The eggs are then extruded from both oviducts in a continual stream and are deposited in the brood chamber, enclosed by the setae of the abdominal pleura. Egg extrusion has been observed in *H. gammarus* as taking several hours (Scott, 1903, cited in Aiken and Waddy, 1980), and once complete the female remains on its back for an additional 20-30 minutes whilst the eggs become firmly attached to the pleopods.

At the time of oviposition, the eggs of *Homarus gammarus* have only one egg membrane, formed during oogenesis by the developing oocyte itself (Cheung, 1966). Hinsch (1971) identified two distinct layers of the primary egg membrane in the mature oocytes of the spider crab, *Libinia emarginata*, (the outer of which is only 0.6μm thick). Aiken and Waddy (1980; 1982) believe that this is probably also the case in *Homarus spp.*. The mechanism by which the further egg membranes are then produced is disputed. Yonge (1937; 1940) proposed that the inner, living egg membrane becomes surrounded by an external chitinous membrane secreted by the oviduct epithelium during egg deposition, and that a third membrane is produced by the tegumental cement glands. Burkenroad (1947) criticized Yonge's hypothesis, after his work on *Palaemonetes vulgaris*, and suggested that all the components of the egg membrane are produced by the oocyte or embryo, with the second membrane being produced on contact with a foreign medium (i.e. sea water). The third membrane is then developed half an hour after the second and a fourth membrane (only formed in fertilised eggs) approximately twelve hours after spawning. Cheung (1966) discussed various theories of egg membrane formation and concluded that Burkenroad's (1947) suggestion that all the egg membranes were formed by the egg itself, was correct. Cheung (1966) stated that the primary egg membrane (or vitelline membrane) formed before spawning, is lined internally by two more membranes, produced by the egg itself after fertilisation, to complete the 'trichromatic membrane' (so named because of the differential stainability of the three layers). Two more chitinous membranes are apparently produced on the inside of the trichromatic layer later in the egg's development. The fifth and innermost layer is suggested by both Burkenroad (1947) and Cheung (1966) to be an embryonic exuvia.

The egg stalk or funiculus of homarids, derived from the vitelline membrane (Cheung, 1966), is thought to be directly attached to the ovigerous setae, and not to a central stalk as in the palinurid *Jasus lalandii* (von Bonde, 1936, and Silberbauer, 1971). Yonge (1937), working on *H. gammarus,* suggested that a secretion from cement glands, which hardens following exposure to water, was responsible for adhering the eggs in place. Burkenroad (1947) noted that there was no sign of any free adhesive material in the brood chamber and that eggs extracted from the ovary adhered to each other, but to a lesser extent than those spawned naturally. Burkenroad (1947) hypothesised that a form of cement is secreted by the eggs and that the fusion of the eggs is then increased by an enzyme-like intensifying-substance secreted by the cement glands on the pleopods. Cheung (1966) also believed that the cement for attachment is produced by the eggs themselves, as a result of fertilisation, although with the eggs themselves containing the adhesive hardening agent. This would also follow the work of Stevenson and Schneider (1962) on crayfish which suggests that cement glands in the brood chamber are responsible for secreting the enzyme tyrosinase for phenolic hardening of the egg epicuticle. Silberbauer (1971) reported that a secretion from the cement glands of *J. lalandii* gelled within two minutes of its exposure to sea water and became tacky within twenty minutes, and concluded that the cement gland secretion is indeed the adhesive for attachment of eggs to the ovigerous setae. Aiken and Waddy (1982) supported Cheung's (1966) theory that cement gland secretion might provide a suitable medium for external fertilisation, thus providing a potential theory for incomplete unfertilised egg attachment in *Homarus spp.*. Different degrees of egg adhesion have been reported by Aiken and Waddy (1980) who suggested that behavioral aberrations by the female at the time of egg extrusion may be a causal factor.

Estimates of the individual fecundity of *Homarus americanus* were first made by Herrick (1909), who used a volumetric method to assess egg number in relation to female length. Further studies by Saila *et al* (1969) and Perkins (1971), using an electronic counter, and Squires (1970), using the volumetric method, also revealed a logarithmic relationship between female carapace length and egg number (it should be noted that in most studies individual fecundity is described as the number of eggs carried by a female, i.e. clutch size (Barnes and Barnes 1968; Sastry 1983)). Apart from variations in fecundity with female size, clutch size has been shown to vary between females of similar sizes in *H. americanus* (Squires, 1970), and was also reported for the blue crab *Portunus pelagicus* (Batoy *et al*, 1987).

Differences between estimates of fecundity have been attributed to methodology and geographic location by Aiken and Waddy (1980), but may also be caused by egg development stage as up to 36 % egg loss may occur during the incubation period (Perkins, 1971). The majority of fecundity estimates have therefore taken place during the final two months of the incubation period, and resulting estimates can be multiplied by a correction factor if the numbers of eggs extruded are required (e.g. Attard and Hudon, 1987).

The work of Herrick (1909), Perkins (1971), and Saila *et al* (1969) all indicate a curvilinear relationship between clutch size and female carapace length on *H. americanus* with Figueiredo and Nunes (1965) and Morizur *et al* (1981) suggesting a similar relationship for *Nephrops norvegicus*. In contrast, the work of

Hepper and Gough (1978) on *H. gammarus* showed a linear relationship (Table 6.1), although this may be owing to a relatively small female size range as a linear relationship was also indicated for *H. americanus* by Squires (1970) work on a reduced sample size range. Jensen (1958) suggested that the clutch size of *H. gammarus* was related to the cube of female total length.

The work of Hepper and Gough (1978), Latrouite *et al* (1984) and Bennett and Howard (1987) suggest a lower fecundity for *H. gammarus* than for *H. americanus*. The paucity of work on the fecundity of the European lobster prevents conclusions being drawn about possible geographical variation of the species, although the work on the fecundity of American lobster throughout its geographic range indicates both spatial and temporal variation in clutch size (Aiken and Waddy, 1980).

Table 6.1 Fecundity estimates of *H. gammarus*

Author	Location	Egg development stage	Fecundity estimate
Hepper and Gough (1978)	North Wales	Eyed	217.74CL-12490.3
Latrouite *et al* (1984)	Brittany	Eyed	305CL-22759
Bennett and Howard (1987)	Yorkshire	Non-eyed	247.5CL-9629
Bennett and Howard (1987)	South Wales	Non-eyed	430.8CL-32782
Bennett and Howard (1987)	South Wales	Eyed	430.8CL-35872

Variation in the fecundity of populations of *H. americanus* has been shown by Squires (1970; 1971) on the northwest coast of Newfoundland, and Attard (1985) on the north west and southeast coasts of Iles de la Madeleine, Quebec. Aiken and Waddy (1986) hypothesised that the apparent influence of location upon fecundity is most probably an indirect effect owing to variation in local environmental conditions. Ennis (1981) commented that the proposed spatial variation in lobster clutch sizes may be difficult to analyze because of geographical differences in SOM and the importance of size-fecundity relationships. Annala and Bycroft (1987) did not find any geographical variations in the fecundity of the palinurid *Jasus edwardsii*, but did suggest a potential, local variation in clutch size because of food availability. The clutch size of the crayfish *Orconecetes virilis* was also shown to be reduced in crowded conditions, probably as a result of increased competition for food resources (Morgan and Momot, 1990). The size of eggs, their development rate and individual fecundity were each related to temperature in the copepod *Pseudocalanus* (McLaren, 1968).

In addition to increases in egg number, an increase in egg size may also be observed with increasing female size in *Homarus gammarus* (Latrouite *et al*, 1984). This is a further indication of the greater degree of female energetic investment into her brood with an increase in her size. The small differences in diameters of *H. americanus* and *H. gammarus* eggs (1.5 to 1.6 mm and 1.8 mm respectively) reflect large differences in egg volumes (Branford, 1978), and may help to explain the curvilinear and linear relationships between female size and egg numbers in the two respective species.

Estimates of the individual fecundity of *Homarus* are influenced by egg loss during the incubation period which may be caused by attrition, unfavourable social conditions or parasitism (Perkins, 1971; Aiken and Waddy, 1980; Campbell and Robinson, 1983). Although *H. americanus* egg masses have been shown to be subject to infestations of the nemertean parasite *Pseudocarcinonemertes homari*, which may result in partial or even complete egg loss, there is no indication that this parasite occurs around the British coast at present. Fleming and Gibson (1981) also reported the presence of *P. homari* individuals in the branchial chamber and on the gills of the host. In populations of *H. americanus* where this parasite has occurred an incidence of 74% infestation has been reported (Campbell and Brattey, 1986), with complete egg loss in 6.3% of those cases, and most infected females hatching only 60% of their eggs. Wickham (1979) estimated that a nemertean, *Carcinonemertes errans*, parasite of the Dungeness crab, *Cancer magister*, destroyed 55% of the eggs from one population over a five year study period. Although Wickham (1978) was able to describe the method by which the parasite could feed on the Dungeness crab egg yolk, he was unable to confirm this theory by direct evidence. Wickham (1979) noted a significant correlation between worm density and filamentous egg fouling and mortality and suggested that fouling is stimulated by the release of yolk material into the egg clutch by worm feeding and defecation. Waddy and Aiken (1985) were able to confirm that *Pseudocarcinonemertes* consumed the egg yolk of the American lobster, using an immunofluorescent test to identify yolk proteins within the parasites intestinal diverticula, but also noted the variety of protozoal, bacterial and fungal organisms associated with the nemeretean infestations, which might also increase egg mortality. Egg loss attributed to other factors has been shown to average 36% in *H. americanus* (Perkins, 1971), 27% in *H. gammarus* (Latrouite *et al,* 1984) and 45%, from oocyte number within the ovary (potential fecundity) to full development, in *Nephrops norvegicus* (Morizur *et al,* 1981). Estimates of individual fecundity in both the American and European lobsters must therefore take the development stage of the eggs into account, and most studies have therefore used the number of eggs carried by females toward the end of incubation in fecundity estimations (Perkins, 1971, Hepper and Gough, 1978). Bennett and Howard (1987) observed a decrease in egg loss with increasing female size for *H. gammarus* in South Wales (58 % at 90 mm CL and 11 % at 150 mm CL).

Individual fecundity is a product of two variables, breeding frequency and the number of young produced per breeding cycle (Chittleborough, 1976). Each of these two factors may respond independently to changes in environmental conditions. Spawning frequency is affected where animal density is high, and female nutritional state is poor, whereas the number of young produced is related to female size and therefore is affected by growth rates (Chittleborough, 1976). Lipcius (1985) examined size-dependent reproduction in palinurid, nephropid and brachyuran decapods, and stated the importance of moulting and reproduction regimes, along with survivorship rates within different size (age) groups, in estimating an individuals lifetime fecundity, and the annual population fecundity. Heydorn (1969), working on *Jasus lalandii,* observed that both moulting and egg bearing cycles were conspicuously size-dependent, with a higher proportion of larger females spawning, and smaller individuals spawning one to three months later over a more extended egg-bearing season. Chittleborough (1976) observed that the majority of smaller *Panulirus cygnus* females moulted twice per year and spawned once, whereas larger females probably moulted once and could spawn twice annually. The frequency of spawning has also been shown to affect the number of eggs carried by females. Creaser (1950) showed that larger *Panulirus argus* females which spawned twice in a year had a second clutch size approximately half the size of the first. Lipcius (1985) suggested that females which spawned twice in a year rather than moulting and then spawning in that year, might show a lower overall fecundity. This would depend largely on the relationship between female size and clutch size and survivorship between moults. Pollock (1986) calculated the percentage egg production by size class for west Cape *Jasus lalandii* by multiplying the frequency of mature females by average fecundity for a given 5 mm size class, and showed that the greatest proportion of egg were produced by females of 70 to 79 mm CL (total size range studied 60 to 114 mm CL) (it should also be noticed that 90 to 99% of this fishery is for males only, and therefore the female stock is relatively unexploited (Pollock, 1986)). Estimating spawning frequency in *Homarus* is more complicated than for most palinurids, as the basic ovarian cycle is two years long (Aiken and Waddy, 1976), and only a proportion of females can therefore be expected to carry eggs in any one year; in addition the catchability of berried females is thought to be different from non-berried individuals during the 9 to 11 month incubation period (Hallback and Warren, 1972; Branford, 1977). Aiken and Waddy (1980; 1982) suggested that two different patterns of reproduction and moult exist in newly matured female *H. americanus*, the occurrence of each pattern apparently being controlled by local temperature regimes. It was estimated that approximately 15 - 20 % of newly matured females moult and extrude eggs in the same year, with the majority of individuals moulting and extruding eggs in alternate years. Larger females are also believed to show variations in spawning frequencies, with a proportion of individuals spawning twice in three years, rather than in alternate years. Waddy and Aiken (1990) suggested that large females (>120 mm CL), unable to store enough sperm for two consecutive spawnings, may use intermoult mating to enable fertilisation of all of the eggs of their second broods.

Squires et al (1974) tried to estimate potential spawning by examining ova size, suggesting that if their ova size was less than 1 mm diameter in June or July, females could not be expected to spawn in that August. Ova of 1.3 mm diameter in September would not be spawned until the following year. This contradicts Ennis' (1971) work which suggested that all females carrying ova larger than the ova of ovigerous females (0.5 mm diameter or less) would spawn that year. Ennis's (1971) method thereby gave an unusually high estimate of percentages of potentially ovigerous females.

The relationship between size and individual spawning patterns and therefore fecundity, may also be complicated by the effect of environmental factors such as food availability, temperature and population density upon annual egg production (Chittleborough, 1976).

Templeman and Tibbo (1945) first suggested that berried females did not trap as readily as nonovigerous females, and that the highest occurrence (33%) of berried females caught in traps was therefore likely to be biased. Squires (1970) also agreed with Templeman and Tibbo (1945), as the annual 17% capture of berried females was invariably smaller than the 58% of non-ovigerous females present with large ova. Squires *et al* (1974) stated that a high proportion of berried females caught in August (70%) was caused by berried females feeding after their recent egg extrusion (although the high percentage berried. might also be caused by lower catchabilities of non-ovigerous females and males as a result of ecdysis). In addition to the potential catchability bias of berried females, Squires (1970) suggested that egg loss and resorption might also influence estimates of the proportion of berried females within the population.

During egg incubation, colour changes are observed, with eggs turning from dark green/black to red, with eye spots becoming apparent after a short period of time. Farmer (1974) suggested that the dark green egg colour changes to red as a result of the formation of chromatophores and the general pigmentation of astaxanthin, which becomes freed from the protein complex in ovoverdin (Goodwin, 1951).

Egg incubation period has been directly related to temperature, increasing in cold waters (Perkins, 1972; Wear, 1974; Branford, 1978). According to Wear (1974), a modification of Belehradek's equation may be used to describe the relationship between egg incubation period and sea temperature. This equation was used by Branford (1978) to estimate the incubation period of *H. gammarus* in the north Irish Sea. Branford (1978) calculated that the egg incubation period would last 11 months at the 10.4°C average local temperature, according to the equation below:

$$D = a(T-\alpha)^b,$$

Where: D = incubation period (days)

T = average water temperature

a, b and α are fitted constants

$a = 215{,}100$, $b = -2.3$, $\alpha = -7$

This equation assumes either a short diapause or none at all.

Perkins (1972) developed an equation to relate egg incubation period duration to the temperature regime so that the expected date of egg hatching might be estimated for *H. americanus* eggs. He also developed an eye index measurement to separate the eggs of *H. americanus* into development stages and to determine their development rate, which was shown to vary with temperature. Field based estimates of the length of the incubation period may be based either on observations of stage I larvae, or the apparent larval release by captured females. Sasaki *et al* (1986) studied nutrition and bioenergetics of *H. americanus* eggs, and showed that although egg size increased until week 10 of the 28 week incubation period, the egg diameters did not increase any further until 3 weeks before hatching and that eye dimensions measured according to Perkins (1972) method also did not increase for most of this 15 week slow growth period. Wet and dry weight did change slightly during this period. Campbell (1986) suggested that ovigerous females in the southern Bay of Fundy migrate seasonally between shallow and deep water in order to gain extra heat units, especially during the most critical early months, so that egg development might be completed successfully. Such migrations, to warmer shallow waters might allow less developed eggs to catch up with well developed eggs, thereby decreasing any delay between releases from different females (Attard and Hudon, 1987).

Egg hatching in *Homarus gammarus* has been observed under laboratory conditions by both Ennis (1973) and Branford (1978). These workers reported a pronounced rhythmic release of larvae, a few hours after darkness, every night for between one and six weeks, although Pandian (1970) recorded the release of approximately 1500 eggs per night, over only five days in *H. americanus*. Each individual female releases her larvae at a similar time each night over a period of just a few minutes (Branford, 1978). Ennis (1975) suggested that *H. americanus* show less control in their hatching rhythm than *H. gammarus* as some batches of larvae were released during the day. The hatching of lobster eggs requires two separate events; firstly the rupture of the egg membrane by the larva and then the final release of the larva by the mother (Branford, 1978). The mechanism controlling the rupturing of the egg membranes is thought to be controlled by the perception of the light regime by the larva (perhaps with an endogenous component), and the vigorous maternal pleopod beating to release the larva is thought to be controlled endogenously by the mother (Branford, 1978), although Pandian (1970) and Ennis (1973) suggested that both parts of the hatching procedure may be controlled by the onset of darkness and an endogenous component acting either upon the adults, the embryos or both. Branford (1978) stated that the time between sunset and larval release is controlled solely by temperature; abnormal lighting regimes (such as continual day or night) produce arhythmic hatching, although the hatching times are not influenced by photoperiod and always occur after sunset.

Hughes and Matthiessen (1962) reported a correlation between the peak in hatching intensity of American lobsters and temperature in Massachusetts, with the majority of larvae released when water temperatures equal 20°C. Hatching had been reported in cooler years to be lighter and more sporadic; at 15°C complete hatching might take 10 to 14 days compared to 2 to 3 days at 20°C.

Measurements of the individual fecundity of decapod crustaceans usually refer to clutch size (Barnes and Barnes, 1968). For fisheries studies, the population fecundity is more relevant to help comprehend potential stock and recruitment relationships. The number of eggs per recruit is said to be influenced by the timing of the fishing season, recruit size, fishing mortality, size at onset of maturity and growth rate (Campbell and Robinson, 1983). Egg production in populations of the palinurid *Palinurus longipes cygnus* was found to be regulated by density-dependent factors, with a high population density resulting in smaller size at maturity with fewer eggs per clutch and fewer clutches per year (Chittleborough, 1976).

Attard and Hudon (1987) investigated the relative energetic investment of female American lobsters according to their size, with respect to egg number, egg size and caloric value, rather than by clutch size alone. This study indicated a dome-shaped curve of relative investment by female size, as female weight increased faster than fecundity, so that females effectively showed a higher fecundity, relative to female weight, between 82 and 90 mm carapace length (CL) than for larger individuals. However, Attard and Hudon (1987), commented that females larger than 90 mm CL contributed 10 % and 40 % of egg production to the south east and north west populations of the iles de la Madeleine respectively, and so were still important in terms of overall population fecundity.

Attard and Hudon (1987) suggested that the time of egg extrusion, the number of eggs, female size and energy content of those eggs at different stages during the female's life span, might all affect larval survival rates. Local variations in these factors may assist in maintaining adequate, if not optimal, larval survival rates and recruitment to the adult population. Larvae released from females larger than 83 mm CL, hatch in early summer and are therefore most likely have higher survival rates because of the higher water temperatures (Caddy, 1979; Hudon *et al*, 1986), and survival of larvae from larger females may be increased because of the higher energetic investment put into the eggs (Sasaki *et al*, 1986). Pollock (1986) suggested that regional variations in the fecundity of *Jasus lalandii*, around the Cape west coast of South Africa, with fewer eggs produced by females where growth rates are retarded. In these regions density dependent regulation, ascribed to food availability, is thought to exist in both adults and juveniles, and lower fecundity can therefore be linked to stock density.

The biochemical composition and calorific value of homarid lobster eggs have been examined by Pandian (1970a; 1970b) and Attard and Hudon (1987).

Attard and Hudon's work on *Homarus americanus*, studied the energy content of eggs from 148 ovigerous females. They assessed the development of the eggs according to Perkin's eye index (1972). The calorific content of the eggs, found using microbomb calorimetry, showed a relationship between female size and energy content per egg. Larger females appeared to extrude eggs earlier than smaller females. These eggs were also shown to be larger with a higher energy content. A female of 72-76 mm CL had eggs averaging 4.6 calories each, whereas the eggs from females of 107-110 mm CL had an average calorific value of 5.2 calories. Females of 82-90 mm CL, invested the greatest amount of energy in egg production relative to their own body weight, (0.155 kcal per gram body weight), when compared with other members of the sample population. It was suggested that smaller females would allocate more resources to somatic growth, whereas larger females would divert their energy investment away from reproductive processes and towards maintenance-orientated functions. Attard and Hudon concluded that the larger females, with a greater number of eggs containing relatively more calories than those of smaller females, would effectively contribute more to lobster recruitment than their greater fecundity would suggest. This is because of the increased chances of survival assumed by larger eggs with an earlier extrusion date and hatching time.

Pandian (1970a; 1970b) assayed the biochemical composition of the eggs of *Homarus spp.* relative to arbitrary developmental stages. The most marked changes in the biochemical composition of the eggs, throughout their embryonic development, were changes in water and fat content (Pandian, 1970b). A net increase in water of 54-83.1% (expressed as a percentage of total weight) occurred during development, owing to the absorption of water and salts from the surrounding sea water. An observed decrease in the lipid content of the eggs, and therefore calorific value with egg development, implies oxidation of the lipids for metabolic processes. Lipid metabolism predominates in marine eggs and larvae (Lucas and Crisp, 1987), and also results in the production of water, which, in the case of *Homarus spp.*, may account for 10-15% of the water increase during development (Pandian, 1970b). Pandian (1970b) also observed a 35 % net increase in non-protein nitrogen during the egg development of *H.americanus*, most probably as a result of an increase in chitin synthesis.

6.2 Methods and statistical analysis

6.2.1. Estimation of Fecundity and Egg Development Stage

Samples of berried females were obtained from fishermen and wholesalers from each of Bridlington, Dale and Selsey between 1989 and 1992. Additional fecundity samples collected from Bridlington during September 1987 and June 1988 were also used in this study. A full list of fecundity study sampling dates is presented in Appendix Tables A2i.1 to A2i.3. Whenever possible, 5 berried females were selected from each of the designated 5 mm CL size classes. Females with clutches exhibiting excessive egg loss (caused by attrition, poor handling or partial egg release) were not selected for fecundity counts.

The egg clutches were weighed and approximately 100 eggs were removed from the first pair of pleopods and placed in 4% formol-saline solution for estimation of development stage. The remaining of eggs were also placed in 4% formol-saline solution for at least 7 days, before being prepared for counting. This procedure dehydrated and toughened the eggs thus making it easier to manipulate them. The eggs were then oven-dried at 60°c for 12 hours and rubbed over a 0.5mm mesh sieve to separate them and remove any "fluff" (connective tissue and detritus). The eggs were then counted either by subsampling or by using an automated electronic counting device. For subsample counts, approximately one quarter of the total egg mass (weighed to 0.001g) was counted by hand.

Eggs were counted automatically using a device which had been developed for assessing fish egg number and size (Witthames and Greer Walker, 1987). The dried eggs were placed in absolute alcohol for 2 hours, washed and resuspended in water before being directed through the counting device and past an electronic sensor with a 2500 μm aperture. The sensor produces a voltage pulse which has an amplitude proportional to the particle size. A HIAC Criterion PC-320 particle size analyser and Tracor Northern pulse height analyser separate the voltage pulses into recording channels, so that the number of particles within an appropriate size range can be obtained. This method was found to slightly underestimate egg number because of clumping between eggs, and because some of the dried eggs still floated after treatment in alcohol. The automatic counting method was abandoned after equipment malfunctions caused by clumping, floating and the large size of the lobster eggs (up to 1.8 mm diameter).

The two types of counting methods were compared statistically against whole clutch counts from a number of females and against each other before their results could be treated as a single data set. The accuracy of manual counting was checked by repeat counts of five whole clutches. Total manual egg counts were estimated to have a 99 % accurracy; subsamples of up to one quarter of the total egg volume were estimated to be 98 % precise and automated counts were found to fall between 1 and 3 % below manual estimates. Squires (1970) suggested that a 98 % accuracy is acceptable for counts made by electronic counters and by subsampling (volumetric methods). Ten estimates of egg number made by hand counted whole samples were compared against subsample counts, and a t-Test was performed to compare the two data-sets. A further ten samples were counted as whole hand counts and then by machine count, and the results compared by t-Test. Additional eggs used for the assessment of development were also counted and added to this total to provide a complete estimate of clutch size in relation to female size (carapace length and abdomen width) and egg development stage.

The developmental stage of the eggs was estimated using Perkins' (1972) eye index. This method provides a relative index of egg development by dividing the summation of eye length and width by 2. The percentages of females with eggs at each Perkins eye index stage (PEI) were calculated for each sample date. Non-eyed embryos obviously cannot be "staged" by this method and are therefore classed together. Fifty eggs from each individual sample were measured using a TDS Digitising Tablet and the mean and standard deviation of the index was then calculated for each clutch of eggs. Egg diameter was measured by averaging the greatest and smallest egg diameters. Egg development stage was then related to time and used for aggregating individual fecundity estimates, and in calculation of egg loss during incubation period.

Theoretical egg incubation times were calculated using Wear's (1974) equation, and average annual sea temperatures for 1986 to 1991, for each of Bridlington (Spurn Point temperature data) and Selsey (Shoreham temperature data)

(Chapter 2). Available Dale temperature data (from St. Gowans Head and Skomer) did not include every month of the year after 1985, and an estimate of mean annual seawater temperature for the area was derived from 1982 to 1985 data.

6.2.2 Data analyses

In this study estimates of clutch sizes were grouped according to site, sampling date and egg development stage. Non-eyed eggs (PEI=0) and those with PEI>300 were used to estimate individual fecundity at the beginning and towards the end of the egg incubation period respectively. Graphs of clutch size against CL, and clutch size against AW were plotted for each sample site and year for eggs of PEI=0 and PEI>300. Linear and 2nd order polynomial regression analyses were performed to assess the relationships between egg number and both CL and abdomen width (AW). Linear regression statistics were calculated as estimates of r (correlation coefficient), R^2 (coefficient of determination) and the standard error of estimation (Sx/y) for measuring variability about the fitted regression line. Regression coefficients, their standard error, t-statistics and their probability (P) of predicting the dependent variable are also presented, along with P(F) (probability of association between the independent and dependent variables; calculated by ANOVA). Second order polynomial results have been presented with estimates of r, R^2, the calculated coefficients and P-values. Linear and second order polynomial regression analyses were also performed to investigate any potential relationship between egg diameter and CL or AW. Linear and polynomial regression analyses were performed on clutch size-CL data, grouped into 5 mm CL classes. ANCOVA were used to assess the covariance of fecundity with CL (5 mm CL groups) between-sites, between-egg development stages and between-years.

The percentage egg loss during egg development was calculated for Bridlington data (1987 to 1988 and 1990 to 1991) and Selsey data (1989 to 1991) from average CL-clutch sizes for 5 mm CL groups (PEI=0 and PEI>300 respectively).

6.3. Results

Size frequency distributions

Size frequency distributions of females used in fecundity work are presented as Appendix Figs. A6.1 to A6.4, and size summary statistics are presented for each sample date in Appendix Table A6i.1.

Comparison of counting methods

The numbers of eggs in ten samples estimated by total hand count did not differ significantly from those estimated by subsample count, nor did those of ten total hand counts from same-sample machine counts, when compared using t-Tests (Appendix Tables A6ii.1 to A6ii.3).

Clutch size and CL

Individual clutch size increases with female carapace length at each of the three study sites (Figs. 6.1, 6.3, 6.5, 6.13 and 6.14; Appendix Tables A6ii.4 to A6ii.10). Linear and polynomial regression statistics both describe clutch size/CL relationships adequately and although estimates of R^2 are slightly higher for a 2nd order polynomial relationship, both for non-eyed eggs (PEI=0) and eyed eggs (PEI>300), the linear model is considered more adequate (Appendix Tables A6ii.11 and A6ii.12). Estimates of R^2 are improved by grouping females into 5 mm CL classes, suggesting individual variation in clutch size (linear model R^2 0.723 to 0.991; 2nd order polynomial model R^2 0.922 to 0.995). ANCOVA, assessing potential differences in clutch size/CL covariance at the start and end of the egg incubation period, indicated significant differences between clutch size/CL for eggs of PEI=0 and those of PEI>300, for Bridlington 1987 and 1988, Bridlington 1990 and 1991 and Selsey 1989 and 1990 data (i.e. egg loss during the incubation period) (Appendix Tables A6ii.21, A6ii.22 and A6ii.23 respectively). Between-year variation in clutch size-CL relationships was also identified by ANCOVA for both non-eyed eggs at Bridlington 1987 and 1990, and eyed eggs at Bridlington 1988 and 1991 (Appendix Tables A6ii.24 and A6ii.25). ANCOVA for Bridlington and Selsey non-eyed eggs, and also Bridlington, Dale and Selsey eyed eggs (PEI>300) suggest between-site variation in fecundity/CL relationships (Appendix Tables A6ii.26 and A6ii.27) (Figs. 6.13 and 6.14).

Clutch size and abdomen width

Clutch size was shown to increase with abdomen width (AW) at each of the three study sites (Figs. 6.2, 6.4 and 6.6) and may be adequately defined by a linear regression model (Appendix Tables A6ii.13 and A6ii.14). Polynomial regression statistics do not suggest as good a correlation between clutch size and AW (R^2 0.235 to 0.9)as between clutch size and CL (R^2 0.258 to 0.931). Multiple linear regressions for clutch size with CL and AW revealed a strong collinearity between AW and CL (as shown in Chapter 4), therefore suggesting that clutch size is more dependent on CL than the width of the second abdominal segment.

Egg diameter and CL

Neither linear nor polynomial regression analyses indicate a relationship between egg diameter and CL (R^2 <0.324 and <0.491 respectively) (Appendix Tables A6ii.15 and A6ii.16). However, graphically egg diameter may be suggested to increase with female CL at Bridlington, and Selsey 1991, but not at Dale (although this may be a result of the small sample size), nor Selsey 1989 or 1990 (Figs. 6.7, 6.9 and 6.11).

Egg diameter and AW

Linear and polynomial regression statistics do not indicate any relationship between egg diameter and AW (R^2<0.313 and <0.398 respectively), except for Dale females (R^2 0.954, polynomial model). The suggested polynomial relationship between the two variables at Dale is most probably caused by the small sample size, as the preferred model is for a U-shape curve, which is not obvious for any of the other data-sets (Figs. 6.8, 6.10 and 6.12) (Appendix Tables A6ii.17 and A6ii.18).

Egg loss during incubation period

Egg loss, calculated for average egg numbers from 5 mm CL classes, is presented in Appendix Table A6ii.28. Percentage egg loss was shown to be changeable throughout the size classes, most probably as a result of individual variability in fecundity. The average egg loss for all size classes was shown to be 12.94 % and 6.63 % at Bridlington (1987 to 1988 and 1990 to 1991) and 20.07 % at Selsey (1989 to 1991) (although the Selsey data may suggest a higher total egg loss because it is not over the same incubation period).

Egg development

The monthly percentages of berried females, presented in Appendix Table

Individual clutch size plotted against female CL (mm) (with linear regression lines), Bridlington 1987 to 1991

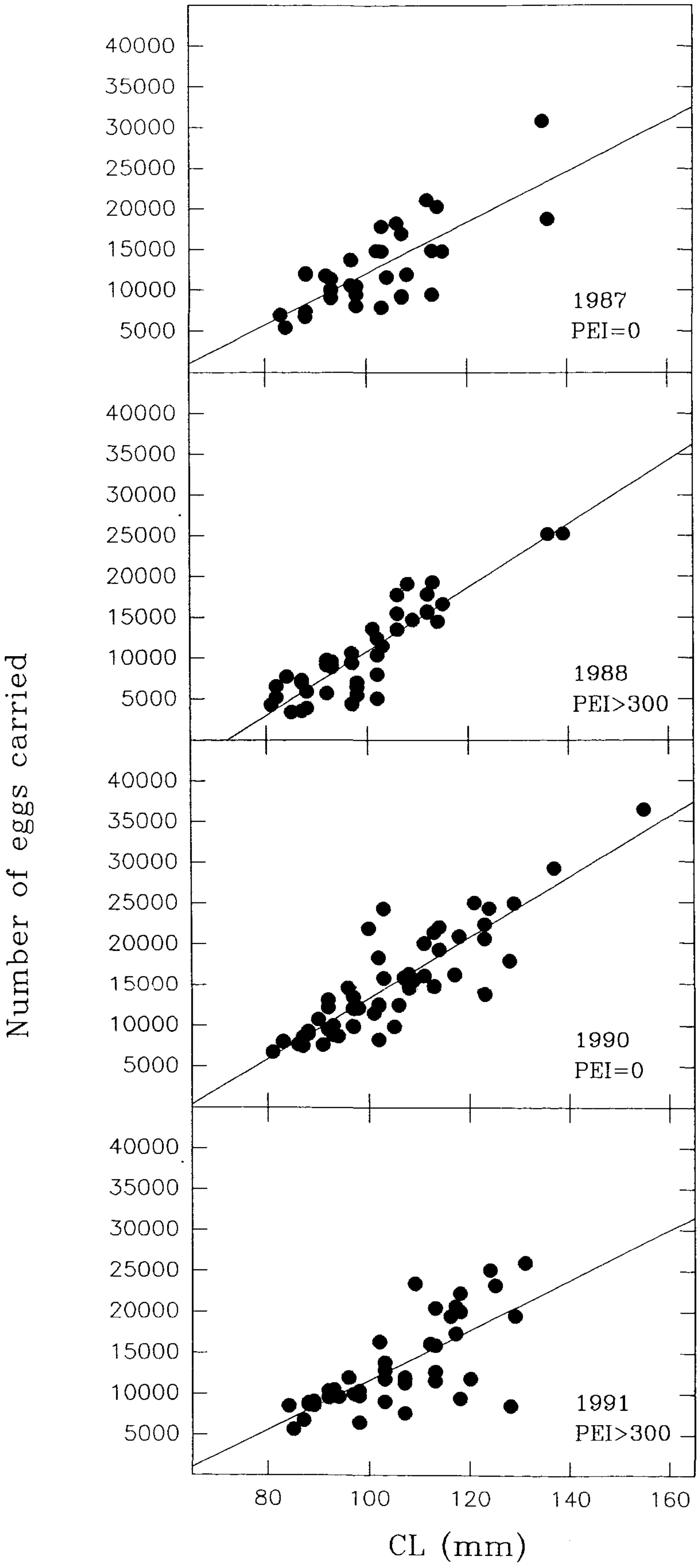


Fig. 6.1

Individual clutch size plotted against female AW (mm) (with linear regression lines), Bridlington 1987 to 1991

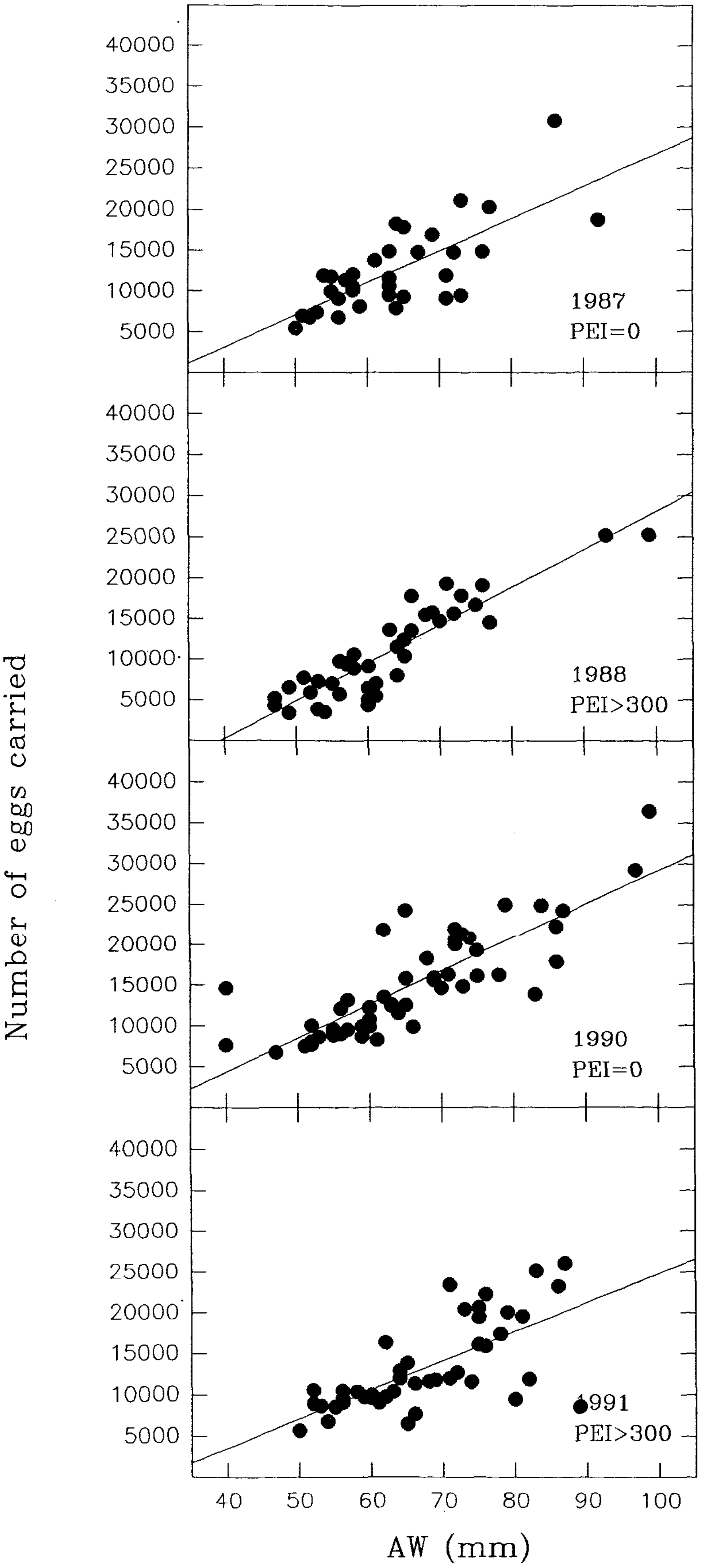


Fig. 6.2

Individual clutch size plotted against female CL (mm)
with linear regression lines), Dale 1992

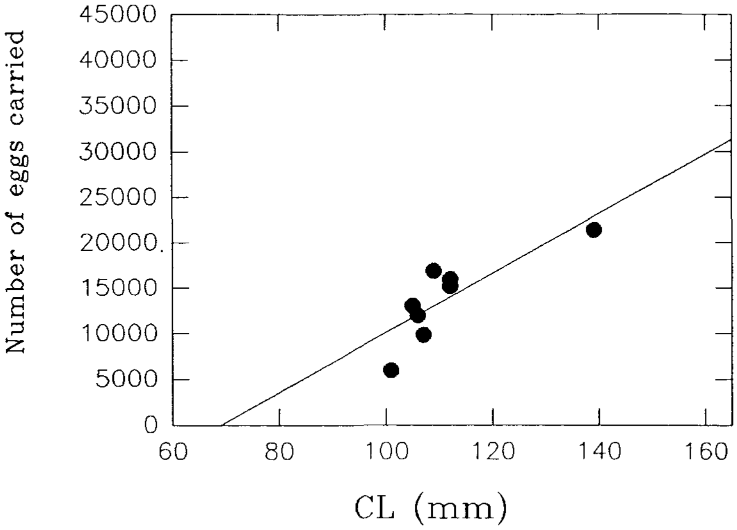


Fig. 6.3

Individual clutch size plotted against female AW (mm)
with linear regression lines), Dale 1992

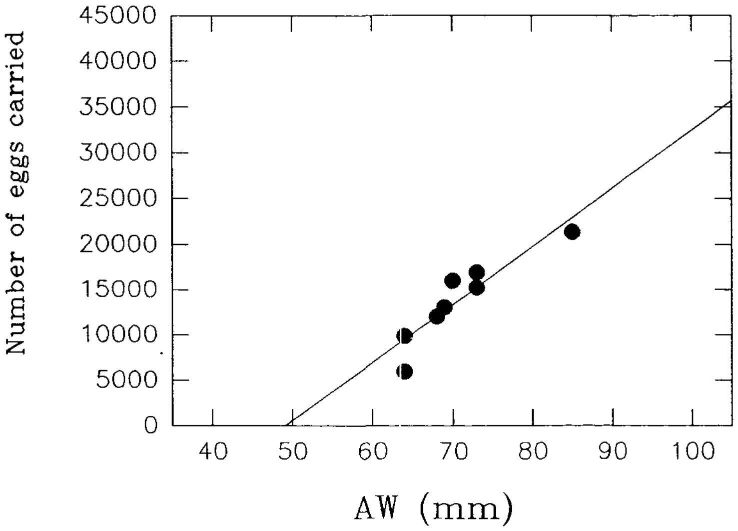


Fig. 6.4

Individual clutch size plotted against female CL (mm) (with linear regression lines), Selsey 1989 to 1991

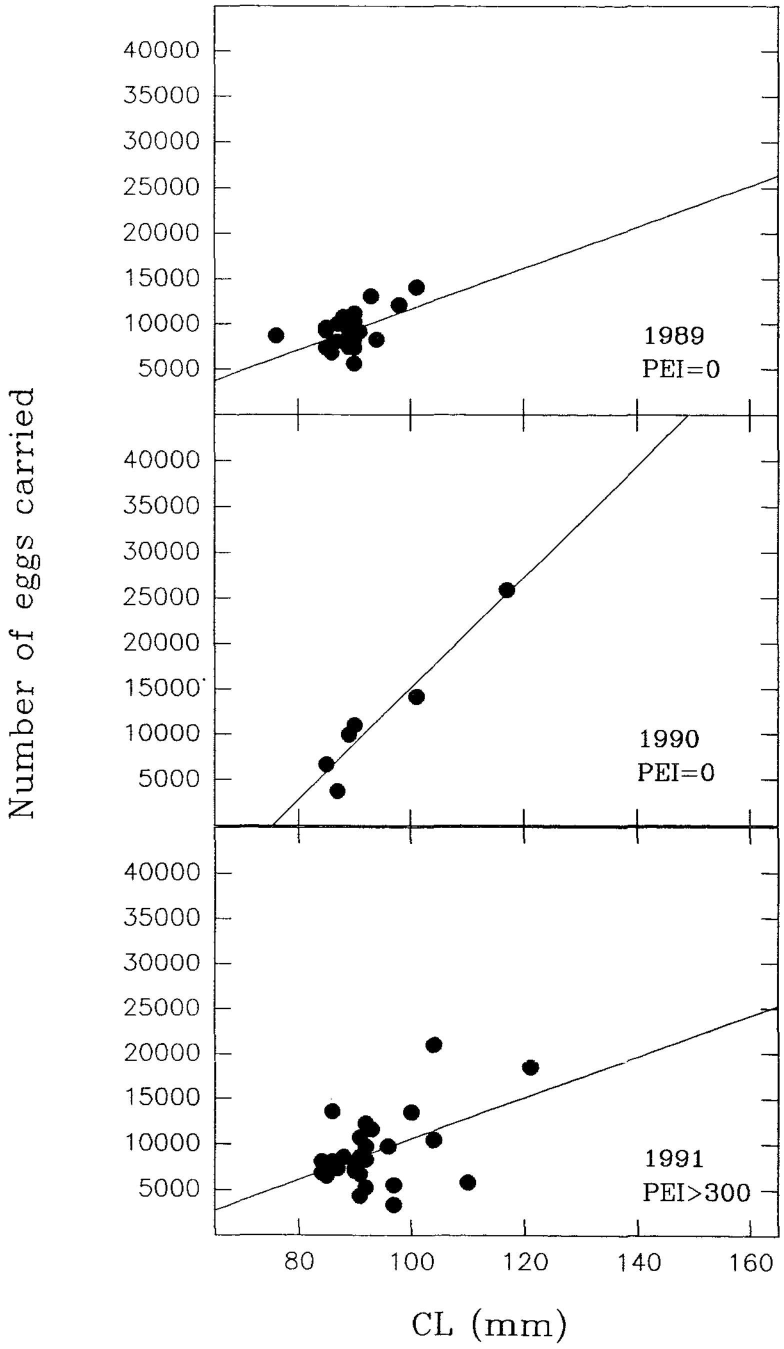


Fig. 6.5

Individual clutch size plotted against female AW (mm) (with linear regression lines), Selsey 1989 to 1991

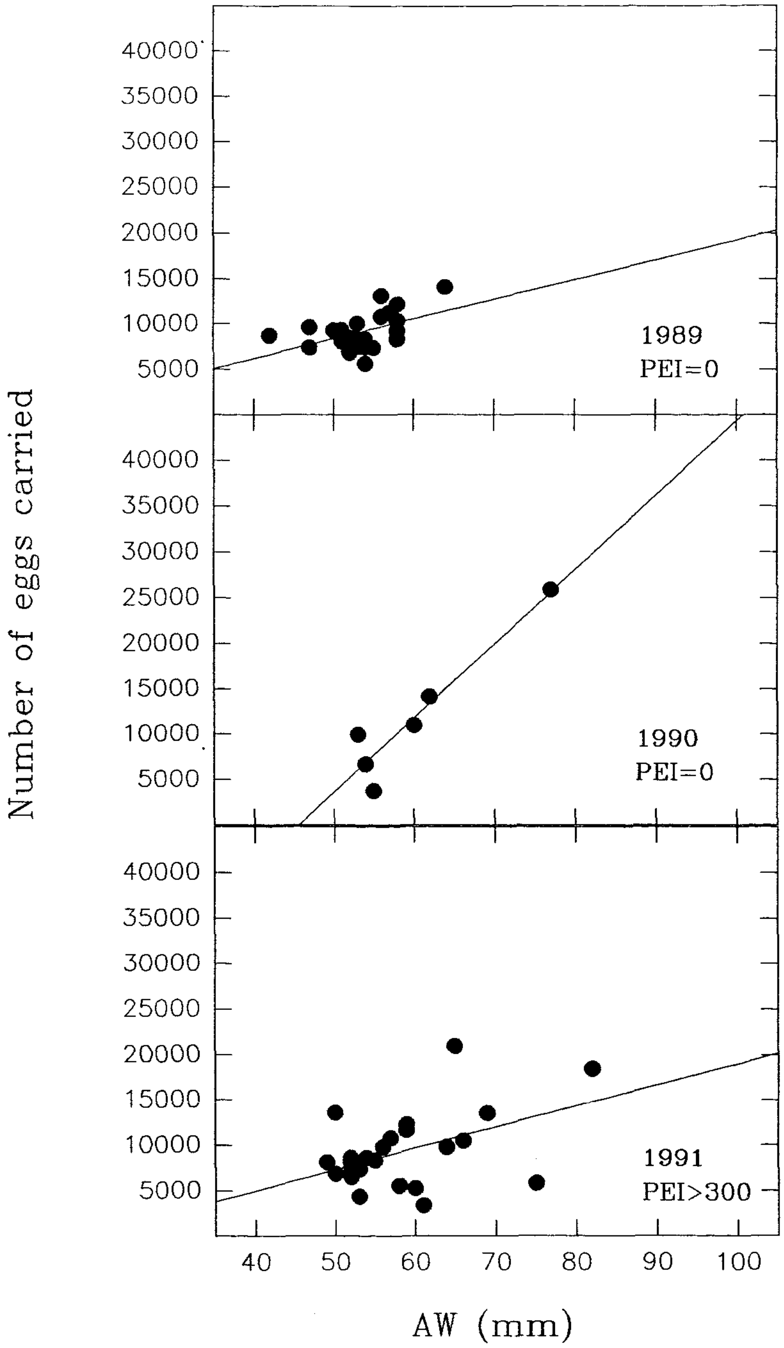


Fig. 6.6

Egg diameter (mm) plotted against female CL (mm) (with linear regression lines), Bridlington 1987 to 1991

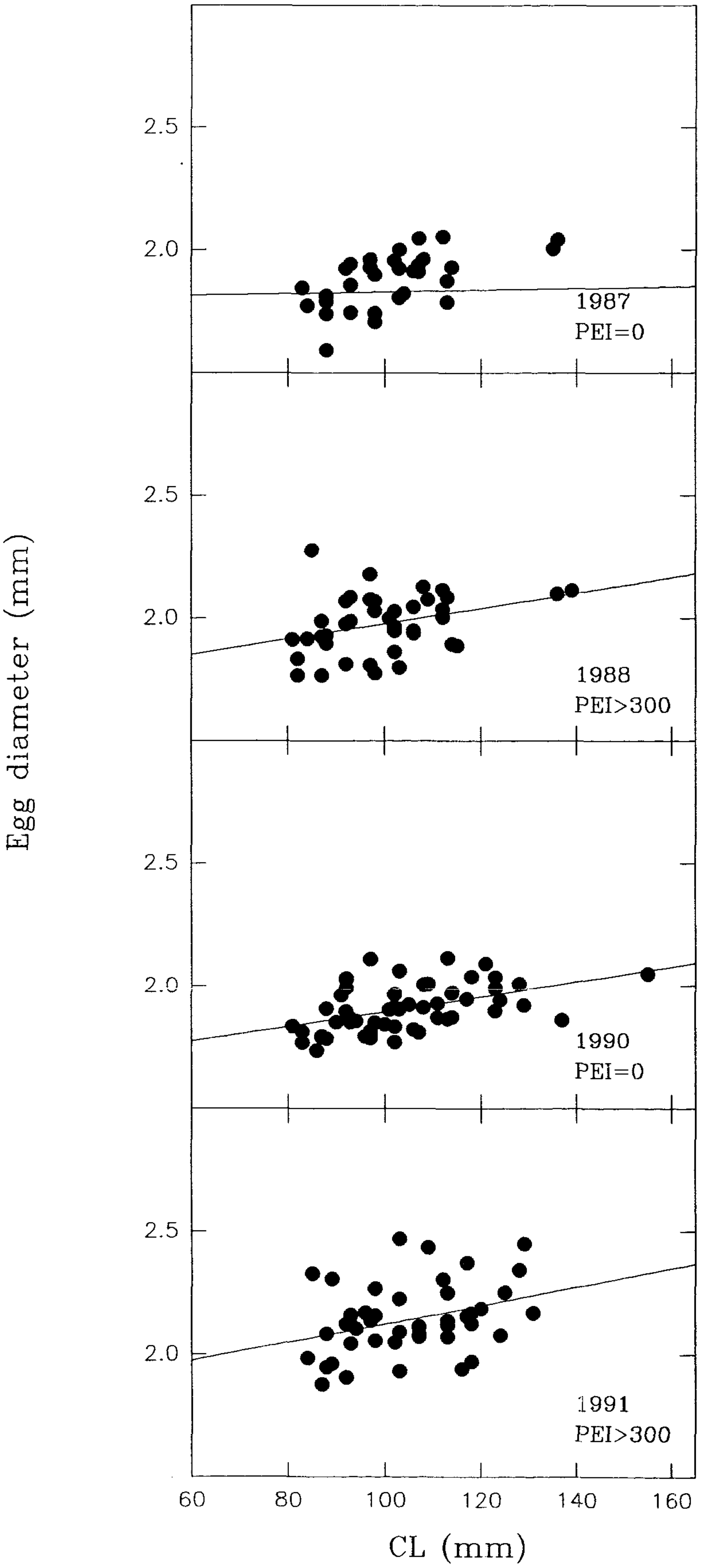


Fig. 6.7

Egg diameter (mm) plotted against female AW (mm)
(with linear regression lines), Bridlington 1987 to 1991

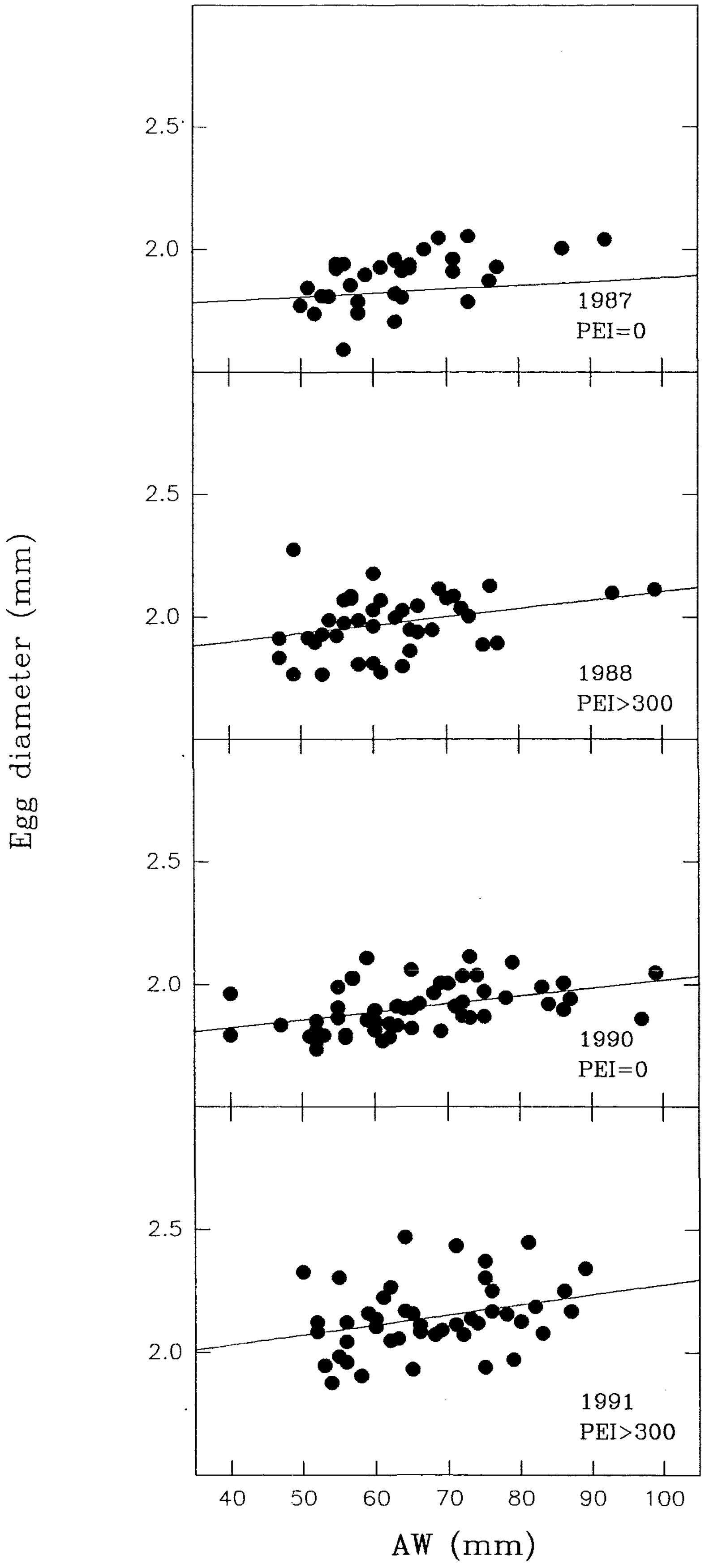


Fig. 6.8

Egg diameter (mm) plotted against female CL (mm) with linear regression lines), Dale 1992

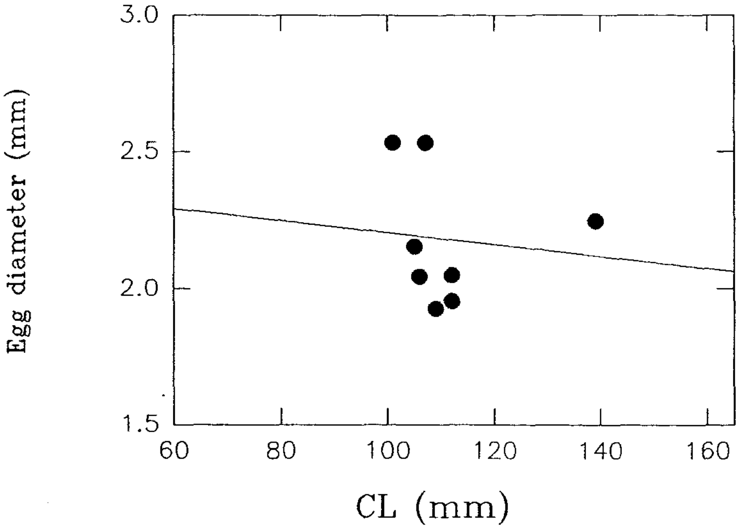


Fig. 6.9

Egg diameter (mm) plotted against female AW (mm) with linear regression lines), Dale 1992

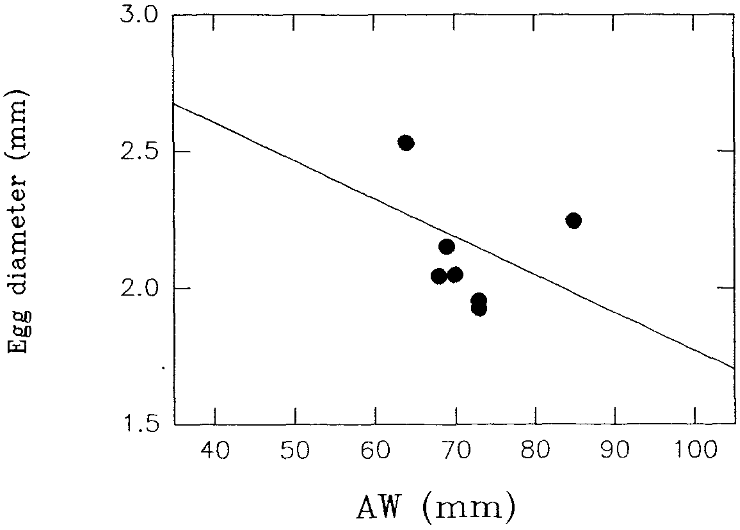


Fig. 6.10

Egg diameter (mm) plotted against female CL (mm)
(with linear regression lines), Selsey 1989 to 1991

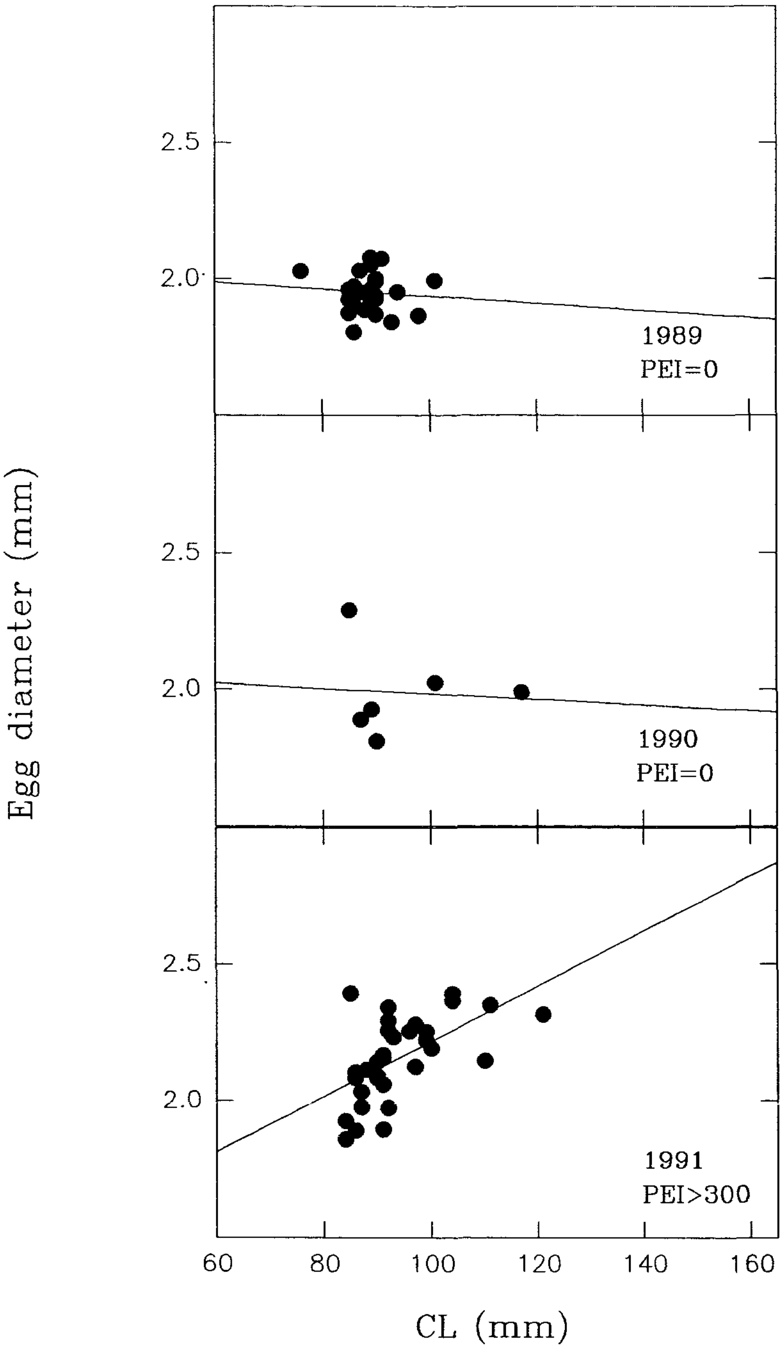


Fig. 6.11

Egg diameter (mm) plotted against female AW (mm) (with linear regression lines), Selsey 1989 to 1991

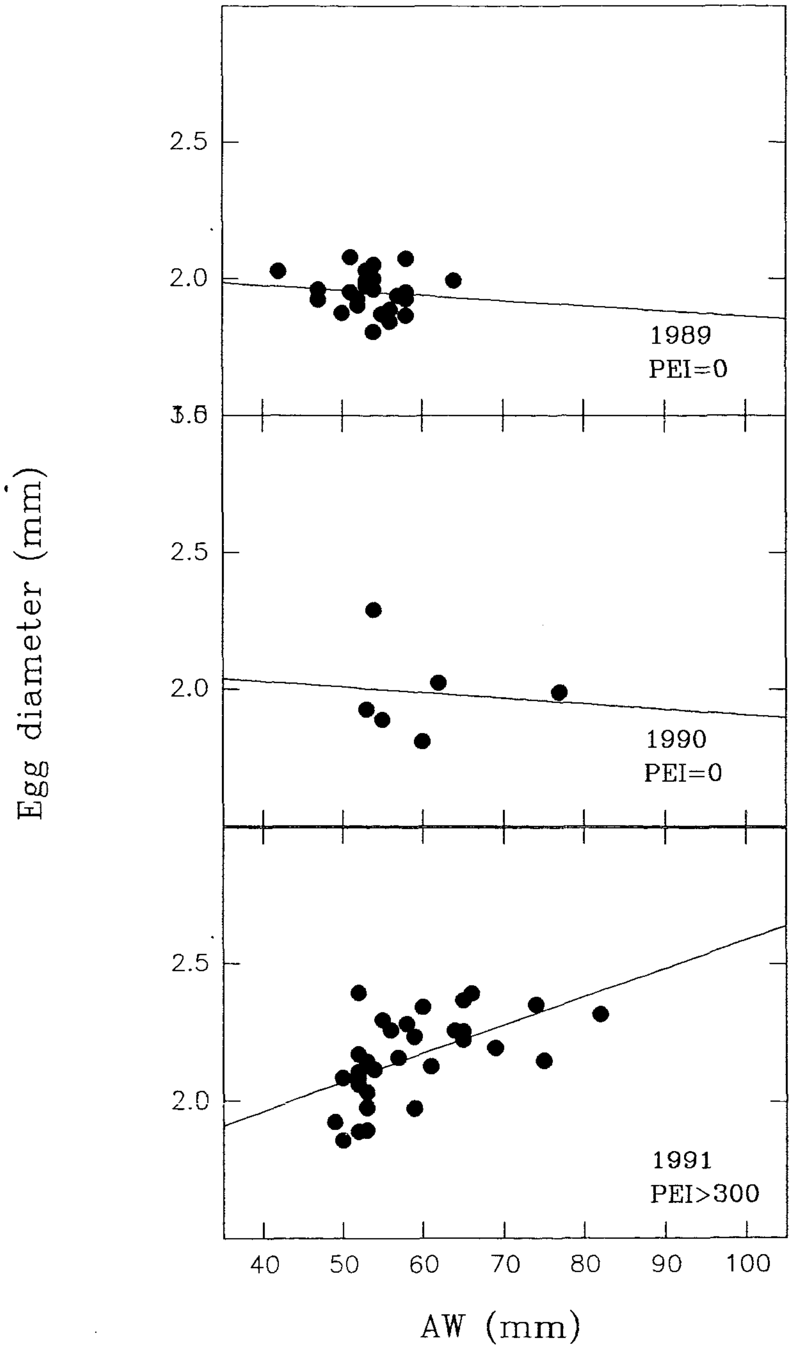


Fig. 6.12

Lobster fecundity against carapace length (mm), Bridlington,
1988 and 1990, and Selsey 1989 (non-eyed eggs).

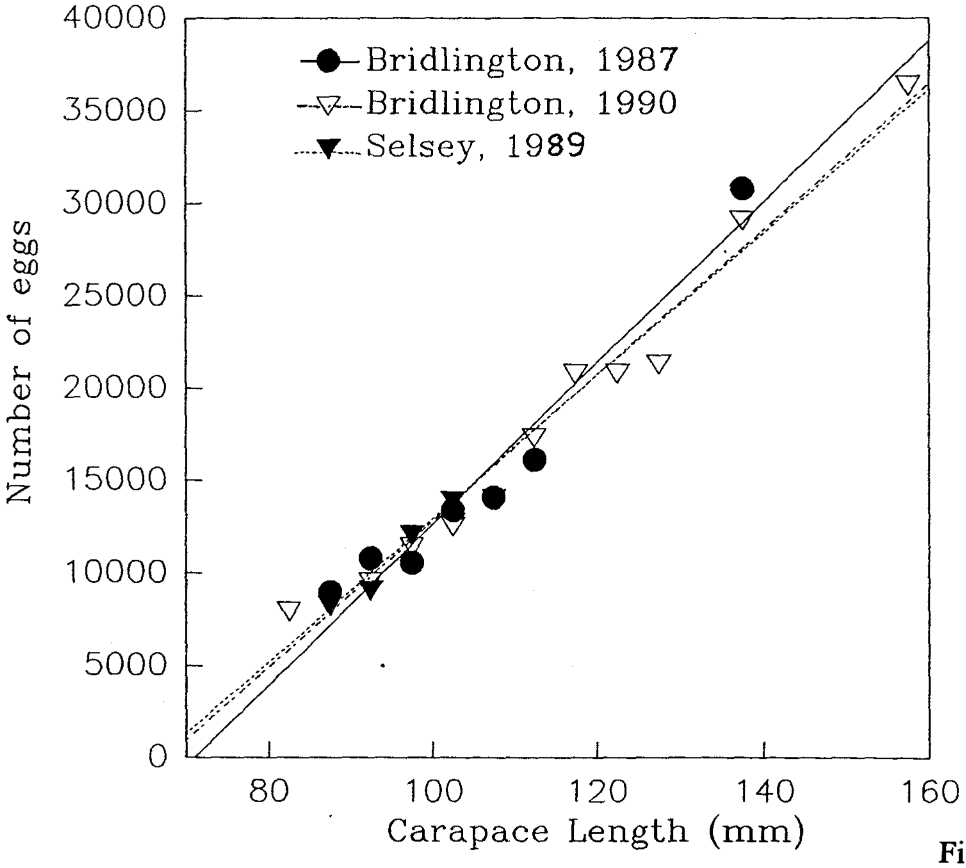


Fig. 6.13

Lobster fecundity against carapace length (mm), Bridlington, 1988 and 1991, Dale 1992 and Selsey 1991 (eyed eggs, PEI >300).

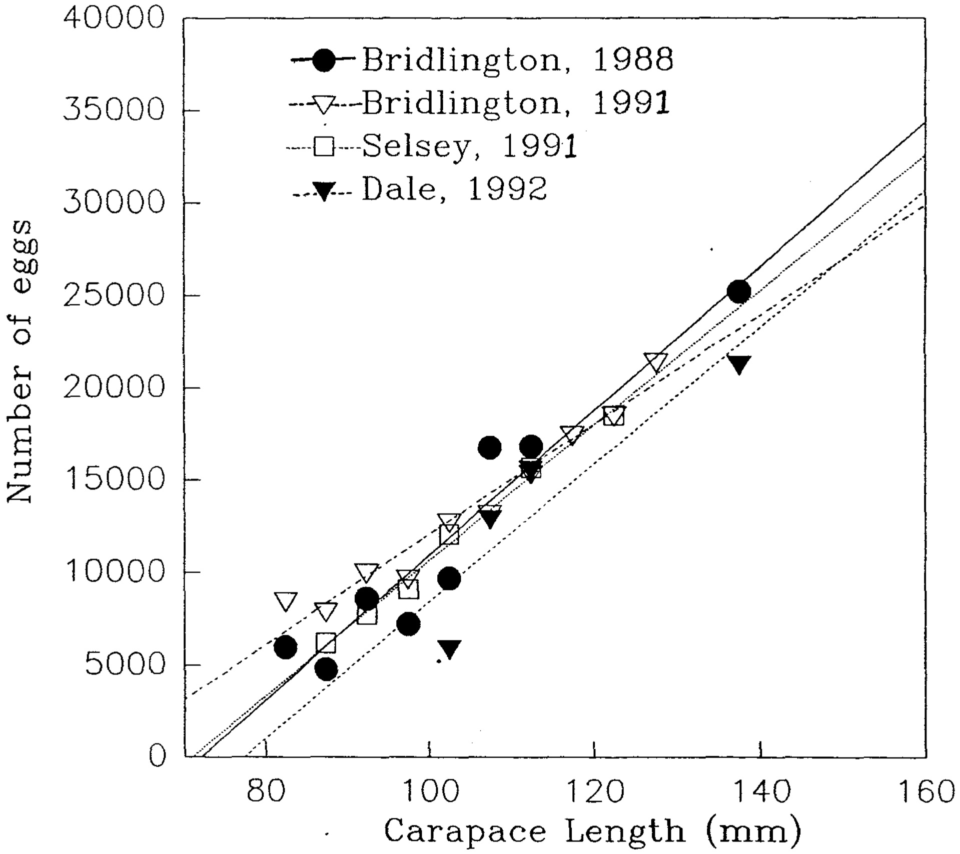


Fig. 6.14

A2iii.14, suggest geographical variation in the seasonality of the egg incubation period. Bridlington 1989 to 1991 data show a lower proportion of berried female during July and August, and the ovigerous females examined in August 1990 were newly berried, with non-eyed eggs (Appendix Table A6iii.1). Some eggs with PEI of 100 to 300 were observed in September 1987 and September 1990, suggesting egg spawning in August and early September and the completion of the egg incubation period in June or July. A moderate proportion of Dale females were berried with eggs of PEI>300, on each of the four sample dates in this study (18.75-36.4%, May to August 1989). Selsey, between 1989 and 1991, had the highest proportion of berried females in September (PEI=0), and non-eyed eggs were still present in the November 1990 sample (Appendix Tables A2iii.14 and A6iii.1). Very few berried Selsey females were seen in July 1989 and 1990 (0 % and 0.5 % respectively), and the majority of ovigerous females observed in July 1991 had well-developed eggs (PEI>400), thereby suggesting an egg incubation period of between September or October through to May or early July for Selsey females. Yorkshire 1972-1974 percentages of berried females (Appendix Table A2iii.14) indicated an egg incubation period of October to July, whereas the percentages of ovigerous females from both Pembrokeshire and Selsey, in 1972 and 1973, suggested an egg incubation period of September through to May or June.

Theoretical egg development time

Theoretical egg development times calculated for each of Bridlington and Selsey between 1986 and 1991 are presented in Appendix Table A6iii.2, along with an estimate made using Dale average seawater temperatures for 1982 to 1985. Bridlington egg incubation periods were calculated to last between 286 and 371 days (9 to 12 months) (at 8.9 to 10.8°C). Selsey eggs, developing in warmer average sea temperatures, (11.1 to 13.2°C) were suggested to be incubated for 214 and 275 days (7 to 9 months). The average Dale annual seawater temperature for 1982 to 1985 was calculated as 10.9°C, leading to an egg incubation period of 283 days (9 months).

6.4 Discussion

The results of this fecundity study suggest that for individual females, either a linear or polynomial regression line may be used to adequately describe the relationship between clutch size and female CL. The use of a wider size range of females for fecundity studies would be useful to either confirm the preference for a second order polynomial model, or suggest that a linear model is adequate (especially for use in the management of English and Welsh *H. gammarus* fisheries which exploit a fairly small size range of individuals (Chapter 2)). Clutch size varied considerably between individuals, and grouping females into 5 mm CL classes was shown to help counteract the effect of outliers on clutch size/CL relationships. The linear regression model can be seen to be adequate for describing the increase of fecundity with CL (5 mm groups) and is therefore preferred to a second order polynomial model for statistical simplicity.

The estimated fecundities of females at both Bridlington and Selsey (1987 to 1991) are higher than that suggested by both Hepper and Gough (1978) and Bennett and Howard (1987) (Free *et al*, 1992). Apparent differences in fecundity between sample sites and dates may be accentuated by individual variation in clutch size (and lack of samples from either end of the sample size range), or differences in the size ranges of the females studied on each sampling trip. Spatial and temporal variation in fecundity may be caused by local environmental conditions (such as seawater temperature or food availabilty) or density dependent factors, which may also be affected by the intensity of fishing effort. Variations in clutch size/CL relationships may also be caused by differences in methodology, as suggested by Aiken and Waddy (1980) when comparing *H. americanus* fecundity estimates.

Egg loss was found to vary considerably between individuals, with no apparent relationship between the number of eggs lost and female size (c.f. Bennett and Howard, 1987). Egg loss calculated in this study may be low compared with previous estimates (e.g. 27 % Latrouite *et al*, 1984) because females PEI >300 were used in order to obtain a reasonable sample size and egg loss caused by hatching was apparent in some females with egg of PEI>500. Females with eggs near to hatching often lost their eggs easily on being handled and egg loss from onset of egg incubation to egg eclosion is therefore difficult to estimate accurately in the field.

The theoretical egg development times calculated using Wear's equation (1974) for Bridlington, Dale and Selsey suggest very different lengths of incubation periods, and imply that local temperature (especially over winter) is important. Unfortunately, no Dale offshore temperature data were available, and the suggested egg incubation period for Dale may not be accurate because of reduced seasonal variation in offshore seawater temperatures.The short duration of egg development time for Selsey females (7 to 9 months) may facilitate females to spawn twice in a three year period, which would not be likely if the egg incubation period lasted 12 months (as may be the case at Bridlington).

CHAPTER 7 GENERAL DISCUSSION AND CONCLUSIONS

Differences between the fisheries, and temperature regimes of the three study sites were reflected by variations in size distributions, catch per unit effort and landing statistics. Annual variation in landings has been suggested to be a result of both weather restrictions on fishing activity, and temperature effects on lobster availability and catchability, which will also affect catch per unit effort (CPUE) (Bennett, 1974; Dow, 1980, Cooper and Uzmann, 1980; Fogarty, 1988, Campbell *et al*, 1991). The relationship between size composition and fishing mortality in *H. gammarus* (Bannister, 1986) confirms that the Dale offshore fishery is relatively unexploited, with a wide size range of individuals caught. In contrast the catches in both Selsey and Bridlington had truncated size distributions (although gear type may also be partially influential) reflecting the sustained exploitation in these fisheries. Differences in size composition of the catch may also be influenced by environmental conditions (such as topography, temperature or food availability) and their effect on lobster behaviour and catchability (Sastry, 1983; Howard, 1986; Addison and Lovewell, 1991). The effect of moult and reproductive cycles, on lobster availability is an important factor which will influence the determination of lobster population structure and therefore more information regarding the growth rate of *H. gammarus* (moult increment and moult frequency) would be useful in determination of the critical factors deciding population size structure.

The results of this study have indicated considerable spatial variation in the size at maturity for both males and females. Geographical variations in growth rate may affect the size at onset of maturity, as might high fishing mortality and differences in environmental conditions such as temperature. Further work is required to help isolate the causes of variations in size at onset of maturity between areas.

Regional variations in functional SOM (using expressed maturity i.e. ovigerous females) have important implications for fisheries management strategy, and may indicate the requirement for local MLS legislation.

The size at onset of maturity will affect local landings, as in areas with high SOM (above MLS) immature, animals, will inevitably be landed. This reinforces the necessity for SOM to be below MLS so that at least 50 % of individuals have a chance to spawn once, thereby protecting spawning stock biomass and reducing the likelyhood of recruitment failure. In areas where SOM is above MLS, there may be a need for local legislation in order to protect the stock-reproductive potential. However, this is complicated by the inadequate knowledge of the locations of spawning stock, as areas where SOM is low may be populated by lobsters spawned from regions where individuals do not become berried until they are larger than the minimum legal landing size. Unfortunately, *H. gammarus* larvae have not been found in abundance (Nichols and Thompson, 1988), and the location of females contributing larvae to local populations is therefore difficult to determine.

This study highlighted a number of problems with the use of both internal and external maturity indicators. The use of egg extrusion as an indicator of maturity is complicated by behavioural effects on feeding and therefore catchability (Hallback and Warren, 1972; Branford, 1977) which require further investigation. The use of the allometric growth of the female abdomen as an external indicator of maturity must be questioned because of poor correlation between the onset of berry and the size at which the growth rate of the abdomen alters. It is suggested that the change in abdomen width/CL ratio for female lobsters occurs two (or possibly one) moults prior to functional maturity, although statistical methodology problems and individual variation in AW/CL relationships complicate determination of this relationship. Internal indicators of female physiological sexual maturity were assessed to be less useful than ovary staging for determination of maturity. Further work using smaller individuals would be useful in clarification of the sizes at which ovary maturation and onset of functional maturity occur. The size at male functional maturity may be indicated by the relationship between crusher propodite length and CL, although claw loss and damage may cause individual variation in this relationship. The relationship between the onset of allometric growth of the crusher claw and functional maturity (as well as physiological maturity) needs further assessment, but appears adequate at least as a relative indicator of SOM.

This study confirms a linear relationship between clutch size and carapace length. This linear relationship exhibits regional and temporal variation, which requires further research for the determination of potential causes. Variation in population structure and local environmental conditions may influence clutch size, as may the duration of the reproductive cycle, as consecutive spawnings may reduce the number of eggs produced in the second clutch. The relationship between stock abundance and female CL/clutch size covariation could be an important parameter in stock-recruitment relationship considerations for management purposes. Differences between the results of this study and previous *H. gammarus* fecundity studies may be caused by food availability, temperature, fishing intensity or methodology (Aiken and Waddy, 1980), and further research into the potential causal factors is therefore required.

Local temperature effects will influence the duration of the reproductive cycle and therefore individual fecundity. Some females from both Bridlington and Selsey have been suggested to have consecutive spawnings, although the potential for this will undoubtably be affected by temperature effects upon egg incubation period duration. In cooler years at Bridlington temperatures may require 12 months for egg development and not allow a second consecutive spawning, thereby influencing individual fecundity.

REFERENCES

Ackers, G. (1977). Mixon Hole project. A project for underwater conservation year adopt a site scheme. Unpubl. Rept. 26pp.

Addison, J.T. (1986). Density-dependant mortality and the relationship between size composition and fishing effort in lobster populations. Can. J. Fish. Aquat. Sci.: **43**, 2360-2367.

Addison, J.T. and Lovewell, S.R.J. (1991). Size composition and pot selectivity in the lobster (*Homarus gammarus* (L)) and crab (*Cancer pagurus* L) fisheries on the east coast of England. Ices J. Mar. Sci.: **48**, 79-90.

Adiyodi, R.G. (1968). On reproduction and moulting in the crab *Paratelphusa hydrodromous*. Physiol.Zool.: **41**, 204-209.

Adiyodi, K.G. and Adiyodi, R.G. (1970). Endocrine control of reproduction in decapod Crustacea. Biol. Rev. Cambridge Philos. Soc.: **45**, 121-165.

Adiyodi, R.G. and Adiyodi, K.G. (1972). Hepatopancreas of *Paratelphusa hydrodomous* (Herbst): Histophysiology and the pattern of proteins in relation to reproduction and moult. Biol.Bull. (Woods Hole, Mass.): **142**, 359-369.

Adiyodi, R.G. and Subramonian, T. (1983). Arthropoda - Crustacea. Chapter 18. In "Reproductive biology of invertebrates. Vol. 1. Oogenesis and Oosorpton. Adiyodi, K.G. and Adiyodi, R.G. (eds.). John Wiley and Sons Ltd.: 443-495.

Aiken, D.E. and Waddy, S.L. (1976). Controlling growth and reproduction in the american lobster. Proc. Ann. Meet.-World Maric. Soc.: **7**, 415-430.

Aiken, D.E. and Waddy, S.L. (1980). Reproductive biology. In "The Biolgy and Management of Lobsters. Vol. 1". Cobb, J. S. and Phillips, B.F. (eds.). Academic Press, New York.: 215-276.

Aiken, D.E. and Waddy, S.L. (1982). Cement gland development, ovary maturation and rperoductive cycles in the american lobster *Homarus americanus*. J.Crust. Biol. 1982: **2**, 315-327.

Aiken, D.E. and Waddy, S.L. (1985a). The uncertain influence of spiny photoperiod on spawning in the american lobster (*Homarus americanus*). Can. J. Fish Aquat. Sci.: **42**, 194-197.

Aiken, D.E and Waddy, S.L (1985b). Photoperiodic control of vitellogenesis in the american lobster (*Homarus americanus*): comment on a recent report. Can. J. Fish Aquat. Sci: **42**, 198-199.

Aiken, D.E. and Waddy, S.L. (1986a). Environmental influence on the recruitment of the american lobster Homarus americanus: A perspective. Can. J. Fish. Aquat. Sci.: **43**, 2258-2270.

Aiken, D.E. and Waddy, S.L. (1986b). Oocyte maturation and spawning in wild american lobsters (*Homarus americanus*): Lack of evidence for significant regulation by photoperiod. Can. J. Fish. Aquat. Sci.: **43**, 1451-1453.

Aiken, D.E. and Waddy, S.L. (1986c). Growth of the Vasa Deferentia of mature *Homarus americanus*: conflicting results from field and laboratory studies. Can. J. Fish. Aquat. Sci.: **43**, 1453-1457.

Aiken, D.E. and Waddy, S.L. (1989a). Interaction of temperature and photoperiod in the regulation of spawning by american lobsters (*Homarus americanus*). Can. J. Fish. Aquat. Sci.: **46**, 145-148.

Aiken, D.E. and Waddy, S.L. (1989b). Allometric growth and onset of maturity in male american lobsters (*Homarus americanus*): the crusher propodite index. J.Shellfish Res.: 8(1), 7-11.

Aiken, D.E. and Waddy, S.L. (1990). Winter temperature and spring photoperiod requirements for spawning in the american lobster, *Homarus americanus*, H. Milne Edwards, 1837. J. Shellfish Res.: 9(1), 41-43.

Aiken, D.E. and Waddy, S.E. (1991). Mating and insemination in the American lobster, *Homarus americanus*. In "Crustacean sexual biology". R.T. Bauer and Martin, J.W. (eds.). Columbia University Press. p126-144.

Aiken, D.E., Waddy, S.L. and Uhazy, L.S. (1985). Aspects of the biology of *Pseudocarcinonemertes homari* and its association with the american lobster, *Homarus americanus*. Can. J. Fish. Aquat. Sci.: **42**, 351-356.

Amoto, G.-D. and Payen, G. (1978). Mise en evidence du controle endocrine des differentes etapes de la spermatogenese chez l'ecrevisse *Pontastacus leptodactylus leptodactylus* (Eschscholtz, 1823) Crustace, Decapode, Reptantia. Gen. Comp. Endocrinol.: **36**, 487-496.

Annala, J.H., McKoy, J.L., Booth, J.D. and Pike, R.B. (1980). Size at the onset of sexual maturity in female *Jasus edwardsii* (Decapoda Palinundae) in New Zealand. New Zealand. J. Mar. Freshwat. Res.: **14**(3), 217-227.

Anon. (1979). Report of the Homarus working group. ICES C.M. 1979/**K:8.**

Anthony, V.C. (1980). Review of lobster mortality estimates in the U.S.. Can. Tech. Rep. Fish. Aquat. Sci.: **932**, 18-25.

Anthony, V.C. and Caddy, J.F. (eds.) (1980). Proceedings of the Canada-U.S. worhshop on status of assessment science for N.W. Atlantic lobster

(*Homarus americanus*) stocks. St.Andrews, New Brunswick, Oct. 24-26, 1978. Can. Tech. Rep. Fish Aquat. Sci.: **932**, 186pp.

Armstrong, J.M. (1988). Reproduction in the paddle crab *Ovalipes catharus* (Decapoda: Portunidae) from Blueskin Bay, Otago, New Zealand. New Zealand J. Mar. Freshwat. Res.: **22**(4), 529-536.

Atkinson, E G. and Wacasey, J.W. (1983). Caloric equivalents for benthic marine organisms from the Canadian Arctic. Can. Tech. Rep. Fish. Aquat. Sci.: **1216**, 31pp.

Attard, J. and Fradette, P. (1985). Developpement des oeufs et fecondite des femelles de homard (*H. americanus*) aux Iles De La Madeleine. C.S.C.P.C.A. Doc. Res.: **85/15**, 22pp.

Attard, J. and Hudon, C (1987). Embryonic development and energetic investment in egg production in relation to size of female lobster (*Homarus americanus*). Can. J. Fish. Aquat. Sci.: **44**, 1157-1164.

Bannister, R.C.A. (1986). Assessment and population dynamics of commercially exploited shellfish in England and Wales. Can. Spec. Publ. Fish. Aquat. Sci.: **92**, 182-194.

Bannister, R.C.A. and Addison, J.T. (1986). Effect of Assumptious about the stock-recruitment relationship on a lobster (*Homarus gammarus*), stock assessment. Can. J. Fish. Aquat. Sci.: **43**, 2353-2359.

Bannister, R.C.A., Addison, J.T., Lovewell, S.R.J. and Howard, A.E. (1983). Results of a recent minimum size assessment for the fisheries for lobster, *Homarus gammarus* (L)., in England and Wales. ICES C.M. 1983/**K:4**.

Bannister, R.C.A. and Lovewell, S.R.J. (1985). Sampling the size composition of catches of the lobster (*Homarus gammarus* L.) on the East Coast of England. ICES C.M. 1985/**K:36**.

Barlow, J. and Ridgeway, G.J.(1969). Changes in serum protein during the molt and reproductive cycles of the american lobster (*Homarus americanus*). J.Fish. Res. Bd. Can.: **26**, 2101-2109.

Barnes, H. and Barnes, M. (1968). Egg numbers, metabolic efficiency of egg production and fecundity: Local and regional variations in a number of common cirrepedes. J. Exp. Mar. Biol. Ecol.: **2**, 135-153.

Barnes, H. and Blackstock, J. (1973). Estimation of lipids in marine animals and tissues: detailed investigation of the sulphanophospho-vanillin method for 'total' lipids. J. Exp. Mar. Biol. Ecol.: **7**, 103-118.

Batoy, C.B., Sarmago, J.F. and Pilapil, B.C. (1987). Breeding season, sexual maturity and fecundity of the blue crab, *Portanus pelagicus* (L) in selected coastal waters in Leyte and vicinity. Ann. Trop. Res.: **9**(3), 157-177.

Bennett, D.B. (1974). The effects of pot immersion time on catches of crabs, *Cancer pagurus* (L.) and lobsters, *Homarus gammarus* (L.). J.Cons. Int. Explor. Mer.: **35**(3), 332-336.

Bennett, D.B. (1980). Perspectives on European lobster management. In " The Biology and Management of lobsters. Vol. 2", Cobb, J.S. and Phillips, B.F. eds.). Acad. Press N.Y.: 317-331.

Bennett, D.B.and Brown, C.G. (1979). The problems of pot immersion time in recording and analysing catch-effort data from a trap fishery. Rapp. P.V. Reun. Cons. Int. Explor. Mer.: **175**, 186-189.

Bennett, D.B., Brown, C.G., Howard, A.E. and Lovewell, S.R.J. (1978). Comparison of lobster (*Homarus gammarus*) growth rates in Norfolk and Yorkshire, England. ICES C.M., 1978/**K:6**.

Bennett, D.B. and Edwards, E. (1981). Should we ban the berried lobster?. ICES C.M. 1981/**K:11**.

Bennett, D.B. and Howard, A.E. (1987). Estimates of lobster and fecundity (*Homarus gammarus*) from East and West Britain. ICES C.M. 1987/**K:47**.

Bennett, D.B. and Lovewell, S.R.J. (1977). The effects of pot immersion time on catches of lobsters, *Homarus gammarus* (L), from the Welsh coast fishery. Fish. Res. Tech. Rep. MAFF Direct. Fish. Res., Lowestoft.: **36,** 4pp.

Berrill, M. (1974). The burrowing behaviour of newly settled lobsters *Homarus vulgaris*. J. Mar. Biol. Assoc. U.K.: **54,** 797-801.

Berry, P.F. (1969). The Biology of *Nephrops andamanicus* Wood-Mason (Decapoda Reptantia). Oceanogr. Res. Inst. (Durban) Invest. Rep.: **22,** 1-55.

Beverton, R.J.H. and Holt, S.J. (1957). On the dynamics of exploited fish populations. Fish. Invest.(Lond). Ser.: **2**(19), 533pp.

Beyers, C.J. de B. and Goosen, P.C. (1987). Variations in feeundity and size at sexual maturity of female rock lobster *Janus Lalandii* in the Benguela Ecosystem. S. Afr. J. Mar. Sci.: **5**, 513-521.

Bliss, D.E. (1966) Neurosecretion of invertebrates other than insects. Part IV Physiological processes and neurosecretion as related to ecolysis and reproduction. Relation between reproduction and growth in Decapod Crustaceans. Am. Zool.: **6**, 231-233.

Booth, J.D. (1984). Size at onset of breeding in female *Jasus verreauxi* (Decapoda:

Palinuridae) in New Zealand. New Zealand J. Mar. Freshwat. Res.: **18**, 159-169.

Branford, J.R. (1977). Aspects of the reproduction and fisheries biology of the lobster (*Homarus gammarus* L.). PhD. Thesis University of Liverpool, Port Erin Marine Lab. Isle of Mann. 193 pp.

Branford, J.R. (1978) Incubation period for the lobster *Homarus gammarus* at various temperatures. Mar. Biol.: **47**, 363-368.

Briggs, P.T. (1976). Aspects of the American lobster in LOng Island Sound, New York. N.O.A.A., N.M.F.S. Comm. Fish. Res. Dev. Act. Rept. New York Proj.: **3-212-R**, 1-37.

Briggs, P.T. and Mushacke, F.M. (1979). The american lobster in Western Long Island Sound. New York Fish. and Game. J.: **26**, 59-86.

Brown, R.S. and Caputi, N. (1985). Factors affecting the growth of undersize western rock lobster, *Panulirus cygnus* (George), returned to the sea. Fish. Bull.: **83**(4), 567-574.

Brown, R.S. and Caputi, N. (1986). Conservation of recruitment of the Western rock lobster (*Panulirus cygnus*) by improving survival and growth of undersize rock lobsters captured and returned by fishermen to the sea. Can. J. Fish. Aquat. Sci.: **43**, 2236-2242.

Brown, C.G. and Bennett, D.B. (1979). Population and catch structure of the edible crab (Cancer pagurus) in the English Channel. J. Cons. Int. Explor. Mer.: **39**(1),88-100.

Bumpus, H.C. (1891). The embryology of the American lobster. Science **4**, 536-537.

Burkenroad, M.D. (1947). Reproductive activities of decapod crustacea. Amer. Nat.: **81**, 392-398.

Byard, E.H. (1975).Female specific protein and reproduction in the lobster. PhD. Thesis, Univeristy of Western Ontario.

Bycroft, B.L. (1986). A technique for separating and counting rock lobster eggs. New Zealand. J. Mar. Freshwat. Res.: **20**, 623-626.

Caddy, J.F. (1977). Approaches to a simplified yield-per-recruit model for Crustacea, with particular reference to the American lobster, *Homarus americanus*. Fish. Mar. Serv. Manuscr. Rept.: **1445**, 14pp.

Caddy, J.F. (1979). The influence of variations in the seasonal temperature regime on survival of larval stages of the american lobster (*Homarus americanus*) in the Southern Gulf of St. Lawrence. Rapp. P.-V. Reun. Cons. Int. Explor. Mer.: **175**, 204-216.

Campbell, A. (1980). A review of mortality estimates of lobster populations in the Canadian Maritimes. Can. Tech. Rep. Fish. Aquat. Sci.: **932**, 28-36.

Campbell, A. (1983). Growth of tagged american lobsters, *Homarus americanus* in the Bay of Fundy. Can. J. Fish. Aquat. Sci.: **40**, 1667-1675.

Campbell, A. (1989). The lobster fishery of south western Nova Scotia and the Bay of Fundy. In "Marine Invertebrate fisheries: their assessment and management. Caddy, J.F. (ed.)". J. Wiley and Sons, New York. 141-158.

Campbell, A. and Robinson, D.G. (1983). Reproductive potential of 3 lobster (*Homarus americanus*) stocks in the Canadian maritimes. Can. J. Fish. Aquat. Sci.: **40**, 1958-1967.

Campbell, A. and Brattey, J. (1986). Egg loss from the american lobster *Homarus americanus* in relation to nemertean *Pseudocarcinonemertes homari* infestation. Can. J. Fish. Aquat. Sci.: **43**, 772-780.

Campbell A. and Pezzack, D.S. (1986). Relative egg production and abundance of berried lobsters, *Homarus americanus*, in the Bay of Fundy and off Southwest Nova Scotia. Can. J. Fish. Aquat. Sci.: **43**, 2190-2196.

Campbell, A. Noakes, D.J. and Elner, R.W. (1991). Temperature and lobster, *Homarus americanus*, yield relationships. Can. J. Fish. Aquat. Sci.: **48**, 2073-2082.

Charniaux-Cotton, H.P., Zerbib, C. and Meusy, J.J (1966). Monographie de la glande androgene des crustaces superieurs. Crustaceana: **10**, 113-116

Cheesman, D.F, Lee, W.L. and Zagalsky, P.F. (1967). Caratenoproteins in invertebrates. Biol. Rev. (Cambridge).: **42**, 131-160.

Cheung, T.S. (1966). The development of egg-membranes and egg attachment in the shore crab, *Carcinus maenas*, and some related decapods. J. Mar. Biol. Ass. U.K.: **46**, 373-400.

Chittleborough, R.G. (1974). Western rock lobster reared to maturity. Aust. J. Mar. Freshwat. Res.: **25**, 221-225.

Chittleborough, R.G. (1975). Environmental factors affecting growth and survival of juvenile Western rock lobsters (*Panulirus longipes* Milne Edwards). Aust. J. Mar. Freshwat. Res.: **26**, 177-196.

Chittleborough, R.G. (1976). Breeding of *Panulirus longipes cygnus* George under natural and controlled conditions. Aust. J. Mar. Freshwater Res.: **27**, 499-

516.

Cobb, J.S., Tamm, G.R. and Wang, D. (1982). Behavioural mechanisms influencing moult frequency in the american lobster, *Homarus americanus* Milne Edwards. J. Exp. Mar. Biol. Ecol.: **62**, 185-200.

Cobb, J.S. and Wang, D. (1985) Fisheries biology of lobsters and crayfishes. In " The Biology of Crustacea. Vol 10; Bliss, D.E. (ed.)" 167-247.

Comita, G.W., Marshall, S.M. and Orr, A.P. (1966). On the biology of Calanus finmarchicus.XIII Seasonal change in weight,calorific value and organic matter. J. Mar. Biol. Assoc. U.K.: **46**,1-17.

Conan, G.Y. (1978). Comparison between growth at moult of the european and american lobsters in different geographical locations, according to sex and state of maturity. ICES C.M.: 1978/**K:18**.

Conan, G.Y. (1985). Periodicity and phasing of molting. In "Crustacean Issues 3: Factors in adult growth". Balkema Press. pp 73-99.

Conan, G.Y., Comeau, M. and Moriyasu (1985). Functional maturity of the american lobster *Homarus americanus*. ICES C.M. 1985/**K:29**.

Conan, G.Y. and Comeau, M. (1986). Functional maturity and terminal molt of male snow crab *Chionoecetes opilio*. Can. J. Fish. Aquat. Sci.: **43**, 1710-1719.

Cooper, R.A. (1970). Retention marks and their effects on growth, behaviour and migrations of the american lobster *Homarus americanus*. Trans. Am. Fish. Soc. (U.S): **99**, 409-417.

Cooper, R.A., Clifford, R.A. and Newell,C.D. (1975). Seasonal abundance of the american lobster, *Homarus americanus* in the Boothbay Region of Maine. Trans. Am. Fish. Soc.: **104**, 669-674.

Cooper, R A. and Uzmann, J.R. (1971). Migrations and growth of deep-sea lobsters, *Homarus americanus*. Science: **171**, 288-290.

Cooper, R.A. and Uzmann, J.R. (1977). Ecology of juvenile and adult clawed lobsters, *Homarus americanus*, *Homarus gammarus* and *Nephrops norvegicus*. Circ. Div. Fish Oceanogr. (Aust): **7**, 187-208.

Cooper, R.A. and Uzmann, J.R. (1980). Ecology of juvenile and adult *Homarus*. In "The Biology and Management of Lobsters. Vol 2" (J.S.Cobb and B.F. Phillips, eds.). Academic Press, New York. pp 97-142..

Creaser, E.P. (1950). Repetition of egg-laying and number of eggs of the Bermuda spiny lobster. Gulf. Caribb. Fish. Inst. Mimai Univ. Proc.: **2**, 30-31.

Daniel, P.C., Bayer, R.C. and Waltz, C. (1989). Egg production of v-notched american lobsters (*Homarus americanus*) along coastal Maine. J. Crust. Biol.: **9**(1), 77-82.

Dehn, P.F., Aiken, D.E. and Waddy, S.L. (1983). Aspects of vitellogenesis in the lobster Homarus americanus. Can. Tech. Rep. Fish. Aquat. Sci.: **1161**, 24pp.

Dow, R.L. (1977). Relationship of sea surface temp to american and european lobster landings. J. Cons. Int. Explor. Mer.: **37**, 186-191.

Dow, R.L. (1980). The clawed lobster fisheries. In "The Biology and Management of Lobsters. Vol 2" (J.S.Cobb and B.F. Phillips, eds.). Academic Press, New York. pp 265-316.

Dow, R.L., Bell F.W and Harriman DM (1975). Bioeconomic relationships for the Maine lobster fishery with consideration of alternative management schemes. NOAA Tech. Rep.,NMFS SSRF **683**.

Dunham, P.J. and Skinner-Jacobs, D. (1978). Intermolt mating in the lobster (*Homarus americanus*). Mar. Behav. Physiol.: **5**, 209-214.

Dybern, B.I. (1973). Lobster burrows in Swedish waters. Helgolander Wiss. Meers.: **24**, 401-414.

Dybern, B.I., Jacobsen, L. and Hallback, H. (1967). On the habitat behaviour of the lobster, *Homarus vulgaris* in Swedish water. ICES C.M. 1967/**K:3**

Elner, R.W. (1980). Lobster gear selectivity- a Canadian overview. Can. Tech. Rep. Fish. Aquat. Sci.: **932**, 77-83.

Ennis, G.P. (1971). Lobster (*Homarus americanus*) fishery and biology in the Bonavista Bay, Newfoundland, 1966-1970. Fish. Res. Bd. Can. Tech. Rep.: **289**, 17-46.

Ennis, G.P. (1972). Growth per moult of tagged lobsters (*Homarus americanus*) in Bonavista Bay, Newfoundland. J.Fish. Res. Bd. Can.: **29**, 143-148.

Ennis, G.P. (1973a). Food, feeding and condition of lobsters, *Homarus americanus*, throughout the seasonal cycle in Bonavista Bay, Newfoundland. J. Fish. Res. Bd. Can.: **30**, 1905-1909.

Ennis, G.P. (1973b). Endogenous rhythmicity associated with the larval hatching in the lobster *Homarus gammarus*. J. Mar. Biol. Assoc. UK.: **53**, 531-538.

Ennis, G.P. (1975). Observations on hatching and larval release in the lobster *Homarus americanus*. J.Fish. Res. Bd. Can.: **32**, 2210-2213.

Ennis, G.P. (1979). Estimates of abundance and recruitment to the standing stock for a Newfoundland population of the lobster *Homarus americanus*, with a method of estimating its natural mortality. Rapp. P.V. Reun. Cons. Int. Explor. Mer.: **175**, 225-228.

Ennis, G.P. (1980) Size-maturity relationships and related observations in Newfoundland populations of the lobster (Homarus americanus). Can. J. Fish. Aquat. Sci.: **37**, 945-956.

Ennis, G.P. (1981). Fecundity of the american lobster *Homarus americanus* in Newfoundland waters. Fish. Bull. U.S.: **79**, 796-800.

Ennis, G.P. (1984). Comparison of physiological and functional size-maturity relationships in two Newfoundland populations of lobsters *Homarus americanus*. Fish. Bull. U.S.: **82**, 244-249.

Estrella, B.T. and McKiernan, D.J. (1989). C.P.U.E. and biological parameters from the Massachusetts coastal lobster (*Homarus americanus*) resource: description and trends. NOAA Tech. Rep. NMFS **81**, Sept.89 21pp.

Evans, C. (1988). Population dynamics of spiny lobsters *Palinururs argus* and *P. guttatus* at Bermuda, 1986/1987. Phd Thesis University of Southampton, Hampshire.

Farmer, A.S.D.(1974). Reproduction in *Nephrops norvegicus* (Decapoda: Nephropidae). J. Zool.: **174**, 161-183.

Figueredo, M.J. and Nunes, M.C. (1965). The fecundity of the Norway lobster *Nephrops norvegicus* (L) in Portuguese waters. ICES C.M.1965/**K:34**.

Fleming, L.C. and Gibson, R. (1981). A new genus and species of mono-stiliferous hoplonemerteans, ectohabitant on lobsters. J. Exp. Mar. Biol. Ecol.; **52**,79-93.

Fogarty, M.J., Cooper, R. A.,Uzmann, J.R. and Burns, T. (1982). Assessment of the USA offshore american lobster *Homarus americanus* fishery. ICES C.M. 1982/**K:14**

Fogarty, M.J. (1988). Time series models of the Maine lobster fishery: the effect of temperature. Can. J/. Fish. Aquat. Sci.: **45**, 1145-1153.

Free, E.K, Tyler, P.T and Addison, J.T. (1992). Lobster (*Homarus gammarus*) fecundity and maturity in England and Wales. ICES C.M. 1992/**K:43.**

Freire, J. and Gonzalez-Guirriaran, E. (1992). Functional maturity in the velvet swimming crab *Necora puber*: a morphometric analysis. ICES C.M. 1992/K:47.

Fullarton, J.H. (1895). The European lobster. Breeding and development. 14th Ann.

Rept. Fish Bd. Scot. 1895.

Garman, S. (1985). Lobster Reproduction. Zool. Analogr. **XIII** Feb. 1895.

George, R.W. and Morgan, G.R. (1980). Linear growth stages in the rock lobster *Panulirus versicolor* as a method for determining size at first physical maturity. Rapp. P-V.Reun.Cons.Int.Explo.Mer.: **175**, 182-185.

Gibson, F.A. (1963). Measurements and growth of Irish lobsters. Rept. Sea and Ind. Fish. Ireland.

Gibson, F.A. (1967). Irish investigations on the lobster (*Homarus vulgaris* Edw.). Irish Fish Invest. Ser. B.: **1**, 13-45.

Gibson, F.A. (1969). Age, growth and maturity of Irish lobsters. Irish Fish Invest. Ser B.: **5**, 37-44.

Giese, A.C. (1966). On the biochemical constitution of some echinoderms. In " Physiology of Echinodermata". Boolootian, R.A. (ed.). John Wiley and Sons, New York. 757-796.

Goodwin, T. W. (1951). Carotenoid metabolism during the development of lobster egg. Nature: **7**, 559.

Graham, M. (1949). A note on the theory of a dwarf race of lobsters on the Norfolk Coast. J. Mar. Biol. Assoc., U.K.: **28**, 481-488.

Grey, K.A. (1979). Estimates of the size of first maturity of the western rock lobster *Palinuris cygnus*, using secondary sexual characteristics. Aust. J. Mar. Freshwater. Res.: **30**, 785-791.

Hallback, H. and Warren, A. (1972) Food ecology of the lobster, *Homarus, vulgaris*, in Swedish waters. Some preliminary results. ICES C.M. 1972/**K:29**

Harding, G.C., Drinkwater, K.F., Vass, W.P. (1983). Factors influencing the size of American lobster (*Homarus americanus*) stocks along the Atlantic coast of Nova Scotia, Gulf of St. Lawrence and Gulf of Maine: a new synthesis. Can. J. Fish. Aquat. Sci.: **40**, 168-184.

Harrison, K.E. (1990). The role of nutrition in maturation reproduction and embryonic development of decapod crustaceans: a review. J. Shellfish. Res.: **9**(1), 1-28.

Hartnoll, R.G. (1978) The determination of relative growth in Crustacea. Crustaceana.: **34**, 281-291.

Heath, J.R. and Barnes, H. (1970). Some changes in biochemical composition with season and during the moulting cycle of the common shore crab *Carcinus maenas* (L). J. Exp. Mar. Biol. Ecol.: **5**, 199-233.

Hepper, B.J. (1965). Pre-moult changes in structure of the integument of the lobster, *Homarus vulgaris*. Rapp. P-V. Reun. Cons. Perm. Int. Explor. Mer.: **156**, 7-14.

Hepper, B.T. (1967). On the growth at moulting of lobsters (*Homarus vulgaris*) in Cornwall and Yorkshire. J. Mar. Biol. Assoc., U.K.: **47**, 629-643.

Hepper, B.T. (1972). The growth at moulting of lobsters, *Homarus vulgaris*, Milne-Edwards, in the Menai Straits, North Wales. J. Cons. Int. Explor. Mer.: **34**(2), 169-173.

Hepper, B.T. (1978). Population dynamics of the lobster *Homarus gammarus* (L) off the coasts of England. Fish Res. Rep.: **41**, 29pp.

Hepper, B. T. and Gough, C.J. (1978). Fecundity and rate of embryonic development of the lobster, *Homarus gammarus* (L) off the coast of North Wales. J. Cons. Int. Explor. Mer.: **38**, 54-57.

Herrick, F.H. (1894). The reproduction of the lobster. Zool Anzeger, 1894: **17**, 289-292.

Herrick, F.H. (1895). The reproduction of the lobster. Zool Anzeger, 1895: **18**, 226-228.

Herrick, F.H. (1909). Natural history of the American lobster. Bull U.S. Bur. Fish.: **29**, 149-408.

Herrick, F.H. (1911). Protecting the lobster. Trans Am. Fish. Soc.: **40**, 359-364.

Hewett, C.J. (1974). Growth and moulting in the common lobster (*Homarus vulgaris*). J. Mar. Assoc., U.K.: **54**, 379-391.

Heydorn, A.E.F. (1964). Notes on the reproductive biology and size limit of South African rock lobsters. Part 2. S. Afr. Ship. News Fish. Ind. Res.: **19**(6), 93.

Heydorn, A.E.F. (1965). The rock lobster of the south African West coast *Jasus lalandii* (H. Milne-Edwards). Part 1. Notes on the reproductive biology and the determination of minimum size limits for commercial catches. Div. Sea Fish. South Africa Invest. Rep.: **53**, 1-32.

Heydorn, A.E.F. (1969). The rock lobster of the South African West coast *Jasus lalandii* (H. Milne-Edwards). 2. Population studies, behaviour, reproduction, moulting, growth and migration. Div. Sea Fish. S. Afr. Invest. Rep.: **71**, 1-52.

Hilton, J., Sutcliffe, D.W., Carrick,T.R. and Rigg, E. (1984). Major inorganic components in some freshwater crustaceans (Malacostraca),their exuviae and food items and thermographic-differential thermal analysis of organic ash components. Comp. Biochem. Physiol.: **77** **A**(1), 13-22.

Hinsch, G.W. (1968). Reproductive behaviour in the spider crab, *Libina emarginata* (L). Biol. Bull., Woods Hole.: **135**, 273-278.

Howard, A.E. (1980). Substrate controls on the size composition of lobster (*Homarus gammarus*) populations. J. Cons. Int. Expl. Mer.: **39**(2), 130-133.

Howard, A.E. (1988). Lobster behaviour, population structure and enhancement. Symp. Zool. Lond.: 59. Aspects of Decapod Biology; eds. A.A. Fineham and P.S. Rainbow Oxford Sci. Publ.: 355-364.

Howard, A.E. and Nunny, R.S. (1983). Effects of near-bed current speeds on the distribution and behaviour of the lobster (*Homarus gammarus* L.). J. Exp. Mar. Biol. Ecol.: 71, 2-42.

Hudon, C., Fradette, P. and Legendre, P. (1986). La repartition hotizontale et verticale des larves de homard (*Homarus americanus*) autour des iles de la Madeleine, golfe du Saint-Laurent. Can. J. Fish. Aquat. Sci.: **43**, 2164-2176.

Hughes, J.T. and Matthiessen, G.C. (1962). Observations on the biology of the American lobster *Homarus americanus*. Limnol. Oceanogr.: 7(3), 414-421.

Hughes, J. T. , Sulivan, J.J. and Shleser, R.A. (1972). Enhancement of lobster growth. Science: **177**, 1110-1111.

Hunt, J.H. and Lyons, W.G. (1986). Factors affecting growth and maturation of spiny lobsters,*Panulirus argus*,in the Florida Keys. Can. J. Fish. Aquat. Sci.: **43**, 2243-2247.

Jamieson, G.S. (1986). A perspective on invertebrate fisheries management- the British Columbia experience. Can. Spec. Publ. Fish. Aquat. Sci.: **92**, 57-74.

Jamieson, J.S. and Caddy, J.F. (1986). Research advice and its application to management of invertebrate resources: an overview. Can. Spec. Publ. Fish. Aquat. Sci.: **92**, 416-424.

Jayakody, D.S. (1989). Size at onset of sexual maturity and onset of spawning in female *Panulirus homarus*, (Crustacea, Decapoda, Palinuridae) in Sri Lanka. Mar. Ecol. prog. Ser.: **57**, 83-87.

Jensen. D. (1958). The relation between body size and the number of eggs in marine malacostraces. Meddr. Danm. Fish. Og. Havunders.: **2**(19), 1-25.

Kamiguichi, Y. (1971). Studies on the moulting of the freshwater prawn, *Palaemon* *paucidens*. II Effects of eyestalk removal in relation to the state of ovarian growth. J. Fac. Sci. Hokkaido. Univ. **18**(1):17-38.

Knight, A.P. (1918). Lobster investigations at Long Beach Pond Nova Scotia. Contrib. Can. Biol. 53-71.

Krouse, J.S. (1989). Peformances and selectivity of trap fisheries for crustaceans. In "Marine Invertebrate Fisheries: their assessment and management. Caddy, J.F. (ed.)." J. Wiley and Sons. New York. 307-326.

Krol, R.M., Hawkins, W.E. and Overstreet, R.M. (1992). Reproductive components. In "Microscopic anatomy of invertebrates. Vol. 10 Decapod crustacea, Harrison, F.W. and Humes, A.G. (eds.). p295-343.

Kuhn, R. and Sorensen, N.A. (1938). Uber Astakarten und ovoverdin. Ber. dt Chem. Ges. Bd.: **71**, 1879-1888

Latrouite, D., Morizur, Y. and Raguenes, G. (1984). Fecundities individuelles et par recrue du homard europeen *Homarus gammarus* (L) des cotes francaises. ICES CM 1984/**K38**.

Lipcius, R.N. (1985). Size dependant reproduction and molting in spiny lobsters and other long-lived decapods. Crustacean Issues **3**: Factors in adult growth. (Balkema Press): 129-148

Lucas, M.I. and Crisp, D.J. (1987). Energy metabolism of eggs during embryogenesis in *Balanoides balanoides*. J. Mar .Biol. Assoc., U.K.: **67**, 27-54.

MacDiarmid, A.B. (1989a). Moulting and reproduction of the spiny lobster *Jasus Edwardsii*, (Decapoda: Palinunidae) in northern New Zealand. Mar. Biol.: **103**, 303-310.

MacDiarmid, A.B. (1989b). Size at onset of maturity and size dependent reproductive output of female and male spiny lobsters *Janus edwardsii* (Hutton) (Decapoda Palinundae) in northern New Zealand. J. Exp. Mar. Biol. Ecol.: **127**, 229-243.

Mauchline, J. (1976). The Hiatt growth diagram for Crustacea. Mar. Biol.: **35**, 79-84.

Mauchline J. (1977). Growth of shrimps, crabs and lobsters,-an assessment. J. Cons. Int. Explor. Mer.: **37**, 162-169.

McLaren, I.A. (1965). Some relationships between temperature and egg size, body size, development rate and fecundity of the copepod *Pseudocalanus*. Limnol. Oceanog.: **10**, 528-538.

Mcleese, D.W. and Wilder, D.G. (1958). The activity and catchability of the lobster (*Homarus americanus*) in relation to temperature. J. Fish. Res. Bd. Can.: **5**(16), 1345-1354.

McLeese, D.W. and Wilder, D.G. (1964). Lobster storage and shipment. Fish. Res. Bd. Can. Bull.: **147**, 69pp.

Miller, R.J. (1983). How many traps should a crab fisherman fish? N. Am. J. Fish. Manag.: **3**, 1-8.

Miller, R.J. (1990). Effectiveness of crab and lobster traps. Can. J. Fish. Aquat. Sci.: **47**, 1228-1251.

Morgan, G.R. (1979). Trap response and the measurement of effort in the fishery for the Western Rock lobster. Rapp. P-V. Reun Cons. Int. Explor. Mer.: **175**, 197-203.

Morgan, G.E. and Momot, W.T. (1990). Population dynamics and exploitation responses of the freshwater crayfish *Orconectes virilis* Hagen. Ices, Shellfish Symp. 1990.

Morizur, Y. (1981). Evaluation de al perte d'oefs lors de l'incubation chez *Nephrops norvegicus* (L) dans la region Sud-Bretagne, France. Crustaceana.: **41**(3), 301-306.

Morizur, Y., Conan, C., Guenole, A., Omries, M.K. (1981). Fecondite de *Nephrops norvegicus* dans le golfe de Gascogne. M. Biol.: **63**, 319-324.

Munro, J.L. (1974). The mode of operation of Antillian fish traps and the relationships between ingrees, escapement, catch and soak. J. Cons. Int. Explor. Mer.: **35**, 337-350.

Nelson, K. (1986). Photoperiod and reproduction in lobsters (*Homarus*). Am. Zool: **26**, 447-457.

Nelson, K. and Hedgecock, D. (1985). Reply to Aiken and Waddy. Can. J. Fish. Aquat. Sci.: **42**, 199-200.

Nelson, K., Hedgecock, D. Borgeson,W. (1983). Photoperiodic and ecolysial control of vitellogenesis in lobsters (*Homarus*) (Decapode, Nephropidae). Can. J. Fish. Aquat. Sci.: **40**, 940.

Nelson, K., Hedgecock, D., Borgson,W., Johnson, E. Daggett, R. and Aronstein. D (1980). Density-dependant growth inhibition in lobsters, *Homarus* (Decapoda, Nephropidae). Biol.Bull.: **159**, 162-176.

Nichols, J.H. and Thompson, B.M. (1988). Quantitive sampling of crustacean larvae and its use in stock size estimation of commercially exploited species. Symp. Zool. Soc. Lond.: **59**, 157-179.

Orsi Relini, L. and Relini, G. (1985). Notes on the distribution, reproductive biology and fecundity of *Nephrops norvegicus* in the Ligurian Sea. FAO Fish. Rept.: **336**, 107-111.

Paloheimo, J.E. (1963). Estimation of Catchabilities and Population sizes of lobsters. J.Fish. Res. Bd. Can.; **20**(1), 59-88.

Pandian, T.J. (1970a). Ecophysiological studies on the developing eggs and embryros of the European lobster *Homarus gammarus*. Mar. Biol.; **5**, 153-167.

Pandian, T.J. (1970b). Yolk utilization and hatching time in the Canadian lobster *Homarus americanus*. Mar.Biol.: **7**, 249-254.

Panouse, J.B. (1943). Influence de l'ablation de pedoncule oculaire sur la croissance de l'ovarie chez la crevette *Leander serratus*. C. R. Hebd. Seances Acad. Sci.: **217**, 553-555.

Passano, L.M. (1960). Moulting and its control. In "The physiology of crustacea" Vol 1. Metabolism and growth. Waterman, T.H. (ed.). Acad. Press, New York. pp 473-536.

Pauly, D. (1980). On the interrelationships between natural mortality, growth parameters and near environmental temperature. J.Cons.: **39**, 175-192.

Perkins, H.C. (1971). Egg loss during incubation from offshore northern lobsters (Decapoda: Homaridae). Fish Bull US.: **69**, 451-453.

Perkins, H.C. (1972). Development rates at various temperatures of embryo of the northern lobster (*Homarus americanus*). Fish. Bull. **70**(1), 95-99.

Phillips, B.F., Cobb, J.S. and George, R.W. (1980). General Biology. In "Cobb, J.S. and Phillips, B.F. (eds). The Biology and Management of lobsters, Vol. 1". Academic Press. 2-82.

Pillay, K.K. and Nair, N.B. (1971). The annual reproductive cycles of *Uca annulipes*, *Portunus pelagicus* and *Metapenaeus affinis* (Decapoda: Crustacea), from the south-west coast of India. Mar. Biol.: **11**, 152-166.

Pillay, K.K. and Nair, N.B. (1973). Observations on the biochemical changes in gonads and other organs of *Uca annulipes*, *Portunus pelagicus* and *Metapenaeus affinis* (Decapoda: Crustacea) during the reproductive cycle. Mar. Biol.: **18**, 167-188.

Pollock, D.E. (1973). Growth of juvenile rock lobster *Jasus lalandii*. Sea Fish Invest. Rept. S. Africa : **106**, 16pp.

Pollock, D.E. (1982). The fishery for, and population dynamics of, west coast rock lobsters related to the environment in the Lamberts Bay and Port Nolloth areas. Sea Fish. Invest. Rept. S. Africa: **124**, 57pp.

Pollock, D.E. (1986). Review of the fishery for, and biology of, the Cape rock lobster *Jasus lalandii* with notes on larval recruitment. Can. J. Fish. Aquat. Sci.: **43**, 2107-2117.

Robinson, D.G. (1980). Consideration of the lobster (*Homarus americanus*), recruitment over fishing hypothesis; with special reference to the Canso Causeway. Can. Fish. Mar. Ser. Tech. Rept.: **834**(3), 77-99.

Rutherford, J.B., Wilder, D.G. and Frick, H.C. (1967). An economic appraisal of the Canadian lobster fishery. Bul. Fish. Res. Bd. Can.: **157**, 126 pp.

Saila, S.B. and Flowers, J.M. (1965). A simulation study of sex ratios and regulation effects with the American lobster *Homarus americanus*. Proc. Gulf. Carrib. Fish. Inst.: **18**, 66-78.

Saila, S.B., Flowers, J.M. and Hughes, J.T. (1969). Fecundity of the American lobster (*Homarus americanus*). Trans. Am. Fish. Soc.: **98**, 537-539.

Saila, S.B. and Marchessault, G. (1980). Population dynamics of clawed lobsters. In "The Biology and Management of lobsters, Vol. 2", Cobb, J.S. and Phillips, B.F. (eds.). 219-242.

Sasaki, G.C., McDowell, J., Capuzzo, M., and Biesiot, P. (1986). Nutritional and bioenergetic considerations in the development of the american lobster *Homarus americanus*. Can. J. Fish. Aquat. Sci.: **43**, 2311-2319.

Sastry, A.N. (1983). Ecological aspects of reproduction. In " The biology of Crustacea Vol. 8, Bliss, D.E. (ed.). Academic Press.

Saunders, J.W. (1949). Histophysiological work on lobsters., 35-43.

Scarratt, D.J. (1968). An artificial reef for lobsters *Homarus americanus*. J. Fish Res. Bd. Can.: **125**, 2683.

Scott, A. (1903). On the spawning of the common lobster. Trans. Liverpool Biol. Soc.: **17**, 106-113.

Silberbauer, B.I. (1971). The biology of the South African rock lobster *Jasus lalandii* (H.Milne Edwards) 2. The reproductive organs, mating and fertilisation. Fish. Invest. Rept. S. Africa: **93**, 46pp.

Simons, M.J. (1981). Relative growth in the New Zealand mud crab *Macrophthalmus hirtipes* (Brachyura: Ocypodidae). New Zealand, J. Mar. Freshwat. Res.: **15**, 193-200.

Simpson, A.C. (1958). The lobster fishery of Wales. Fish. Invest. Lond. Ser. II: **23**, 1-23.

Simpson, A.C. (1961). A contribution to the economics of the lobster (*Homarus vulgaris* Edw.) on the coast of North Wales. Fish. Invest.(Lond).Ser 2.: **23**, 1-28.

Simpson, A.C. (1975). Effort measurement in the trap fisheries for crustacea. Rapp. P.-V. Reun. Cons. Int. Explor. Mer.: **168**, 50-53.

Skud, B.E. (1979). Soak time and catch per pot in an offshore fishery for lobsters (*Homarus americanus*). Rapp. P-.V. Reun. Cons. Int. Explor. Mer.: **175**, 190-196.

Skud, B.E. and Perkins, H.C. (1969). Size composition, sex ratio and size at maturity of offshore northern lobster. U.S. Fish. Wildl. Serv. Spec. Sci. Rep.- Fish.: **598**, 1-10.

Smith, G.F.M. (1944). The catchability of lobsters. Fish. Res. Bd. Can.: **6**(3), 291-301.

Squires, H.J. (1965). Decapod crustaceans of Newfoundland, Labrador and the Canadian eastern Arctic. Fish. Res. Bd. Can. Manu. Rept. Ser (Biol): **810**, 212pp.

Squires, H.J. (1970). Lobster (*Homarus americanus*) fishery and ecology in Port-au-Port Bay, Newfoundland 1960-1965. Proc. Nat. Shellfish Assoc.: **60**, 22-39.

Squires, H.J. and Ennis, G.P. (1968). Lobsters from 95 fathoms deep off St.John's, Newfoundland. J. Fish Res. Bd. Can.: **25**(12), 2723-2724.

Squires HJ, Tucker, G.Z. and Ennis G.P.(1971). Lobsters (*Homarus americanus*) in Bay of Islands, Newfoundland 1963-1965. Fish. Res. Bd. Can. Manuscr. Rept.: **1151**, 58pp.

Squires HJ, Ennis G.P. and Tucker, G.Z. (1974) Lobsters of the Northwest coast of Newfoundland 1964-67. Proc. Natn. Shellf. Ass. 64:16-27.

Steel, C.G.H. (1980). Mechanisms of cocordination between moulting and reproduction in terrestrial isopod crustacea. Biol. Bull.: **159**, 206-218. .

Stern, K.G. and Salomon, K. (1938). On ovoverdin, the carotenid-protein pigment of the egg of the lobster. J. Biol. Chem.: **122**, 461-475.

Sutcliffe, W.H.J. (1952). Some observations of the breeding and migration of the Bermuda spiny lobster, *Panulirus argus*. Proc. Gulf. Caribb. Fish. Inst.: **4**, 64-68.

Templeman, W. (1934). Local differences in the body proportions of the lobster *Homarus americanus*. J. Biol. Bd. Can.: **1**, 213-226.

Templeman, W. (1936). The influence of temperature, salinity, light and food conditions on the survival and growth of the larvae of the lobster (*Homarus americanus*). J. Biol. Bd. Can.: **2**, 485-497.

Templeman, W. (1937). Egg laying and hatching postures of the american lobster, *Homarus americanus*. J. Fish. Res. Bd. Can.: **3**, 339-342.

Templeman, W. (1939). Investigation into the life history of the lobster (*Homarus americanus*) on the West Coast of Newfoundland 1938. Newf. Dept. Nat. Reserves Res. Bull. (Fish): 7, 1-52.

Templeman, W. (1940a). Lobster tagging on the West Coast of Newfoundland, 1938. Newf. Dept. Nat. Reserves Res. Bull. (Fish): **8**, 1-16.

Templeman W. (1940b) Embryonic development rates and egg-laying of the Canadian lobster. J.Fish Res. Bd. Can.5:71-83.

Templeman, W. (1944). Abdominal width and sexual maturity of female lobsters on Canadian Atlantic Coast. J. Fish Res. Bd. Can.: **6**(3), 281-290.

Templeman, W. and Tibbo, S.N. (1945). Lobster investigations in Newfoundland 1938-1941 Res. Bull. Div. Fish. Res. Newfl.: **16**, 98 pp.

Thomas, H.J. (1951). Fluctuations in the lobster (*Homarus vulgaris*) population of the Scottish Coast. Rapp. P.- V. Cons. Int. Explor. Mer.: **218**, 84-91.

Thomas, H.J. (1954). Some observations on the distribution biology and exploitation of the Norway lobster, (*Nephrops norvegicus* L.) in Scottish waters. SHD Mar. Res: **1**, 12pp.

Thomas, H.J. (1958). Some seasonal variations in the catch and stock composition of the lobster. J. Cons. Perm. Int. Explor. Mer.: **24**(1), 147-154.

Thomas, H.J.(1965). Berried lobsters. Scot. Fish Bull.: **23**, 10-12.

Thomas, T.H. (1955). Observations on the sex ratio and mortality ratio in the lobster (*Homarus vulgaris* Edw.). J. Cons. Perm. Int. Explor. Mer.: **20**, 295-305.

Thomas, J.C. (1973). An analysis of the commercial lobster (*Homarus americanus*) fishery along the coast of Maine, August 1966 through December 1970. US Dept. Comm. NOAA Tech. Rep. NMFS SSRF: **667**, 1-57.

Uzmann, J.R., Cooper, R.A. and Pecci, K.J. (1977). Migration and dispersion of tagged American lobsters, *Homarus americanus*, on the southern New

England continental shelf. N.O.A.A. Tech. Rep. N.M.F.S., S.S.R.F.: **705**, 1-92.

Van Engel, W.A. (1980). Maturity and fecundity in the American lobster H*omarus americanus* - A review. Can. Tech. Rep. Fish. Aquat. Sci.: **932**, 52-57.

Von Bonde, C. (1936). The reproduction, embryology and metamorphosis of the Cape crayfish (*Jasus lalandii*) (Milne-Edwards) Ortman. Invest. Rep. Div. Sea Fish. S. Afr.: **6**, 1-25.

Wacasey, J.W. and Atkinson, E.G. (1987). Energy values of marine benthic invertebrates from the Canadian Arctic. Mar. Ecol. Prog. Ser.: **39**, 243-250.

Waddy, S.L. and Aiken, D.E. (1979). Natural reproductive cycles of female american lobsters, *Homarus americanus*. Proc. Intern. Symp. Invert. Reprod.: **2**.

Waddy, S.L. and Aiken, D.E. (1985). Immunefluorescent localization of American lobster egg yolk protein in the alimentary tract of the Nemertean *Pseudocarcino-nemertes homari*. Can. J. Fish. Aquat. Sci.: **42**, 357-359.

Waddy, S.L. and Aiken, D.E. (1990). Intermolt insemination, an alternative mating strategy for the American lobster (*Homarus americanus*). Can. J. Fish. Aquat. Sci.: **47**, 2402-2406.

Wallace, R.A., Walker, S.L. and Hauschka, P.V. (1967). Crustacean lipovitellin: isolation and charachterisation of the major high density lipoprotein from the eggs of decapods. Biochem.: **6**, 1582-1590.

Wear, R.G. (1974). Incubation in British Decapod Crustacea and effects of temperature on the rate and success of embryonic development. J. Mar. Biol. Assoc. UK.: **54**, 745-762.

Wenner, A.M., Fusaro, C. and Oater, A. (1974). Size at onset of sexual maturity and growth rate in crustacean populations. Can. J. Zool.: **52**, 1095-1106.

Wenner, A.M., Page, H.M. and Siegel, P.R. (1985). Variation in size at onset of egg production. In "Crustacean Issues 3: Factors in adult Growth". Balkema Press.: 149-164.

Wickham, D.E. (1979). *Carcinonemertes errans* and the fouling mortality of eggs of the Dungeness crab, *C. magister.* J. Fish. Res. Bd.Can.: **36**, 1319-1324..

Wilder, D.G. (1953). The growth rate of the American lobster (*H.americanus*). J. Fish. Res. Bd. Can.: **10**(7), 371-412.

Wilder, D.G. (1963). Movements, growth and survival of marked and tagged lobsters liberated in Egremont Bay, Prince Edward Island. J. Fish. Res. Bd.

Can.: **20**, 305-311.

Witthames, P.R. and Greer-Walker, M. (1987). An automated method for counting and sizing fish eggs. J. Fish Biol.: **30**,: 225-235.

Yonge, C.M. (1937). The nature and significance of the membrane surrounding the developing eggs of *Homarus vulgaris* and other decapods. Proc. Zool. Soc. Lond. Ser. A: **107**, 499-517.

Yonge, C.M. (1946). Permeabilitity and properties of egg membranes surrounding the developing egg of *Homarus vulgaris*. J. Mar. Biol. Assoc. U.K. 1946: **26**, 432-438.

Table A2i.1 Bridlington sample types and dates.

Date	Sample Type and Origin
22/09/1987 to 29/09/1987	Fecundity *
07/06/1988 to 24/06/1988	Fecundity *
30/03/1989	Boat and laboratory
23/05/1989	Boat and laboratory
24/05/1989	Boat *
28/06/1989	Boat and laboratory
29/06/1989	Boat *
30/06/1989	Boat *
18/07/1989	Boat *
19/07/1989	Boat *
26/07/1989	Boat and laboratory
06/08/1989	Boat *
13/09/1989	Boat *
16/08/1990	Boat, fecundity and laboratory
18/08/1990	Boat *
10/09/1990	Boat *
11/09/1990	Boat * and morphometric data
17/09/1990	Fecundity and laboratory
10/06/1991	Boat *
11/06/1991	Boat *
13/06/1991	Boat *, fecundity and laboratory
14/06/1991	Boat *
11/06/1991 to 12/06/1991	Fecundity
20/06/1991	Fecundity

* Data collected by J.T. Addison, R.C.A. Bannister and S.R.J. Lovewell

Table A2i.2 Dale sample types and dates.

Date	Sample Type and Origin
11/05/1989	Boat and laboratory
15/06/1989	Boat and laboratory
20/07/1989	Boat and laboratory
23/08/1989	Boat and laboratory
02/06/1992	Fecundity and laboratory

Table A2.3 Selsey sample types and dates.

Date	Sample Type and Origin
26/04/1989	Boat and laboratory
06/07/1989	Boat and laboratory
09/08/1989	Boat and laboratory
07/09/1989	Boat and laboratory
14/09/1989	Fecundity
11/10/1989	Fecundity
23/11/1989	Fecundity and laboratory
04/04/1990	Fecundity and laboratory
23/05/1990	Boat, fecundity and laboratory
11/07/1990	Fecundity and laboratory
19/07/1990	Boat and laboratory
27/09/1990	Fecundity and laboratory
15/10/1990	Laboratory
07/11/1990	Fecundity and laboratory
07/02/1991	Fecundity and laboratory
12/04/1991	Fecundity and laboratory
08/07/1991	Fecundity and laboratory

Table A2.4 Additional sample dates and sites.

Date	Site
August 1972	Pembrokeshire
May 1973	Pembrokeshire
July 1973	Pembrokeshire
August 1973	Pembrokeshire
September 1973	Pembrokeshire
March 1972	Yorkshire
April 1972	Yorkshire
May 1972	Yorkshire
June 1972	Yorkshire
July 1972	Yorkshire
August 1972	Yorkshire
September 1972	Yorkshire
October 1972	Yorkshire
1973	Yorkshire
1974	Yorkshire
April 1972	South Coast
May 1972	South Coast
June 1972	South Coast
July 1972	South Coast
August 1972	South Coast
September 1972	South Coast
October 1972	South Coast
April 1973	South Coast
May 1973	South Coast
June 1973	South Coast
July 1973	South Coast
August 1973	South Coast
September 1973	South Coast

Appendix A2i Table 5 Growth Rate Estimates for *Homarus gammarus.*

Moult increment for an individual of 80 mm carapace length.

YORKSHIRE	Males	11.30 mm
	Females	9.15 mm
WEST WALES	Males	10.482 mm
	Females	7.99 mm
SELSEY	Males	11.246 mm
	Females	9.65 mm

Appendix A 2ii.1 Moult staging of *Homarus spp*

Appendix Table A 2ii.1 Determination of the moult stages of *Homarus* (after Aiken, 1973)

STAGE	CHARACTERISTICS	DURATION	ASSESSMENT
A_1	Body flaccid; water absorption continuing	0.3	Entire body soft
A_2	Integument soft; mineralisation begins; able to eat exuvia	1.1	Body soft but tips of chela and mouthparts hard
B	Integument flexible; new endocuticle secretion begins	2.0	
C_1	Integument flexible; thin lamina endocuticle forms in the merus of the cheliped; appendages hard; active foraging begins.	6.0	Region "A" may be depressed by finger pressure.
C_2	Carapace rigid posteriodorsal to rostrum but flexible elsewhere; thin lamina endocuticle forms in anteriodorsal carapace.	7.6	Region "A" cannot be depressed by light finger pressure. Region "B" can still be.
C_3	Carapace rigid except for branchial region; thin lamina endocuticle forms in all areas of the carapace	9.0	Region "C" only may depressed by light finger pressure
C_4	Carapace rigid; membraneous layer formed; organic reserves accumulate.	30.0	
D_0	Passive premoult; may remain in this state for an extended period.	>26.0	Pleopods examined for setal development
D_1	Active premoult (irreversable); new epicuticle forms; new setae form and invaginate	9.0	
D_2	New exocuticle formed	7.0	
D_3	Extensive resorption of minerals from exoskeleton; decalcification of dorsal surface of merus and ecdysial stutures.	2.0	
E	Passive phase of ecdysis (may be delayed); water absorption increased; ecdysial sutures open.		
	Active phase of ecdysis (irreversable); thoraco-abdominal membranr ruptures; carapace is thrown forward and emergence occurs.		

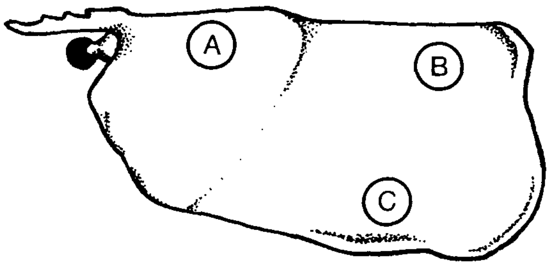


Figure A3ii.1 Regions of the carapace of *Homarus* for use in moult staging (after Aiken, 1980).

Appendix A2ii.2 Cement gland staging in *Homarus spp*.

Appendix Table A2ii.2 Determination of the cement gland stages of *Homarus* (after Aiken and Waddy, 1982)

Stage 1. Tissue thickened between nodes along lateral and medial edges, but the glands not visible to the unaided eye. Glands visible as spots with X20 magnification.

Stage 2. Some cement gland activity in central region. Glands just visible as spots to the naked eye.

Stage 3. Gland rosettes well developed in central region of endopodite. Visible to unaided eye as distinct white dots in central region, and as a continuous white mass in the medial and lateral regions.

Stage 4. All glands engorged and visible to the naked eye as a white mass in the medial and lateral regions, and in the proximal portion of the central region.

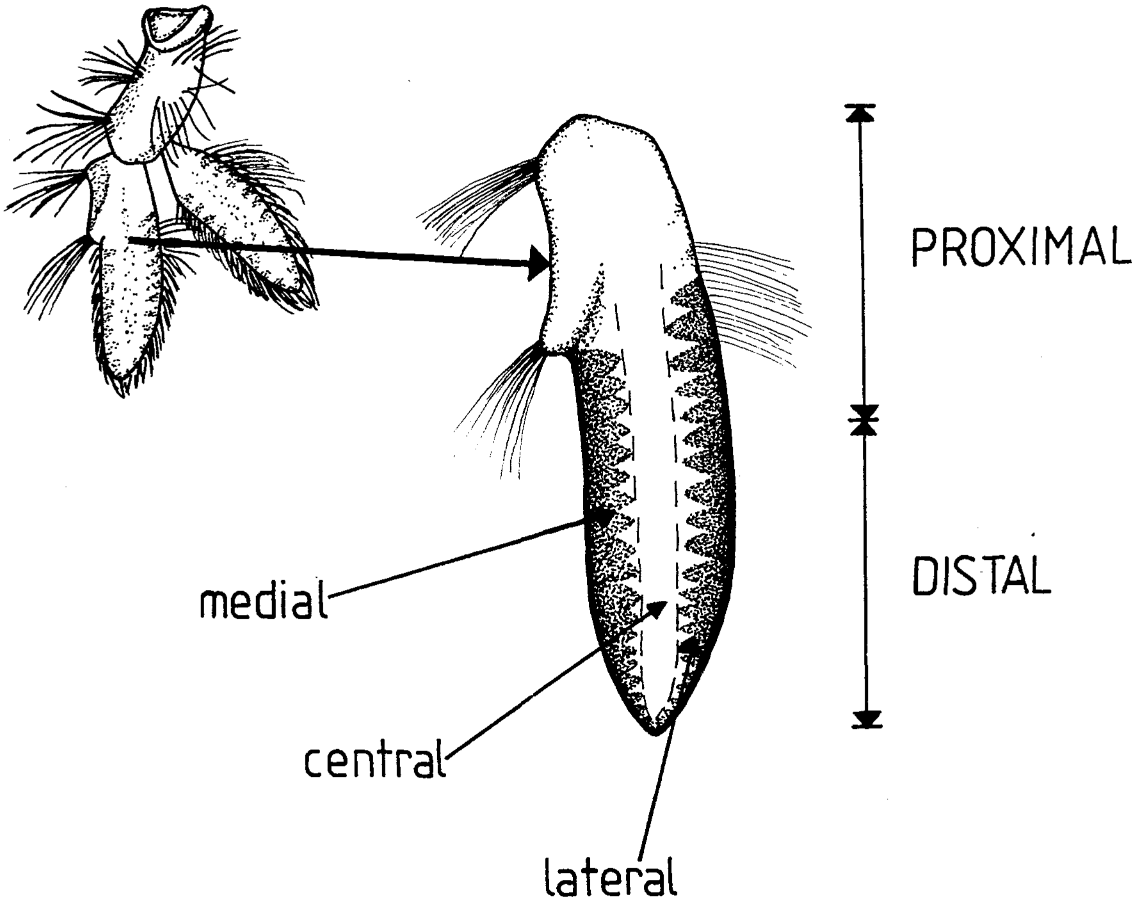


Fig A2ii.2 Regions of pleopod endopodite useful for staging cement gland development

Table A2iii.1 Bridlington catch size distribution summary statistics.

Sample Date	Sex	Sample size	Average CL (mm)	Median CL (mm)	Mode CL (mm)	Minimum CL (mm)	Maximum CL (mm)	Std Dev. CL (mm)	Distribution Skewness	Distribution Kurtosis
30/03/1989	Males	28	81.0357	81.5	83	68	98	6.13117	0.396691	1.51315
30/03/1989	Females	23	78	79	72	64	100	7.48939	0.745888	2.46393
23/05/1989	Males	56	80.8929	80	82	66	108	7.51406	1.26461	2.95033
23/05/1989	Females	70	84.8857	84	86	68	126	9.01133	1.24858	5.09493
24/05/1989	Males	74	81.3784	81	82	67	106	8.066	0.883011	1.23536
24/05/1989	Females	151	81.4768	81	82	63	101	7.33197	0.008556	0.267962
28/06/1989	Males	57	85.5965	84	84	72	105	7.59666	0.44193	-0.472747
28/06/1989	Females	69	84.1159	83	80	72	111	7.34554	1.57339	4.07835
29/06/1989	Males	43	87.8605	87	90	66	107	8.5261	0.0747029	0.313056
29/06/1989	Females	46	82.8261	82.5	82	64	100	7.27646	-0.234494	1.04435
30/06/1989	Males	39	84.8462	83	80	66	107	8.95468	0.415219	0.139994
30/06/1989	Females	45	82.2444	82	83	73	95	5.8704	0.192856	-0.799479
18/07/1989	Males	69	85.1159	84	83	60	102	7.63417	-0.414278	0.664998
18/07/1989	Females	76	84.1842	85	87	68	99	6.07445	-0.260862	0.0588892
19/07/1989	Males	100	85.4	85	83	62	136	9.95647	1.16799	5.80866
19/07/1989	Females	91	83.9341	85	85	64	108	7.16752	-0.096183	1.24728
26/07/1989	Males	78	85.6795	86.5	84	63	106	8.52726	-0.313217	-0.067484
26/07/1989	Females	96	84.7708	85	81	68	124	8.2774	0.877495	4.12919
06/08/1989	Males	198	86.4646	86	86	65	116	9.71347	0.452771	0.347696
06/08/1989	Females	204	85.2353	86	85	70	108	7.10051	-0.019138	-0.12818
13/09/1989	Males	118	85.1017	84	81	62	111	8.30033	0.415894	0.908939
13/09/1989	Females	169	85.8107	85	92	63	111	7.55454	0.129228	0.449486
1989	Males	860	84.936	84	83	60	136	8.85989	0.541787	1.39939
1989	Females	1040	84.0558	84	84	63	126	7.54587	0.356463	1.66508
16/08/1990	Males	12	82.25	81	75	72	95	7.33764	0.62534	-0.455359
16/08/1990	Females	10	84.1	83.5	80	68	98	9.39799	0.0064454	-0.434294
18/08/1990	Males	51	86.7647	86	82	72	113	9.13365	0.65482	0.288082
18/08/1990	Females	60	82.7333	82	76	72	95	6.3242	0.267914	-0.708047
10/09/1990	Males	35	88.6	88	77	75	112	9.03978	0.610801	-0.133241
10/09/1990	Females	28	88.5	88	81	77	106	7.50555	0.641572	-0.011482
11/09/1990	Males	32	84.625	82.5	80	64	103	9.28318	0.054758	-0.678644
11/09/1990	Females	47	82.3617	82	82	57	102	8.70638	-0.374899	0.674381
1990	Males	130	86.3154	85	80	64	113	9.10578	0.472658	-0.03629
1990	Females	145	83.8207	83	86	57	106	7.88253	0.0217366	0.551961
10/06/1991	Males	66	84.2121	84.5	81	68	104	8.27697	0.28605	-0.26157
10/06/1991	Females	62	81.0484	80.5	80	64	112	8.24308	0.795582	2.31465
11/06/1991	Males	15	82.3333	84	79	59	98	10.8672	-0.522809	0.066082
11/06/1991	Females	21	82.0476	81	81	70	103	8.91334	0.955828	0.299823
13/06/1991	Males	24	81.4167	82	85	68	97	6.03552	-0.066236	1.5507
13/06/1991	Females	28	79	80	80	64	98	8.3887	0.166621	-0.313026
14/06/1991	Males	7	84	85	81	74	92	6.37704	-0.356299	-0.834292
14/06/1991	Females	23	77.8696	78	78	67	91	5.90304	0.31004	-0.215203
1991	Males	112	83.3482	83.5	85	59	104	8.1348	0.0573374	0.264418
1991	Females	134	80.2313	80	80	64	112	8.07941	0.701504	1.33715

Table A2iii.2 Dale catch size distribution summary statistics.

Sample Date	Sex	Sample size	Average CL (mm)	Median CL (mm)	Mode CL (mm)	Minimum CL (mm)	Maximum CL (mm)	Std Dev. CL (mm)	Distribution Skewness	Distribution Kurtosis
11/05/1989	Males	3	115.33	106	105	105	135	17.039	1.7253	-
11/05/1989	Females	11	102.09	104	128	81	128	15.921	0.47714	-0.5544
15/06/1989	Males	10	112	109	109	91	136	16.282	0.15811	-1.5103
15/06/1989	Females	24	110.38	106.5	102	89	141	14.385	0.7335	-0.3611
20/07/1989	Males	26	117.31	122	127	87	150	17.239	-0.2731	-0.614
20/07/1989	Females	29	116.79	120	122	92	140	14.436	-0.09957	-0.9514
23/08/1989	Males	45	111.04	114	91	71	148	18.518	6.84E-05	-0.83511
23/08/1989	Females	52	110.77	122.5	125	74	148	17.341	-0.12614	-0.7689
1989	Males	84	113.25	114	103	71	150	17.753	-0.07743	-0.84602
1989	Females	115	111.41	111	128	74	148	16.36	-0.34861	-0.8018

Table A2iii.3 Selsey catch size distribution summary statistics.

Sample Date	Sex	Sample size	Average CL (mm)	Median CL (mm)	Mode CL (mm)	Minimum CL (mm)	Maximum CL (mm)	Std Dev. CL (mm)	Distribution Skewness	Distribution Kurtosis
26/04/1989	Males	66	79.152	79	78	68	95	5.201	0.6889	1.3307
26/04/1989	Females	103	79.941	81	82	64	99	6.1498	-0.12397	0.5267
06/07/1989	Males	184	78.147	79	80	64	99	5.5717	-0.07328	0.80238
06/07/1989	Females	183	81.328	82	85	60	100	7.0921	-0.30431	-0.0501
09/08/1989	Males	44	79.977	80.5	82	61	96	7.296	-0.358	0.7401
09/08/1989	Females	56	81.5	81	85	64	97	7.8601	0.02982	-0.72272
07/09/1989	Males	55	80.455	80	80	61	93	6.6272	-0.5517	0.21153
07/09/1989	Females	70	82.657	82	90	64	100	7.5602	0.00218	-0.45996
1989	Males	349	78.932	79	80	61	99	5.9674	-0.05817	0.65036
1989	Females	412	81.231	82	82	60	100	7.0922	-0.09752	-0.14793
23/05/1990	Males	60	83.1	83	83	63	123	10.3804	1.5825	4.9132
23/05/1990	Females	57	83.597	82	82	66	103	7.1436	0.23739	1.14458
19/07/1990	Males	166	79.398	80	82	63	96	6.0762	-0.24985	0.49596
19/07/1990	Females	231	81.909	82	82	60	105	8.7231	0.099313	-0.25906
1990	Males	226	80.381	81	82	63	123	7.6167	1.2864	6.7511
1990	Females	288	82.243	822	82	60	105	8.4493	0.0809	-0.08503

Table A2iii.4 Additional Yorkshire size distribution summary statistics.

Sample Date	Sample size	Median class CL (mm)	Modal class CL (mm)	Minimum class CL (mm)	Maximum class CL (mm)
March 1972	108	80-85	80-85	75-80	110-115
April 1972	331	80-85	80-85	75-80	110-115
May 1972	320	85-90	80-85	75-80	110-115
June 1972	443	85-90	80-85	75-80	140-145
July 1972	172	85-90	80-85	75-80	120-125
August 1972	814	85-90	80-85	75-80	125-130
September 1972	143	85-90	80-85	75-80	105-110
October 1972	166	85-90	85-90	75-80	115-120
1972	2497	85-90	85-90	75-80	140-145
1973	2708	85-90	85-90	75-80	135-140
1974	1616	85-90	85-90	75-80	130-135

Table A2iii.5 Additional Pembrokeshire size distribution summary statistics.

Sample Date	Sample size	Median class CL (mm)	Modal class CL (mm)	Minimum class CL (mm)	Maximum class CL (mm)
August 1972	635	90-95	90-95	75-80	145-150
May 1973	91	100-105	90-95	80-85	135-140
July 1973	414	95-100	90-95	75-80	140-145
August 1973	303	90-95	85-90,95-100	75-80	145-150
September 1973	110	90-95	80-85	75-80	130-135
1973	918	95-100	90-95	75-80	145-150

Table A2iii.6 Additional South coast size distribution summary statistics.

Sample Date	Sample size	Median class CL (mm)	Modal class CL (mm)	Minimum class CL (mm)	Maximum class CL (mm)
April 1972	140	85-90	85-90	75-80	125-130
May 1972	516	95-100	85-90	75-80	125-130
June 1972	560	85-90	90-95	75-80	130-135
July 1972	875	90-95	85-90	75-80	135-140
August 1972	91.	90-95	80-85	75-80	120-125
September 1972	381	95-100	80-85	75-80	115-120
October 1972	603	85-90	80-85	75-80	115-120
1972	3166	90-95	80-85	75-80	135-140
April 1973	202	95-100	85-90	75-80	145-150
May 1973	155	90-95	85-90	75-80	125-130
June 1973	938	85-90	80-85	75-80	135-140
July 1973	472	80-85	80-85	75-80	120-125
August 1973	424	85-90	80-85	75-80	125-130
September 1973	561	85-90	80-85	75-80	125-130
1973	2752	85-90	80-85	75-80	145-150

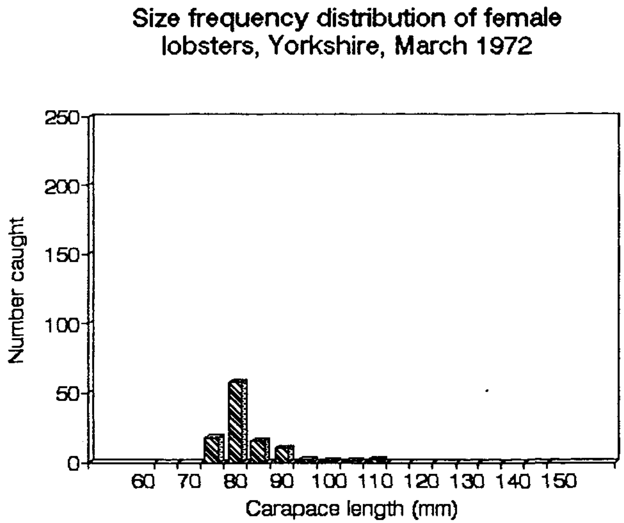


Fig.A2.1

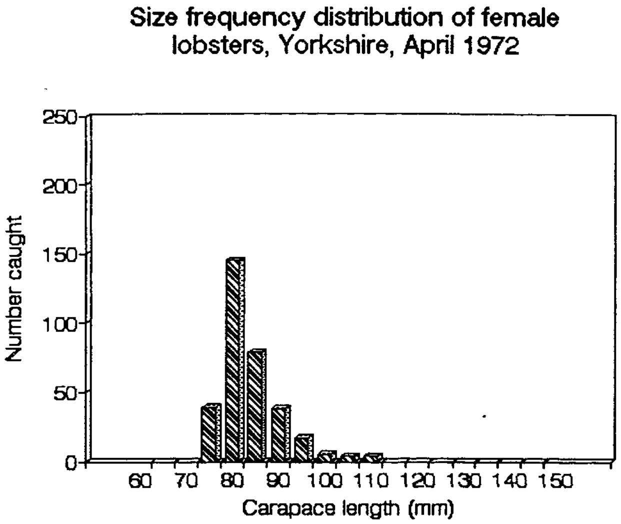


Fig.A2.2

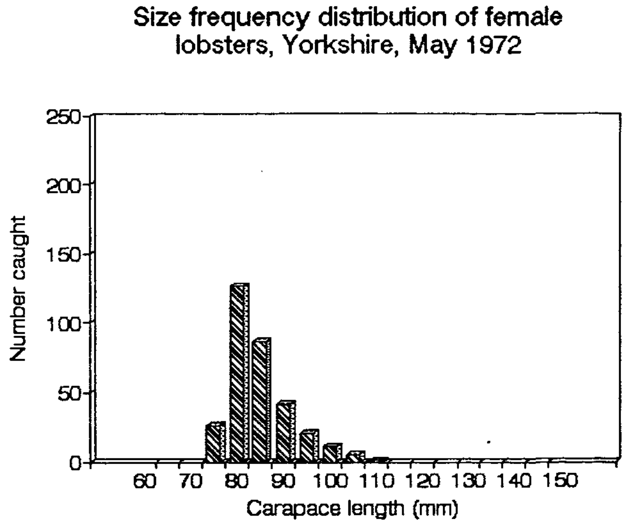


Fig.A2.3

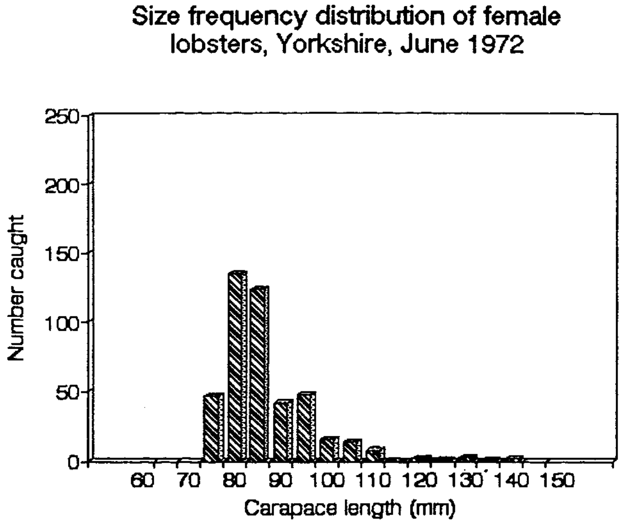


Fig.A2.4

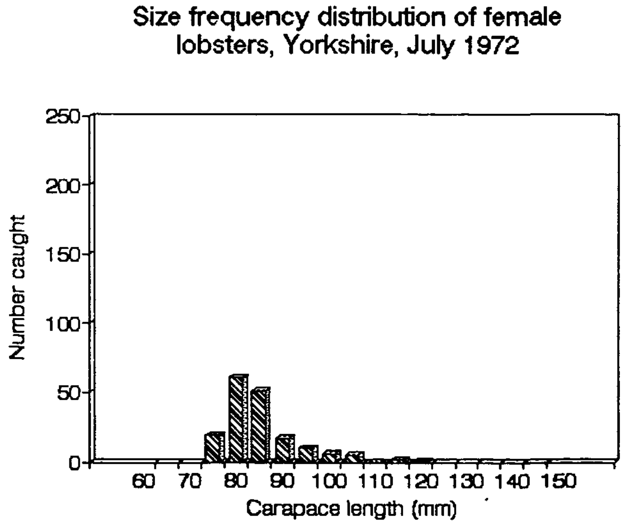


Fig.A2.5

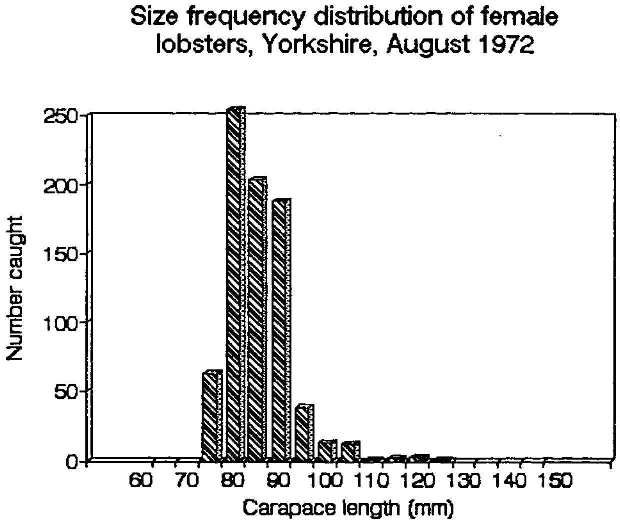
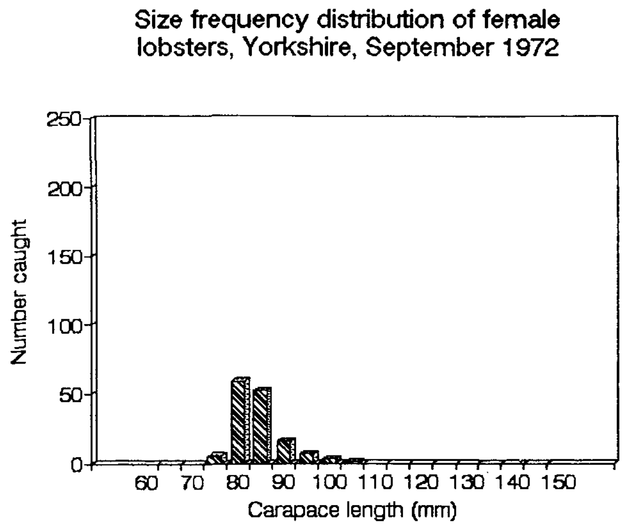
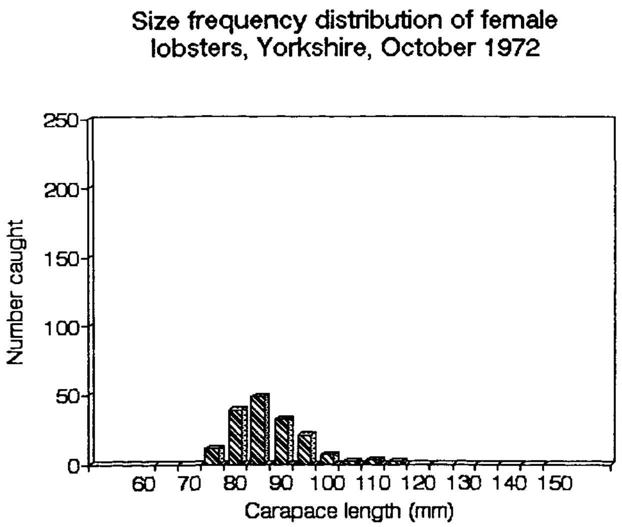


Fig.A2.6



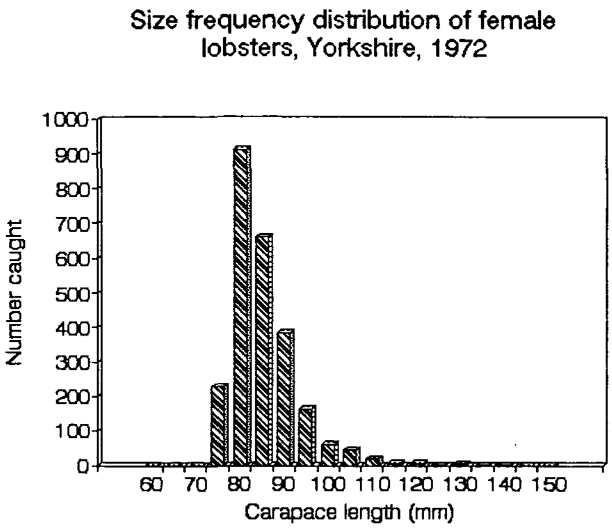
Size frequency distribution of female lobsters, Yorkshire, September 1972

Fig.A2.7



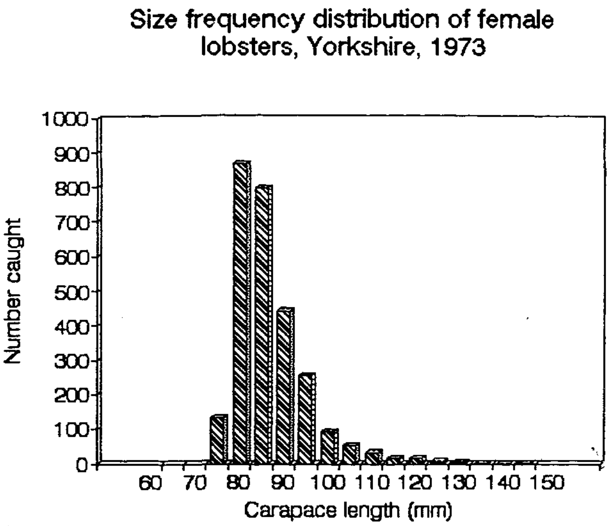
Size frequency distribution of female lobsters, Yorkshire, October 1972

Fig.A2 8



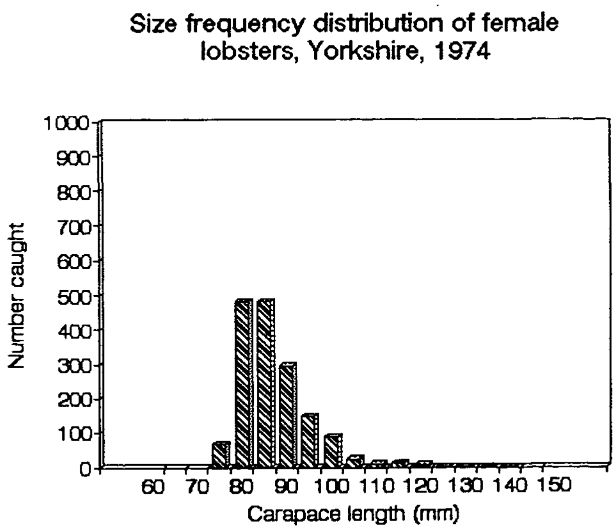
Size frequency distribution of female lobsters, Yorkshire, 1972

Fig.A2.9



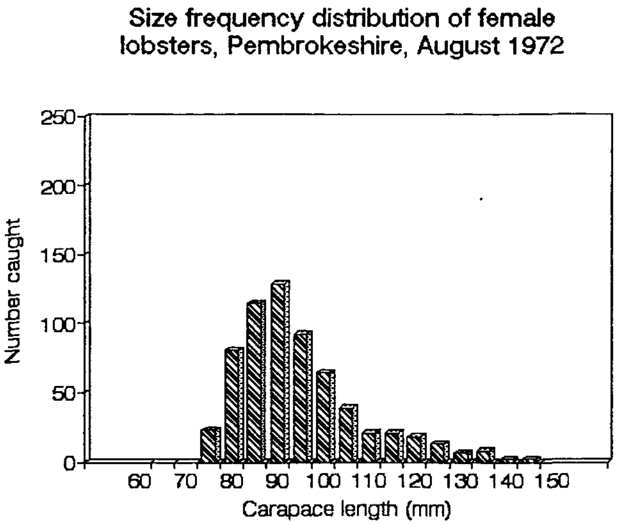
Size frequency distribution of female lobsters, Yorkshire, 1973

Fig.A2.10



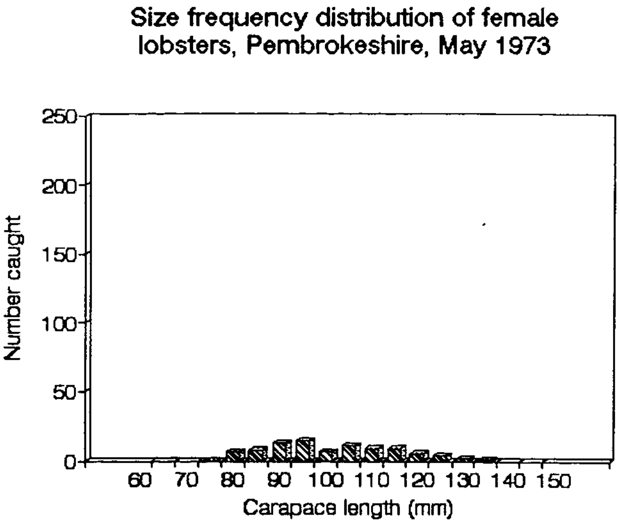
Size frequency distribution of female lobsters, Yorkshire, 1974

Fig.A2.11



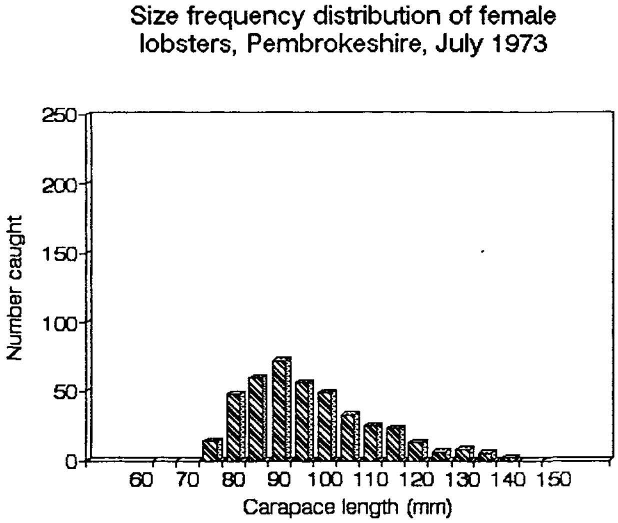
Size frequency distribution of female lobsters, Pembrokeshire, August 1972

Fig.A2.12



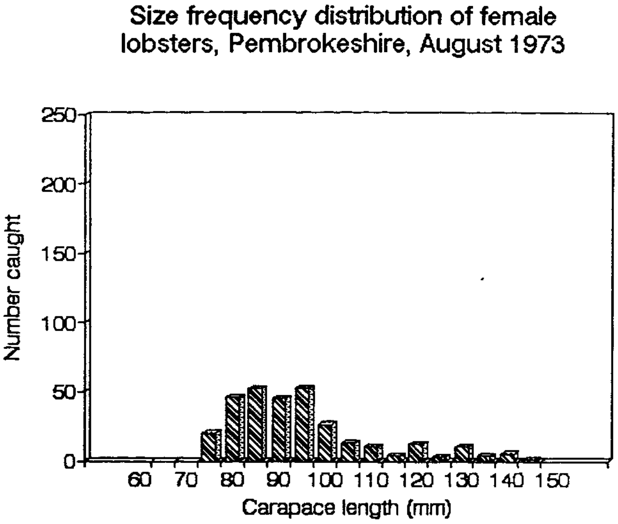
Size frequency distribution of female lobsters, Pembrokeshire, May 1973

Fig.A2.13



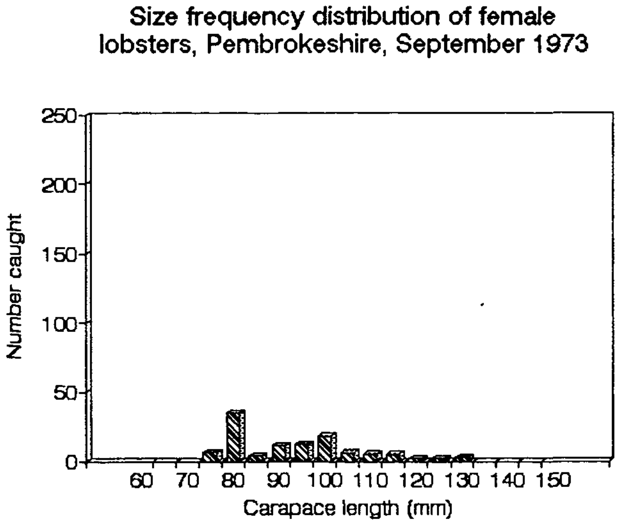
Size frequency distribution of female lobsters, Pembrokeshire, July 1973

Fig.A2.14



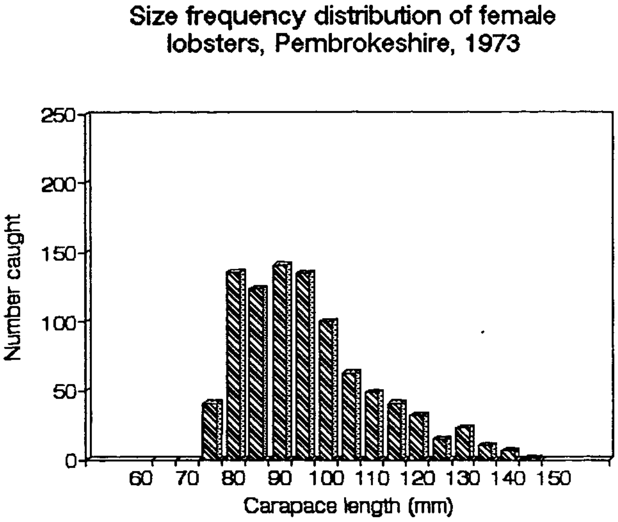
Size frequency distribution of female lobsters, Pembrokeshire, August 1973

Fig.A2.15



Size frequency distribution of female lobsters, Pembrokeshire, September 1973

Fig.A2.16



Size frequency distribution of female lobsters, Pembrokeshire, 1973

Fig.A2.17

Table A2iii.2 Dale catch size distribution summary statistics.

Sample Date	Sex	Sample size	Average CL (mm)	Median CL (mm)	Mode CL (mm)	Minimum CL (mm)	Maximum CL (mm)	Std Dev. CL (mm)	Distribution Skewness	Distribution Kurtosis
11/05/1989	Males	3	115.33	106	105	105	135	17.039	1.7253	-
11/05/1989	Females	11	102.09	104	128	81	128	15.921	0.47714	-0.5544
15/06/1989	Males	10	112	109	109	91	136	16.282	0.15811	-1.5103
15/06/1989	Females	24	110.38	106.5	102	89	141	14.385	0.7335	-0.3611
20/07/1989	Males	26	117.31	122	127	87	150	17.239	-0.2731	-0.614
20/07/1989	Females	29	116.79	120	122	92	140	14.436	-0.09957	-0.9514
23/08/1989	Males	45	111.04	114	91	71	148	18.518	6.84E-05	-0.83511
23/08/1989	Females	52	110.77	122.5	125	74	148	17.341	-0.12614	-0.7689
1989	Males	84	113.25	114	103	71	150	17.753	-0.07743	-0.84602
1989	Females	115	111.41	111	128	74	148	16.36	-0.34861	-0.8018

Table A2iii.3 Selsey catch size distribution summary statistics.

Sample Date	Sex	Sample size	Average CL (mm)	Median CL (mm)	Mode CL (mm)	Minimum CL (mm)	Maximum CL (mm)	Std Dev. CL (mm)	Distribution Skewness	Distribution Kurtosis
26/04/1989	Males	66	79.152	79	78	68	95	5.201	0.6889	1.3307
26/04/1989	Females	103	79.941	81	82	64	99	6.1498	-0.12397	0.5267
06/07/1989	Males	184	78.147	79	80	64	99	5.5717	-0.07328	0.80238
06/07/1989	Females	183	81.328	82	85	60	100	7.0921	-0.30431	-0.0501
09/08/1989	Males	44	79.977	80.5	82	61	96	7.296	-0.358	0.7401
09/08/1989	Females	56	81.5	81	85	64	97	7.8601	0.02982	-0.72272
07/09/1989	Males	55	80.455	80	80	61	93	6.6272	-0.5517	0.21153
07/09/1989	Females	70	82.657	82	90	64	100	7.5602	0.00218	-0.45996
1989	Males	349	78.932	79	80	61	99	5.9674	-0.05817	0.65036
1989	Females	412	81.231	82	82	60	100	7.0922	-0.09752	-0.14793
23/05/1990	Males	60	83.1	83	83	63	123	10.3804	1.5825	4.9132
23/05/1990	Females	57	83.597	82	82	66	103	7.1436	0.23739	1.14458
19/07/1990	Males	166	79.398	80	82	63	96	6.0762	-0.24985	0.49596
19/07/1990	Females	231	81.909	82	82	60	105	8.7231	0.099313	-0.25906
1990	Males	226	80.381	81	82	63	123	7.6167	1.2864	6.7511
1990	Females	288	82.243	822	82	60	105	8.4493	0.0809	-0.08503

Table A2iii.4 Additional Yorkshire size distribution summary statistics.

Sample Date	Sample size	Median class CL (mm)	Modal class CL (mm)	Minimum class CL (mm)	Maximum class CL (mm)
March 1972	108	80-85	80-85	75-80	110-115
April 1972	331	80-85	80-85	75-80	110-115
May 1972	320	85-90	80-85	75-80	110-115
June 1972	443	85-90	80-85	75-80	140-145
July 1972	172	85-90	80-85	75-80	120-125
August 1972	814	85-90	80-85	75-80	125-130
September 1972	143	85-90	80-85	75-80	105-110
October 1972	166	85-90	85-90	75-80	115-120
1972	2497	85-90	85-90	75-80	140-145
1973	2708	85-90	85-90	75-80	135-140
1974	1616	85-90	85-90	75-80	130-135

Table A2iii.5 Additional Pembrokeshire size distribution summary statistics.

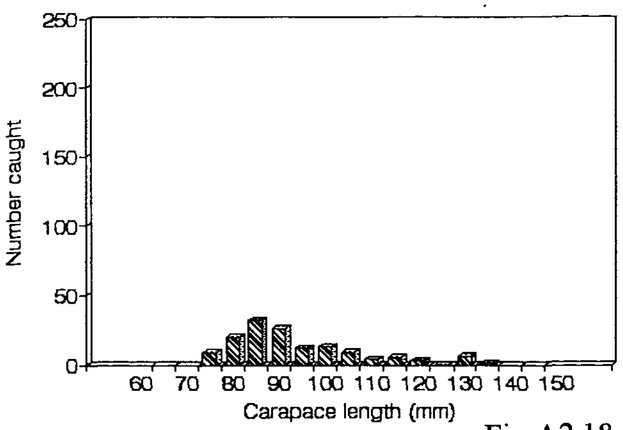
Sample Date	Sample size	Median class CL (mm)	Modal class CL (mm)	Minimum class CL (mm)	Maximum class CL (mm)
August 1972	635	90-95	90-95	75-80	145-150
May 1973	91	100-105	90-95	80-85	135-140
July 1973	414	95-100	90-95	75-80	140-145
August 1973	303	90-95	85-90,95-100	75-80	145-150
September 1973	110	90-95	80-85	75-80	130-135
1973	918	95-100	90-95	75-80	145-150

Table A2iii.6 Additional South coast size distribution summary statistics.

Sample Date	Sample size	Median class CL (mm)	Modal class CL (mm)	Minimum class CL (mm)	Maximum class CL (mm)
April 1972	140	85-90	85-90	75-80	125-130
May 1972	516	95-100	85-90	75-80	125-130
June 1972	560	85-90	90-95	75-80	130-135
July 1972	875	90-95	85-90	75-80	135-140
August 1972	91.	90-95	80-85	75-80	120-125
September 1972	381	95-100	80-85	75-80	115-120
October 1972	603	85-90	80-85	75-80	115-120
1972	3166	90-95	80-85	75-80	135-140
April 1973	202	95-100	85-90	75-80	145-150
May 1973	155	90-95	85-90	75-80	125-130
June 1973	938	85-90	80-85	75-80	135-140
July 1973	472	80-85	80-85	75-80	120-125
August 1973	424	85-90	80-85	75-80	125-130
September 1973	561	85-90	80-85	75-80	125-130
1973	2752	85-90	80-85	75-80	145-150

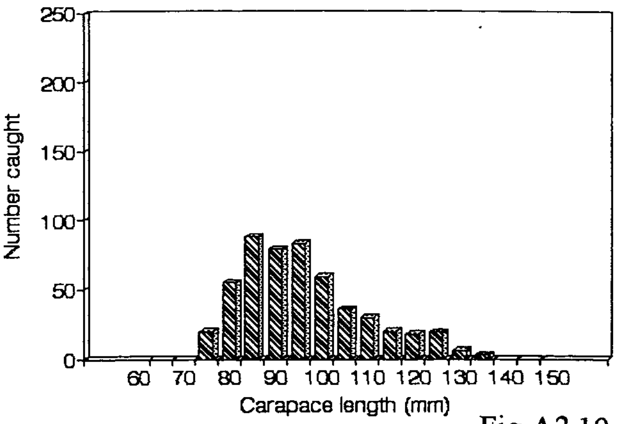
Table A2iii.1 Bridlington catch size distribution summary statistics.

Sample Date	Sex	Sample size	Average CL (mm)	Median CL (mm)	Mode CL (mm)	Minimum CL (mm)	Maximum CL (mm)	Std Dev. CL (mm)	Distribution Skewness	Distribution Kurtosis
30/03/1989	Males	28	81.0357	81.5	83	68	98	6.13117	0.396691	1.51315
30/03/1989	Females	23	78	79	72	64	100	7.48939	0.745888	2.46393
23/05/1989	Males	56	80.8929	80	82	66	108	7.51406	1.26461	2.95033
23/05/1989	Females	70	84.8857	84	86	68	126	9.01133	1.24858	5.09493
24/05/1989	Males	74	81.3784	81	82	67	106	8.066	0.883011	1.23536
24/05/1989	Females	151	81.4768	81	82	63	101	7.33197	0.008556	0.267962
28/06/1989	Males	57	85.5965	84	84	72	105	7.59666	0.44193	-0.472747
28/06/1989	Females	69	84.1159	83	80	72	111	7.34554	1.57339	4.07835
29/06/1989	Males	43	87.8605	87	90	66	107	8.5261	0.0747029	0.313056
29/06/1989	Females	46	82.8261	82.5	82	64	100	7.27646	-0.234494	1.04435
30/06/1989	Males	39	84.8462	83	80	66	107	8.95468	0.415219	0.139994
30/06/1989	Females	45	82.2444	82	83	73	95	5.8704	0.192856	-0.799479
18/07/1989	Males	69	85.1159	84	83	60	102	7.63417	-0.414278	0.664998
18/07/1989	Females	76	84.1842	85	87	68	99	6.07445	-0.260862	0.0588892
19/07/1989	Males	100	85.4	85	83	62	136	9.95647	1.16799	5.80866
19/07/1989	Females	91	83.9341	85	85	64	108	7.16752	-0.096183	1.24728
26/07/1989	Males	78	85.6795	86.5	84	63	106	8.52726	-0.313217	-0.067484
26/07/1989	Females	96	84.7708	85	81	68	124	8.2774	0.877495	4.12919
06/08/1989	Males	198	86.4646	86	86	65	116	9.71347	0.452771	0.347696
06/08/1989	Females	204	85.2353	86	85	70	108	7.10051	-0.019138	-0.12818
13/09/1989	Males	118	85.1017	84	81	62	111	8.30033	0.415894	0.908939
13/09/1989	Females	169	85.8107	85	92	63	111	7.55454	0.129228	0.449486
1989	Males	860	84.936	84	83	60	136	8.85989	0.541787	1.39939
1989	Females	1040	84.0558	84	84	63	126	7.54587	0.356463	1.66508
16/08/1990	Males	12	82.25	81	75	72	95	7.33764	0.62534	-0.455359
16/08/1990	Females	10	84.1	83.5	80	68	98	9.39799	0.0064454	-0.434294
18/08/1990	Males	51	86.7647	86	82	72	113	9.13365	0.65482	0.288082
18/08/1990	Females	60	82.7333	82	76	72	95	6.3242	0.267914	-0.708047
10/09/1990	Males	35	88.6	88	77	75	112	9.03978	0.610801	-0.133241
10/09/1990	Females	28	88.5	88	81	77	106	7.50555	0.641572	-0.011482
11/09/1990	Males	32	84.625	82.5	80	64	103	9.28318	0.054758	-0.678644
11/09/1990	Females	47	82.3617	82	82	57	102	8.70638	-0.374899	0.674381
1990	Males	130	86.3154	85	80	64	113	9.10578	0.472658	-0.03629
1990	Females	145	83.8207	83	86	57	106	7.88253	0.0217366	0.551961
10/06/1991	Males	66	84.2121	84.5	81	68	104	8.27697	0.28605	-0.26157
10/06/1991	Females	62	81.0484	80.5	80	64	112	8.24308	0.795582	2.31465
11/06/1991	Males	15	82.3333	84	79	59	98	10.8672	-0.522809	0.066082
11/06/1991	Females	21	82.0476	81	81	70	103	8.91334	0.955828	0.299823
13/06/1991	Males	24	81.4167	82	85	68	97	6.03552	-0.066236	1.5507
13/06/1991	Females	28	79	80	80	64	98	8.3887	0.166621	-0.313026
14/06/1991	Males	7	84	85	81	74	92	6.37704	-0.356299	-0.834292
14/06/1991	Females	23	77.8696	78	78	67	91	5.90304	0.31004	-0.215203
1991	Males	112	83.3482	83.5	85	59	104	8.1348	0.0573374	0.264418
1991	Females	134	80.2313	80	80	64	112	8.07941	0.701504	1.33715



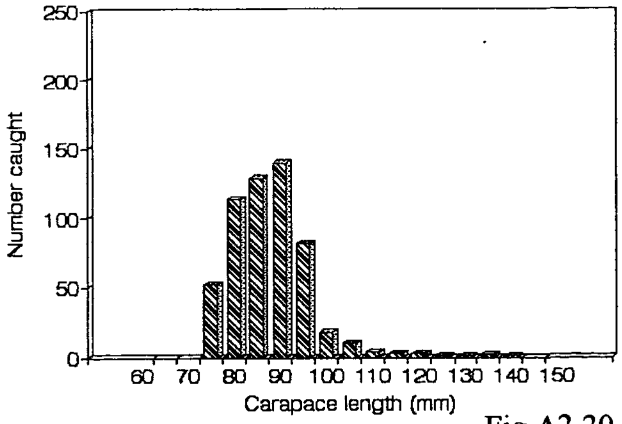
Size frequency distribution of female lobsters, South Coast, April 1972

Fig.A2.18



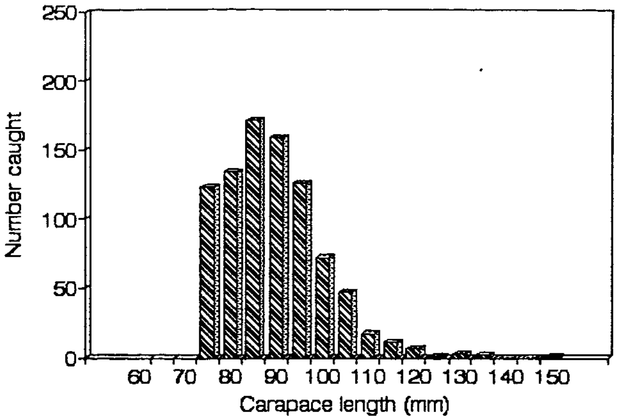
Size frequency distribution of female lobsters, South Coast, May 1972

Fig.A2.19



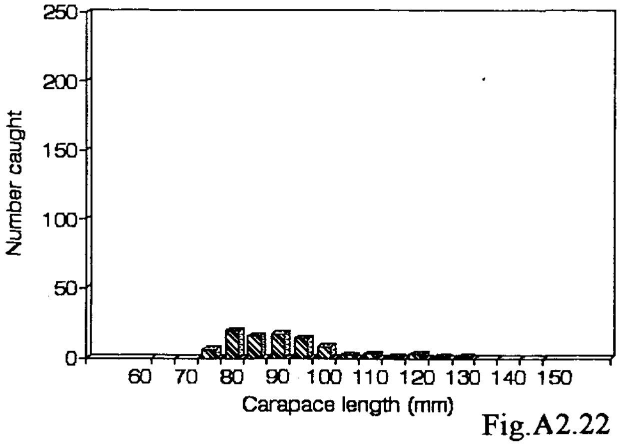
Size frequency distribution of female lobsters, South Coast, June 1972

Fig.A2.20



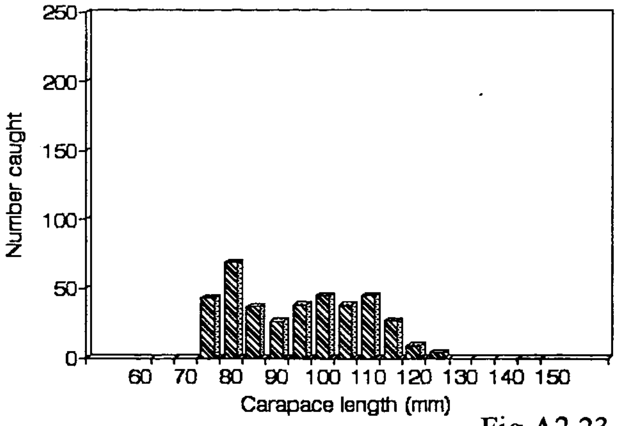
Size frequency distribution of female lobsters, South Coast, July 1972

Fig.A2.21



Size frequency distribution of female lobsters, South Coast, August 1972

Fig.A2.22



Size frequency distribution of female lobsters, South Coast, September 1972

Fig.A2.23

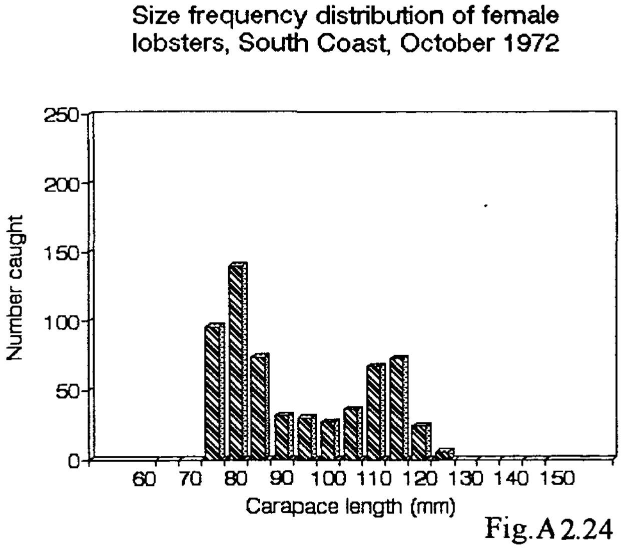


Fig.A2.24

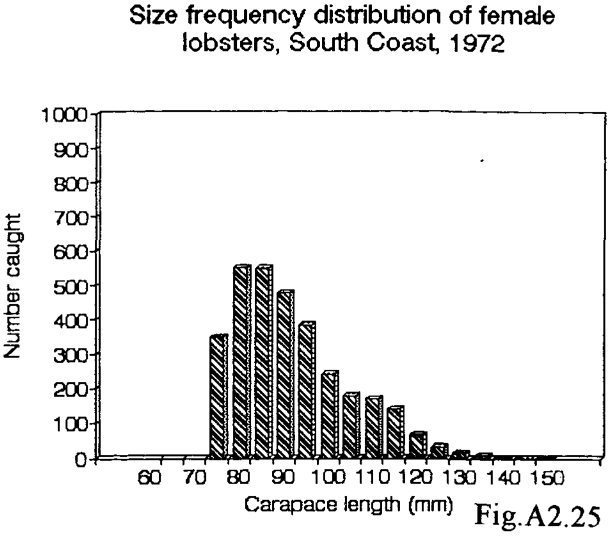


Fig.A2.25

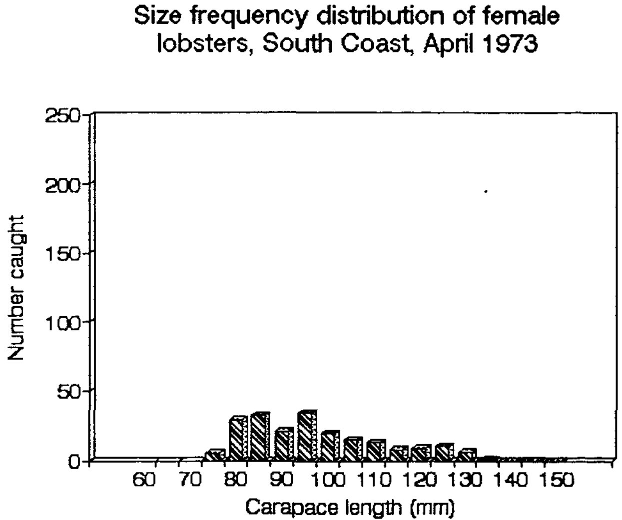


Fig.A2.26

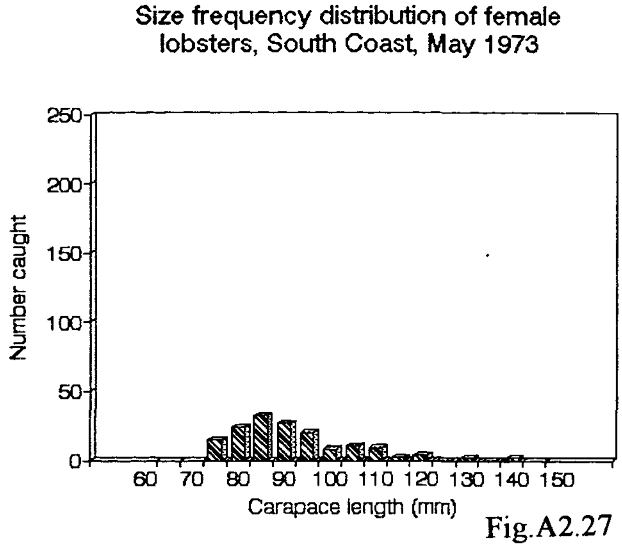


Fig.A2.27

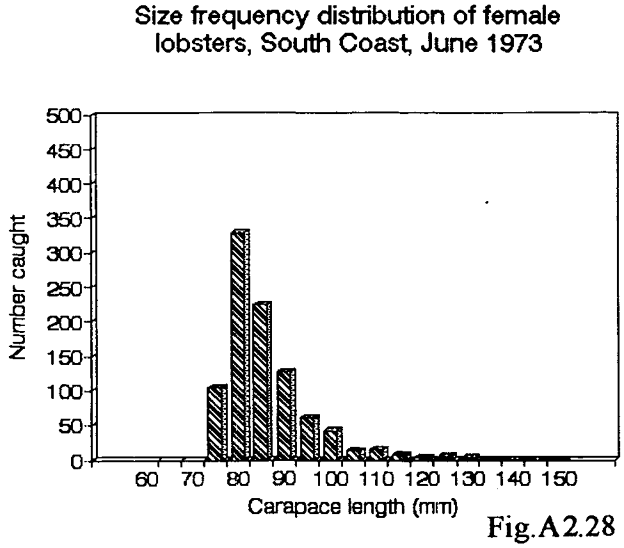


Fig.A2.28

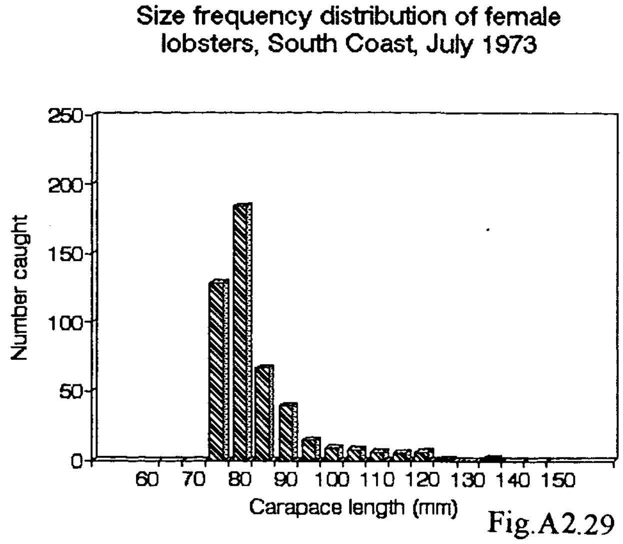


Fig.A2.29

Size frequency distribution of female lobsters, South Coast, August 1973

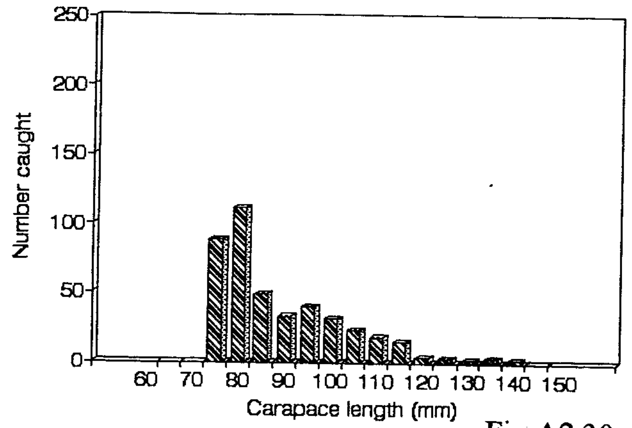


Fig.A2.30

Size frequency distribution of female lobsters, South Coast, September 1973

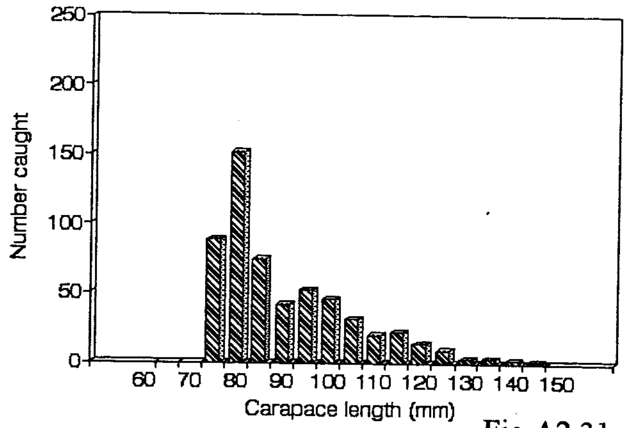


Fig.A2.31

Size frequency distribution of female lobsters, South Coast, 1973

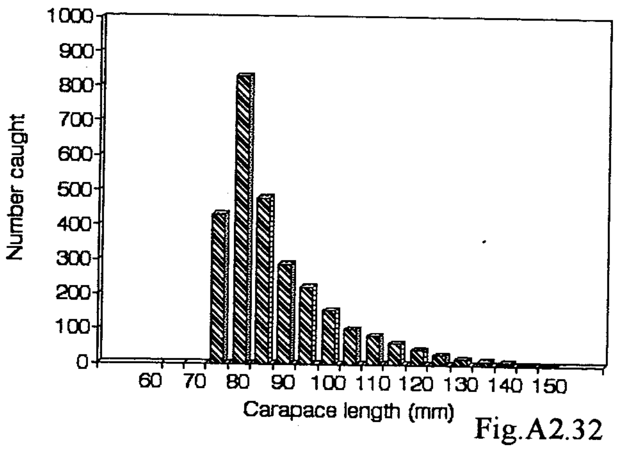


Fig.A2.32

Table A2iii.7 Estimates of CPUE (kg lobsters), derived from log book statistics for Bridington, Dale and Selsey, 1987 - 1989.

Date		Site		
		Dale	Bridlington	Selsey
1987	Jan			4.3
	Feb			2.78
	Mar			3.04
	Apr		2.3	3.56
	May		4.15	4.46
	Jun		9.17	4.97
	Jul		7.41	7.72
	Aug		26.99	6.72
	Sep		19.97	4.21
	Oct		16.62	2.09
	Nov			3.84
	Dec			4.2
1988	Jan			2.57
	Feb			5.89
	Mar			5.02
	Apr	5.995	1.56	6.7
	May		4.71	6.16
	Jun	14.965	6.75	8.77
	Jul	21.196	24.07	7.76
	Aug	18.003	18.24	9.42
	Sep	22.605	12.96	8.55
	Oct	18.206		4.82
	Nov	11.099		6.29
	Dec	10.646		3.52
1989	Jan	7.795		3.633
	Feb			5.565
	Mar		4.06	5.3044
	Apr	16.34	0.87	6.872
	May	18.906	5.63	5.47
	Jun	16.375	5.44	6.621
	Jul	15.112	14.95	8.155
	Aug	17.106	15.38	5.57
	Sep	20.473	10.11	6.1475
	Oct	25.624		6.556
	Nov	19.845		3.896
	Dec	7.664		2.891

Table A2iii.8 CPUE (weight of lobsters) calculated for sampling trips, Bridlington, 1989 - 1991.

Date	Total catch **		Sized catch (>85 mm CL)**		Percentage of catch sized
	CPUE w/o soak	CPUE with soak	CPUE w/o soak	CPUE with soak	
30/03/1989	5.3836	2.191	1.2223	0.4975	15.686
23/05/1989	25.9295	6.4824	11.8169	2.9542	50
24/05/1989	28.447	4.7032	11.8273	1.9554	31.11
28/06/1989	15.2739	2.6885	7.4746	1.3157	37.01
29/06/1989	16.4977	3.5435	11.4452	2.4583	50.562
30/06/1989	12.2269	7.437	6.0865	3.7021	38.1
18/07/1989	22.4302	11.2151	13.2476	6.6238	47.973
19/07/1989	23.6834	11.8417	15.0413	7.5206	51.5625
26/07/1989	24.8962	9.8651	16.4004	6.4987	54.4
16/08/1990	6.2028	2.6583	2.9903	1.2816	36.36
18/08/1990	16.9433	3.3887	9.3346	1.8669	42.857
10/09/1990	11.0781	1.4507	8.5948	1.1255	63.492
11/09/1990	19.0453	9.5227	12.1133	6.0567	40.51
10/06/1991	12.5742	2.7663	7.7605	1.7073	39.063
11/06/1991	3.7405	1.2111	1.882	0.6093	36.111
13/06/1991	8.4946	3.6181	4.2463	1.8086	30.769
14/06/1991	4.0328	1.1369	1.4619	0.4121	26.667

** weight of lobsters caught (kg)

Table A2iii.9 CPUE (weight of lobsters) calculated for sampling trips, Dale, 1989.

Date	Total catch **		Sized catch (>85 mm CL)**		Percentage of catch sized
	CPUE w/o soak	CPUE with soak	CPUE w/o soak	CPUE with soak	
11/05/1989	5.02859	5.02859	4.8765	4.8765	92.857
15/06/1989	9.79375	2.44844	9.79375	2.44844	100
20/07/1989	24.433	5.1404	24.433	5.1404	100
23/08/1989	35.9188	4.48985	35.164	4.3955	95.876

** weight of lobsters caught (kg)

Table A2iii10 CPUE (weight of lobsters) calculated for sampling trips, Selsey, 1989 -1991.

Date	Total catch **		Sized catch (>85 mm CL)**		Percentage of catch sized
	CPUE w/o soak	CPUE with soak	CPUE w/o soak	CPUE with soak	
26/04/1989	13.107	13.107	2.7795	2.7795	23.711
06/07/1989	39.165	39.165	12.611	12.611	23.913
09/08/1989	11.1918	11.1918	4.67	4.67	33.33
07/09/1989	14.5419	14.5419	7.2517	7.2517	40.8
23/05/1990	27.4644	13.7322	14.0379	7.019	34.95
19/07/1990	42.5524	42.5524	16.5775	16.5775	30.27

** weight of lobsters caught (kg)

Table A2iii11 CPUE (number of lobsters) calculated for sampling trips, Bridlington, 1989 - 1991.

Date	Total catch **		Sized catch (>85 mm CL)**		Percentage of catch sized
	CPUE w/o soak	CPUE with soak	CPUE w/o soak	CPUE with soak	
30/03/1989	14.571	5.93	2.286	0.93	15.686
23/05/1989	61.463	15.37	20.488	5.12	50
24/05/1989	72.58	12	22.58	3.78	31.11
28/06/1989	34.332	6.043	12.807	2.254	37.01
29/06/1989	29.18	3.169	14.75	6.286	50.562
30/06/1989	28.47	17.32	10.85	6.6	38.1
18/07/1989	52.28	26.14	24.91	12.46	47.973
19/07/1989	53.33	26.667	27.5	13.75	51.5625
26/07/1989	54.89	21.75	29.653	11.75	54.4
16/08/1990	14.67	6.29	5.33	2.29	36.36
18/08/1990	38.62	7.72	16.55	3.31	42.857
10/09/1990	22.09	3	14.55	1.9	63.492
11/09/1990	35.111	17.56	14.222	7.111	40.51
10/06/1991	36.36	8	14.2	3.125	39.063
11/06/1991	9.114	2.95	3.29	1.07	36.111
13/06/1991	22.61	9.63	6.96	2.96	30.769
14/06/1991	11.32	3.19	3.02	0.851	26.667

** catch in number of lobsters caught

Table A2iii12 CPUE (number of lobsters) calculated for sampling trips, Dale, 1989.

Date	Total catch **		Sized catch (>85 mm CL)**		Percentage of catch sized
	CPUE w/o soak	CPUE with soak	CPUE w/o soak	CPUE with soak	
11/05/1989	6.36	6.36	5.91	5.91	92.857
15/06/1989	10.625	2.66	10.625	2.66	100
20/07/1989	23	4.84	23	4.84	100
23/08/1989	38.8	4.85	37.2	4.65	95.876

** catch in number of lobsters caught

Table A2iii13 CPUE (number of lobsters) calculated for sampling trips, Selsey, 1989 -1991.

Date	Total catch **		Sized catch (>85 mm CL)**		Percentage of catch sized
	CPUE w/o soak	CPUE with soak	CPUE w/o soak	CPUE with soak	
26/04/1989	32.89	32.89	10.22	10.22	23.711
06/07/1989	111.515	111.515	11.52	11.52	23.913
09/08/1989	30.3	30.3	10	10	33.33
07/09/1989	38.2	38.2	15.6	15.6	40.8
23/05/1990	56.2	29.6	20.69	10.34	34.95
19/07/1990	107.8	107.8	32.37	32.37	30.27

** catch in number of lobsters caught

Table A2iii14 Percentage of females berried, calculated for each sample trip, 1989 -1991.

Site	Bridlington		Dale		Selsey	
Date	30/03/1989	4.1667				
					26/04/1989	18.4466
	23/05/1989	22.222	11/05/1989	36.364		
	24/05/1989	22.5166				
	28/06/1989	17.3913	15/06/1989	20.833		
	29/06/1989	19.1489				
	30/06/1989	13.3333				
	18/07/1989	5	20/07/1989	31.034	06/07/1989	0
	19/07/1989	2.1978				
	26/07/1989	1.0417				
	06/08/1989	7.8049	23/08/1989	18.75	09/08/1989	0
	13/09/1989	37.2781			07/09/1989	27.1429
					23/05/1990	8.6957
					19/07/1990	0.4854
	16/08/1990	0				
	18/08/1990	0				
	10/09/1990	21.4286				
	11/09/1990	6.383				
	10/06/1991	4.8387				
	11/06/1991	4.7649				
	13/06/1991	0				
	14/06/1991	0				

Table A2iii15 Monthly percentage of females berried, Yorkshire and Bridlington, 1972 - 1991.

	Year					
	1972	1973	1974	1989	1990	1991
Month						
Jan						
Feb						
Mar	3.7	3.774		4.1667		
Apr	7.3	7.667	13.4			
May	13.4	13.576	20.2	37.45		
Jun	15.8	24.385	29.4	16.875		2.985
Jul	22.1	20.854	20.5	2.622		
Aug	12.9	8.172	10.3	7.805	0	
Sep	15.4	8.352	12.2	37.278	12	
Oct	22.9	33.191				
Nov						
Dec						

Table A2iii16 Monthly percentage of females berried, Pembrokeshire and Dale, 1972 - 1989.

	Year		
	1972	1973	1989
Month			
Jan			
Feb			
Mar			
Apr			
May		44	36.364
Jun		14.3	20.833
Jul		3.6	31.034
Aug	5.2	9.1	18.75
Sep		13.1	
Oct			
Nov			
Dec			

Table A2iii17 Monthly percentage of females berried, South coast and Selsey, 1972 - 1990.

	Year			
	1972	1973	1989	1990
Month				
Jan				
Feb				
Mar				
Apr	42.857	44.335	18.447	
May	30.233	41.818		8.696
Jun	8.571	11.407		
Jul	4.8	2.542	0	0.485
Aug	0	6.84	0	
Sep	15.486	17.469	27.143	
Oct	20.3			
Nov				
Dec				

Table A2iii18 Sample trip sex ratios, Bridlington, 1989 - 1991.

Date	Percentage female		
	<85 mm CL	>85 mm CL	Total
30/03/1989	48.837	25	45.098
23/05/1989	45.238	76.19	55.556
24/05/1989	64.52	72.857	67.111
28/06/1989	41.026	47.1667	45.238
29/06/1989	65.909	37.778	51.685
30/06/1989	59.62	43.75	53.57
18/07/1989	53.846	53.521	53.691
19/07/1989	47.312	47.47	47.396
26/07/1989	55.172	53.191	57.5
06/08/1989	47.753	53.125	50.746
13/09/1989	55.556	62.238	58.885
16/08/1990	35.71	62.5	45.45
18/08/1990	60.937	43.75	53.571
10/09/1990	44.444	45	43.478
11/09/1990	61.7	56.25	59.49
10/06/1991	57.69	34	48.44
11/06/1991	65.22	46.15	58.333
13/06/1991	58.333	43.75	53.846
14/06/1991	86.36	50	76.667

Table A2iii19 Sample trip sex ratios, Dale, 1989.

Date	Percentage female		
	<85 mm CL	>85 mm CL	Total
11/05/1989	100	76.923	78.574
15/06/1989	-	70.588	70.588
20/07/1989	-	52.73	52.73
23/08/1989	100	56.613	53.608

Table A2iii20 Sample trip sex ratios, Selsey, 1989 - 1990.

Date	Percentage female		
	<85 mm CL	>85 mm CL	Total
26/04/1989	56.0811	43.478	53.093
06/07/1989	41.071	78.409	50
09/08/1989	50.746	66.667	56
07/09/1989	51.35	62.75	56
23/05/1990	46.27	41.667	44.66
19/07/1990	45.211	78.57	55.228

Table A2iii21 Percentage of "soft" lobsters, calculated for each sample trip, 1989 - 1991.

Site	Bridlington			Dale			Selsey		
Sex		females	males		females	males		females	males
Date	30/03/1989	0	10.71429						
							26/04/1989	0	1.098901
	23/05/1989	0	1.785714	11/05/1989	0	0			
	28/06/1989	11.5942029	15.78947	15/06/1989	0	0			
	26/07/1989	0	1.282051	20/07/1989	0	0	06/07/1989	0	0
				23/08/1989	0	0	09/08/1989	0	2.272727
							07/09/1989	0	3.636364
							23/05/1990	0	0
							19/07/1990	0	0

Table A2iii.22 Carapace length and weight summary statistics for male lobsters

Site and Date	No.	CL (mm), Weight (g)	Average	Std.	Var.	Min.	Max.
Bridlington, 1989 to 1991	13	CL	86.7692	6.89388	47.5256	76	97
		Weight	486.812	107.917	11646	300.8	616.14
Dale, 1989	8	CL	96.875	19.5772	383.268	71	135
		Weight	612.053	364.166	132617	246.59	1324.2
Selsey, 1989 to 1991	21	CL	84.333	9.20507	84.7333	61	95
		Weight	423.02	130.689	17079.5	150.98	614.92

Table A2iii.23 Carapace length and weight summary statistics for all female lobsters

Site and Date	No.	CL (mm), Weight (g)	Average	Std.	Var.	Min.	Max.
Bridlington, 1989 to 1991	105	CL	95.7333	12.7944	163.697	68	130
		Weight	633.287	280.391	78619	231.11	1525.2
Bridlington, 1989	28	CL	88.0357	11.1902	125.221	68	124
		Weight	484.656	195.103	38065	231.11	1198.2
Bridlington, 1990	47	CL	93.5319	8.20618	67.3414	73	112
		Weight	545.607	132.969	17680.8	259.32	894.6
Bridlington, 1991	30	CL	106.367	13.4766	181.62	84	130
		Weight	909.374	325.297	105818	419.94	1525.2
Dale, 1989 and 1992	27	CL	105.407	13.7205	188.251	81	139
		Weight	761.54	373.829	139748	113.25	1837.9
Dale, 1989	19	CL	102.895	13.9917	195.766	81	128
		Weight	626.564	303.771	92276.8	113.25	1342.6
Dale, 1992	8	CL	111.375	11.7466	137.982	101	139
		Weight	1082.11	338.949	114887	692.85	1837.9
Selsey, 1989 to 1991	161	CL	90.2981	8.85639	78.4356	64	126
		Weight	528.812	184.504	34041.6	167.03	1390.2
Selsey, 1989	32	CL	83.8438	8.03665	64.588	64	97
		Weight	405.126	106.6952	11383.9	167.03	622.9
Selsey, 1990	67	CL	89.4627	7.34708	53.9797	66	117
		Weight	496.8328	146.42	21438.8	202.03	1061.7
Selsey, 1991	62	CL	94.53226	8.58271	73.6629	84	126
		Weight	627.207	203.272	41319.3	323.66	1390.2

Table A2iii.24 Carapace length and weight summary statistics for berried and non-berried females

Site and Date	No.	CL (mm), Weight (g)	Average	Std.	Var.	Min.	Max.
Bridlington, 1989 to 1991	105	CL	95.7333	12.7944	163.697	68	130
All females		Weight	633.287	280.391	78619	231.11	1525.2
Bridlington, 1989 to 1991	47	CL	102.532	13.4647	181.298	84	130
Berried females		Weight	798.845	321.723	103531	380.2	1525.2
Bridlington, 1989 to 1991	58	CL	90.2241	9.13071	83.3699	68	112
Non-berried females		Weight	499.128	137.632	18978.7	231.11	901.9
Dale, 1989 and 1992	27	CL	105.407	13.7205	188.251	81	139
All females		Weight	761.54	373.829	139748	113.25	1837.9
Dale, 1989 and 1992	19	CL	111.375	11.7466	137.982	101	139
Berried females		Weight	1082.11	338.949	114887	692.85	1837.9
Dale, 1989 and 1992	8	CL	91.25	7.81482	61.0714	81	102
Non-berried females		Weight	460.205	132.849	17648.8	253.84	701.48
Selsey, 1989 to 1991	161	CL	90.2981	8.85639	78.4356	64	126
All females		Weight	528.812	184.504	34041.6	167.03	1390.2
Selsey, 1989 to 1991	59	CL	94.0678	9.80827	96.2022	79	126
Berried females		Weight	620.421	228.2876	52115.25	325.43	1390.15
Selsey, 1989 to 1991	102	CL	88.1177	7.47709	55.9068	64	114
Non-berried females		Weight	475.822	127.521	16261.7	167.03	1007.35

Table A2iii.25 :s for female lobster carapace length-weight relationships

Site and Date	RSSQ	Mean of Y	Std. Error	STD Y	R-squared	r	F(df, df)	Signif F		Coeff.	Std. Error	t-statistic	Signif.
Bridlington, 1989 to 1991									a	-3.43407	0.30082	-11.4156	0.0000
Females	0.790368	2.77549	0.087598	0.19765	0.805454	0.897471	1,103	0.0000	b	3.140315	0.15207	20.65036	0.0000
Bridlington, 1989									a	-2.53195	0.3195	-7.92475	0.0000
Females	0.052401	2.65911	0.044893	0.147172	0.910397	0.954147	1,26	0.0000	b	2.67373	0.1645	16.2532	0.0000
Bridlington, 1990									a	-2.3682	0.28429	-8.3301	0.0000
Females	0.877054	2.72451	0.037253	0.105082	0.877054	0.936512	1,45	0.0000	b	2.586	0.14433	17.9169	0.0000
Bridlington, 1991									a	-2.77284	0.31651	-8.76058	0.0000
Females	0.06026	2.9305	0.463912	0.161837	0.920664	0.959512	1,28	0.0000	b	2.81865	0.15637	18.0257	0.0000
Dale, 1989 and 1992									a	-3.5124	0.55861	-6.2877	0.0000
Females	0.15763	2.8752	0.0794	0.19441	0.83959	0.91629	1,25	0.0000	b	3.16317	0.27652	11.4391	0.0000
Dale, 1989									a	-2.97722	0.72631	-2.6581	0.0008
Females	0.120116	2.77863	0.086645	0.186605	0.797088	0.892798	1,17	0.0000	b	2.8712	0.36216	6.49703	0.0000
Dale, 1992									a	-2.19276	1.10556	-1.9834	0.0946
Females	0.022007	3.01836	0.060563	0.121614	0.78743	0.88737	1,6	0.0033	b	2.54837	0.54055	4.7144	0.0033
Selsey, 1989 to 1991									a	-3.4131	0.1734	-19.684	0.0000
Females	0.35308	2.70054	0.04712	0.13953	0.886655	0.94162	1,159	0.0000	b	3.12935	0.08874	35.2664	0.0000
Selsey, 1989									a	-2.72146	0.39359	-6.91449	0.0000
Females	0.07495	2.59036	0.049982	0.13078	0.858644	0.92663	1,30	0.0000	b	2.764555	0.204793	13.4993	0.0000
Selsey, 1990									a	-3.36631	0.30455	-11.0533	0.0000
Females	0.125069	2.68035	0.043865	0.115718	0.858485	0.92654	1,65	0.0000	b	3.10043	0.156135	19.8573	0.0000
Selsey, 1991									a	-3.23876	0.306614	-10.563	0.0000
Females	0.121434	2.77922	0.044988	0.121559	0.865278	0.930203	1,60	0.0000	b	3.04868	0.155303	19.6306	0.0000

** According to the equation log W = a + b(log CL)

Table A2iii.26 Regression statistics for male lobster carapace length- weight relationships

Site and Date	RSSQ	Mean of Y	Std. Error	STD Y	R-squared	r	F(df, df)	Signif F		Coeff.	Std. Error	t-statistic	Signif.
Bridlington, 1989 to 1991									a	-2.93285	0.535032	-5.4816	0.0002
Males	0.012187	2.67623	0.033285	0.10567	0.909046	0.95365	1,11	0.0000	b	2.89563	0.276163	10.4852	0.0000
Dale, 1989									a	-2.82677	0.67999	-4.15706	0.0060
Males	0.035502	2.7237	0.076922	0.24795	0.917507	0.957866	1,6	0.0000	b	2.80491	0.34336	8.16908	0.0002
Selsey, 1989 to 1991									a	-3.1382	0.534577	-5.8706	0.0000
Males	0.079639	2.60011	0.064742	0.16777	0.858535	0.92657	1,19	0.0000	b	2.98376	0.277864	10.7328	0.0000

Table A2iii.27 Regression statistics for berried and non-berried female carapace length-weight relationships

Site and Date	RSSQ	Mean of Y	Std. Error	STD Y	R-squared	r	F(df, df)	Signif F		Coeff.	Std. Error	t-statistic	Signif.
Bridlington, 1989 to 1991									a	-3.4341	0.30082	-11.4156	0.0000
All females	0.79037	2.7755	0.087598	0.197645	0.805454	0.897471	1,103	0.0000	b	3.14032	0.15207	20.6504	0.0000
Bridlington, 1989 to 1991									a	-2.26442	0.24713	-9.16293	0.0000
Berried females	0.100008	2.68221	0.042272	0.119685	0.877424	0.93501	1,56	0.0000	b	2.53268	0.12650	20.0215	0.0000
Bridlington, 1989 to 1991									a	-3.04265	0.23897	-12.7323	0.0000
Non-berried females	0.940166	2.73983	0.045152	0.170703	0.931557	0.931116	1,45	0.0000	b	2.94521	0.11901	24.7483	0.0000
Dale, 1989 and 1992									a	-3.51238	0.55861	-6.28774	0.0000
All females	0.157628	2.87518	0.079405	0.194409	0.839592	0.916292	1,25	0.0000	b	3.16317	0.27652	11.4391	0.0000
Dale, 1989 and 1992									a	-2.09378	0.77979	-2.68508	0.0157
Berried females	0.076907	2.97151	0.06726	0.12199	0.712893	0.84433	1,17	0.0000	b	2.47711	0.38127	6.49703	0.0000
Dale, 1989 and 1992									a	-2.66969	1.78348	-1.4969	0.1851
Non-berried females	0.482393	2.64638	0.089665	0.130764	0.59698	0.77265	1,6	0.0246	b	2.71389	0.91033	2.98121	0.0246
Selsey, 1989 to 1991									a	-3.41313	0.1734	-19.684	0.0000
All females	0.353079	2.70054	0.047124	0.139528	0.886649	0.94162	1,159	0.0000	b	3.12935	0.08874	35.2664	0.0000
Selsey, 1989 to 1991									a	-3.32536	0.30767	-10.8084	0.0000
Berried females	0.147254	2.76841	0.050827	0.141494	0.873187	0.934445	1,57	0.0000	b	3.09126	0.15604	19.8111	0.0000
Selsey, 1989 to 1991									a	-3.19853	0.22033	-14.5167	0.0000
Non-berried females	0.188795	2.66127	0.004345	0.122863	0.876171	0.93604	1,100	0.0000	b	3.01516	0.11335	26.6001	0.0000

** According to the equation $\log W = a + b(\log CL)$

Table A2iii.26 Regression statistics for male lobster carapace length- weight relationships

Site and Date	RSSQ	Mean of Y	Std. Error	STD Y	R-squared	r	F(df, df)	Signif F		Coeff.	Std. Error	t-statistic	Signif.
Bridlington, 1989 to 1991 Males	0.012187	2.67623	0.033285	0.10567	0.909046	0.95365	1,11	0.0000	a	-2.93285	0.535032	-5.4816	0.0002
									b	2.89563	0.276163	10.4852	0.0000
Dale, 1989 Males	0.035502	2.7237	0.076922	0.24795	0.917507	0.957866	1,6	0.0000	a	-2.82677	0.67999	-4.15706	0.0060
									b	2.80491	0.34336	8.16908	0.0002
Selsey, 1989 to 1991 Males	0.079639	2.60011	0.064742	0.16777	0.858535	0.92657	1,19	0.0000	a	-3.1382	0.534577	-5.8706	0.0000
									b	2.98376	0.277864	10.7328	0.0000

Table A2iii.27 Regression statistics for berried and non-berried female carapace length-weight relationships

Site and Date	RSSQ	Mean of Y	Std. Error	STD Y	R-squared	r	F(df, df)	Signif F		Coeff.	Std. Error	t-statistic	Signif.
Bridlington, 1989 to 1991 All females	0.79037	2.7755	0.087598	0.197645	0.805454	0.897471	1,103	0.0000	a	-3.4341	0.30082	-11.4156	0.0000
									b	3.14032	0.15207	20.6504	0.0000
Bridlington, 1989 to 1991 Berried females	0.100008	2.68221	0.042272	0.119685	0.877424	0.93501	1,56	0.0000	a	-2.26442	0.24713	-9.16293	0.0000
									b	2.53268	0.12650	20.0215	0.0000
Bridlington, 1989 to 1991 Non-berried females	0.940166	2.73983	0.045152	0.170703	0.931557	0.931116	1,45	0.0000	a	-3.04265	0.23897	-12.7323	0.0000
									b	2.94521	0.11901	24.7483	0.0000
Dale, 1989 and 1992 All females	0.157628	2.87518	0.079405	0.194409	0.839592	0.916292	1,25	0.0000	a	-3.51238	0.55861	-6.28774	0.0000
									b	3.16317	0.27652	11.4391	0.0000
Dale, 1989 and 1992 Berried females	0.076907	2.97151	0.06726	0.12199	0.712893	0.84433	1,17	0.0000	a	-2.09378	0.77979	-2.68508	0.0157
									b	2.47711	0.38127	6.49703	0.0000
Dale, 1989 and 1992 Non-berried females	0.482393	2.64638	0.089665	0.130764	0.59698	0.77265	1,6	0.0246	a	-2.66969	1.78348	-1.4969	0.1851
									b	2.71389	0.91033	2.98121	0.0246
Selsey, 1989 to 1991 All females	0.353079	2.70054	0.047124	0.139528	0.886649	0.94162	1,159	0.0000	a	-3.41313	0.1734	-19.684	0.0000
									b	3.12935	0.08874	35.2664	0.0000
Selsey, 1989 to 1991 Berried females	0.147254	2.76841	0.050827	0.141494	0.873187	0.934445	1,57	0.0000	a	-3.32536	0.30767	-10.8084	0.0000
									b	3.09126	0.15604	19.8111	0.0000
Selsey, 1989 to 1991 Non-berried females	0.188795	2.66127	0.004345	0.122863	0.876171	0.93604	1,100	0.0000	a	-3.19853	0.22033	-14.5167	0.0000
									b	3.01516	0.11335	26.6001	0.0000

** According to the equation log W = a + b(log CL)

Table A2iii.28 ANCOVA results for male log weight with log length, between sites.

Source of Variation	SSQ	df.	MSQ	Fs	Signif
Log length	1.077	1	1.077	319.407	0.0000
Site	0.026	2	0.013	3.890	0.0290
Error	0.128	38	0.003		
Total	1.232	41	0.030		

Table A2iii.29 ANCOVA results for female log weight with log length, between sites.

Source of Variation	SSQ	df.	MSQ	Fs	Signif
Log length	6.301	1	6.301	1019.216	0.0000
Site	0.096	2	0.048	7.736	0.0005
Error	1.7	275	0.06		
Total	8.097	278	0.029		

Table A2iii.30 ANCOVA results for female log weight with log length at Bridlington, between years

Source of Variation	SSQ	df.	MSQ	Fs	Signif
Log length	2.835	1	2.835	1615.616	0.0000
Year	0.053	2	0.027	15.121	0.0000
Error	0.177	101	0.02		
Total	3.065	104	0.029		

Table A2iii.31 ANCOVA results for female log weight with log length at Dale, between years

Source of Variation	SSQ	df.	MSQ	Fs	Signif
Log length	0.495	1	0.495	13.015	0.0014
Year	0.221	1	0.221	5.816	0.0239
Error	0.912	24	0.038		
Total	1.628	26	0.063		

Table A2iii.32 ANCOVA results for female log weight with log length at Selsey, between years

Source of Variation	SSQ	df.	MSQ	Fs	Signif
Log length	2.762	1	2.762	1331.194	0.0000
Year	0.027	2	0.014	6.592	0.0018
Error	0.326	157	0.002		
Total	3.115	160	0.019		

Table A2iii.33 ANCOVA results for female log weight with log length at Bridlington, between berried and non-berried females

Source of Variation	SSQ	df.	MSQ	Fs	Signif
Log length	2.835	1	2.835	1492.931	0.0000
Berried/ non-berried	0.037	1	0.037	19.276	0.0000
Error	0.194	102	0.002		
Total	3.065	104	0.029		

Table A2iii.34 ANCOVA results for female log weight with log length at Dale, between berried and non-berried females

Source of Variation	SSQ	df.	MSQ	Fs	Signif
Log length	0.825	1	0.825	157.700	0.0000
Berried/ non-berried	0.032	1	0.032	6.129	0.0207
Error	0.126	24	0.005		
Total	0.983	26	0.038		

Table A2iii.35 ANCOVA results for female log weight with log length at Selsey, between berried and non-berried females

Source of Variation	SSQ	df.	MSQ	Fs	Signif
Log length	2.762	1	2.762	1297.150	0.0000
Berried/ non-berried	0.017	1	0.017	7.831	0.0058
Error	0.336	158	0.002		
Total	3.115	160	0.019		

Table A2iii.36 ANCOVA results for berried female log weight with log length between sites

Source of Variation	SSQ	df.	MSQ	Fs	Signif
Log length	3.112	1	3.112	1158.848	0.0000
Site	0.002	2	0.001	0.404	0.6684
Error	0.325	121	0.003		
Total	3.440	124	0.028		

Table A2iii.37 ANCOVA results for non-berried female log weight with log length between sites

Source of Variation	SSQ	df.	MSQ	Fs	Signif
Log length	2.104	1	2.104	980.351	0.0000
Site	0.025	2	0.012	5.810	0.0036
Error	0.352	164	0.002		
Total	2.481	167	0.015		

Table A2iii.38 ANCOVA results for lobster log weight with log length between sites and sexes

Source of variation	SSQ	df.	MSQ	Fs	Signif.
Log length	7.815	1	7.815	1367.254	0.0000
Main effects	0.121	3	0.040	7.074	0.0001
Sex	0.002	1	0.002	0.288	0.5919
Site	0.121	2	0.060	10.581	0.0000
Sex within site	0.012	2	0.006	1.091	0.3369
Explained Var.	7.949	6	1.325	231.777	0.0000
Error	1.875	328	0.006		
Total	9.824	334	0.029		

Table A2iii.39 ANCOVA results for lobster log weight with log length between sites and between berried and non-berried females

Source of variation	SSQ	df.	MSQ	Fs	Signif.
Log length	7.215	1	7.215	3092.466	0.0000
Main effects	0.083	3	0.028	11.831	0.0000
Berried/ non-berried	0.019	2	0.010	4.080	0.0179
Site	0.070	1	0.070	30.021	0.0000
Berry within site	0.012	2	0.006	2.501	0.0838
Explained Var.	7.310	6	1.218	522.160	0.0000
Error	0.667	286	0.002		
Total	7.977	292	0.027		

Table A2iii.40 Kolmogorov-Smirnov D-statistics and test results for comparisons of size frequency distributions, Bridlington 1989 to 1991

Part i

Sample Date	Sex	30/03/1989	23/05/198		24/05/198		28/06/198		29/06/198		30/06/198		18/07/198		19/07/198		26/07/198		08/08/198		13/09/198		1989	
		Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males
30/03/1989	Females	0.1243	0.2143	0.1103	0.13907	0.1093	0.174	0.2105	0.1739	0.2558	0.133	0.1795	0.3118	0.2609	0.2972	0.2	0.2188	0.2179	0.25552	0.173	0.2462	0.1835	0.183546	0.1593
	Males		0.1786	0.0714	0.10337	0.056	0.1092	0.1748	0.1165	0.2201	0.0973	0.1436	0.2124	0.2252	0.1978	0.1443	0.1831	0.1822	0.17508	0.1108	0.2069	0.12532	0.15069	0.1236
23/05/1989	Females			0.1714	0.0775	0.1602	0.184	0.1138	0.0814	0.105	0.0857	0.0513	0.1839	0.0598	0.1693	0.2	0.0682	0.122	0.12803	0.0719	0.03698	0.05328	0.057446	0.055
	Males				0.12117	0.0637	0.127	0.1926	0.1343	0.2379	0.1151	0.1616	0.2639**	0.243	0.2693**	0.1821	0.2009	0.2	0.22762**	0.1266	0.2447	0.1432	0.162669	0.1414
24/05/1989	Females					0.08497	0.19353	0.09735	0.08895	0.11673	0.09303	0.0665	0.17649	0.12183	0.16189	0.2	0.07973	0.09247	0.12021	0.08775	0.10353	0.09855	0.0536	0.06931
	Males						0.1675	0.1835	0.1252	0.2268	0.106	0.1525	0.2202	0.2339	0.2056	0.153	0.1918	0.1909	0.16376	0.139	0.2156	0.13402	0.153769	0.1323
28/06/1989	Females							0.1801	0.1522	0.269	0.1005	0.1962	0.2249	0.1884	0.2323	0.2383	0.2283	0.266	0.29203**	0.2359**	0.1883	0.16474	0.1975	0.20156
	Males								0.0662	0.1351	0.0631	0.0743	0.2676	0.0618	0.253	0.1825	0.1519	0.1302	0.21132**	0.1042	0.10364	0.09027	0.141146	0.07974
29/06/1989	Females									0.1168	0.0676	0.0552	0.1814	0.1087	0.1671	0.1825	0.0761	0.13338	0.13983	0.0837	0.0904	0.05457	0.054946	0.06086
	Males										0.1665	0.0763	0.146	0.0809	0.1314	0.1535	0.0746	0.0536	0.06972	0.1093	0.08064	0.10426	0.06265	0.0965
30/06/1989	Females											0.224	0.2594	0.2387	0.1651	0.1378	0.2528	0.1855	0.22584	0.1354	0.25354	0.21678	0.225868	0.21252**
	Males												0.224	0.0614	0.1669	0.1487	0.0856	0.0898	0.14522	0.0456	0.0631	0.0513	0.0746	0.0327
18/07/1989	Females													0.2104	0.0477	0.1553	0.1157	0.1374	0.1023	0.1634	0.16595	0.1773	0.12645	0.1676
	Males														0.1956	0.0809	0.0947	0.0976	0.15412	0.1144	0.04964	0.09968	0.063946	0.1016
19/07/1989	Females															0.1407	0.1011	0.16812	0.16209	0.1488	0.0668	0.16273	0.059931	0.25256
	Males																0.2	0.1672	0.1951	0.1747	0.19408	0.2	0.19712	0.1614
26/07/1989	Females																	0.0609	0.06373	0.0723	0.05025	0.06356	0.03603	0.07216
	Males																		0.08112	0.0714	0.09764	0.12126	0.068469	0.08444
08/08/1989	Females																			0.10712	0.10967	0.12729	0.094499	0.13158
	Males																				0.101	0.101	0.101	0.09667
13/09/1989	Females																					0.08158	0.08183	0.0833
	Males																						0.050676	0.03662
1989	Females																							0.06141
	Males																							
16/08/1990	Females																							
	Males																							
18/08/1990	Females																							
	Males																							
10/09/1990	Females																							
	Males																							
11/09/1990	Females																							
	Males																							
1990	Females																							
	Males																							
10/06/1991	Females																							
	Males																							
11/06/1991	Females																							
	Males																							
13/06/1991	Females																							
	Males																							
14/06/1991	Females																							
	Males																							
1991	Females																							

** significant difference at 95% level

Sample Date	Sex	16/08/199		18/08/199		10/09/199		11/09/199		1990		10/06/199		11/06/199		13/06/199		14/06/199		1991	
		Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males
30/03/198	Females	0.2174	0.1667	0.1732	0.1765	0.2857	0.2174	0.25444	0.2174	0.24616	0.17692	0.1175	0.1989	0.0662	0.2376	0.146	0.2895	0.0869	0.2425	0.0759	0.21453
	Males	0.1643	0.131	0.0738	0.1408	0.25	0.1072	0.1658	0.1631	0.1574	0.14122	0.0772	0.131	0.0834	0.1643	0.1072	0.1901	0.1538	0.2503	0.05365	0.11603
23/05/198	Females	0.1429	0.1714	0.1524	0.079	0.0714	0.0858	0.1654	0.1617	0.12809	0.06598	0.161	0.0719	0.1667	0.1187	0.1072	0.2143	0.2038	0.1713	0.12475	0.08753
	Males	0.1464	0.1488	0.1453	0.1586	0.2678	0.1572	0.2265	0.1786	0.21626**	0.15902	0.161	0.171	0.0834	0.1821	0.1072	0.2616	0.1538	0.2681	0.07165	0.18753
24/05/198	Females	0.18675	0.17881	0.07465	0.10435	0.146663	0.13245	0.17825	0.20555	0.15437	0.10983	0.1548	0.06359	0.09147	0.1268	0.09654	0.15419	0.126245	0.14693	0.05941	0.08012
	Males	0.1108	0.1397	0.0816	0.1495	0.2587	0.1274	0.1639	0.1765	0.20133	0.14992	0.161	0.1397	0.0824	0.2036	0.0868	0.1979	0.1528	0.259	0.06255	0.12744
28/06/198	Females	0.2783	0.1304	0.1783	0.243	0.1926	0.2497	0.3294**	0.2908	0.29209**	0.22445	0.161	0.2359	0.1926	0.2783	0.1926	0.2026	0.2609	0.3353	0.17979	0.2283**
	Males	0.1123	0.1185	0.129	0.0712	0.1567	0.1409	0.2102	0.1623	0.20196**	0.05867	0.161	0.1547	0.1629	0.1614	0.1429	0.2453	0.2258	0.1983	0.12095	0.17123
29/06/198	Females	0.1783	0.1739	0.071	0.0959	0.1335	0.1212	0.1772	0.1971	0.316299*	0.13692	0.10138	0.1393	0.0837	0.147	0.1113	0.0994	0.1591	0.2174	0.1338	0.09829
	Males	0.1558	0.2093	0.1737	0.0793	0.0806	0.1129	0.1069	0.1933	0.0836	0.07888	0.161	0.0691	0.2082	0.1097	0.1467	0.2558	0.2376	0.1197	0.16625	0.12187
30/06/198	Females	0.2	0.2611	0.1444	0.2209	0.3064	0.2349	0.2714	0.2884	0.30883	0.20857	0.1843	0.2414	0.1397	0.31111	0.1635	0.2528	0.0735	0.2638	0.15392	0.23494
	Males	0.1231	0.1538	0.1129	0.0468	0.1062	0.0769	0.1441	0.1419	0.13586	0.04618	0.161	0.0886	0.1319	0.133	0.1173	0.1795	0.164	0.1391	0.08995	0.10513
18/07/198	Females	0.1737	0.35553	0.1483	0.1984	0.1541	0.1267	0.1652	0.1925**	0.13232	0.21684**	0.2263	0.1129	0.2601	0.2233	2482	0.1316	0.2498	0.1544	0.2359	0.09637
	Males	0.1609	0.1449	0.1776	0.0844	0.1025	0.118	0.153	0.1984	0.14476	0.08398	0.148	0.0975	0.2133	0.1072	0.1538	0.2609	0.2309	0.1469	0.17135	0.12697
19/07/198	Females	0.2	0.39252	0.27852	0.21112	0.26152	0.17582	0.26152	0.20442	0.1915	0.2188	0.16203	0.22967	0.31452	0.21822	0.26152	0.35082	0.29004	0.1322	0.27433	0.22852
	Males	0.2	0.2	0.2	0.1804	0.1643	0.1714	0.1805	0.2078	0.17931	0.18462	0.2	0.2	0.2	0.2	0.2	0.2	0.2**	0.2**	0.2	0.2
26/07/198	Females	0.1538	0.2396	0.1417	0.0827	0.0938	0.1012	0.1498	0.1771	0.11692	0.10114	0.161	0.0521	0.1712	0.1226	0.1325	0.2188	0.1793	0.107	0.12925	0.08487
	Males	0.1179	0.2244	0.1513	0.061	0.0934	0.0769	0.0889	0.1554	0.07176	0.07944	0.1482	0.0723	0.1703	0.01074	0.1173	0.2179	0.1889	0.1026	0.12635	0.08397
06/08/198	Females	0.15098	0.29902**	0.12748	0.14212	0.09943	0.09388	0.14248	0.16978	0.1096	0.16056	0.17002	0.05662	0.20382	0.16602	0.19192	0.21078	0.1861	0.07522	0.11224	0.07685
	Males	0.101	0.1919	0.1354	0.101	0.1392	0.101	0.106	0.1178	0.101	0.101	0.161	0.101	0.1198	0.101	0.1176	0.1465	0.1902**	0.1395**	0.101	0.101
13/09/198	Females	0.1426	0.18935	0.1593	0.0661	0.0532	0.0997	0.14104	0.1801	0.10373	0.06568	0.15508	0.0759	0.195	0.1093	0.13698	0.2426	0.21356**	0.14694**	0.15305	0.10867
	Males	0.12373	0.17797	0.10568	0.07826	0.12468	0.08496	0.16466	0.14253	0.12735	0.05971	0.15253	0.0722	0.1568	0.11356	0.11748	0.16102	0.227	0.17056**	0.10789	0.08096
1989	Females	0.166346	0.22885	0.114777	0.083946	0.104931	0.109246	0.157846	0.18146	0.124966	0.09039	0.15692	0.046177	0.13365	0.118577	0.124631	0.18077	0.182054	0.13777	0.10945	0.04684
	Males	0.11744	0.16774	0.10042	0.04144	0.1264	0.06628	0.13016	0.13624	0.12192	0.04052	0.15635	0.07466	0.12422	0.10974	0.11616	0.16526	0.19462	0.13374	0.07551	0.09119
16/08/199	Females		0.2167	0.15	0.1	0.1857	0.1	0.1	0.125	0.13103	0.1	0.1639	0.1697	0.1905	0.1333	0.1643	0.175	0.2609	0.2	0.17015	0.15536
	Males			0.2167	0.1814	0.2143	0.2286	0.2979	0.25	0.28966	0.16285	0.161	0.2424	0.131	0.2167	0.1429	0.333	0.1993	0.286	0.1194	0.25893
18/08/199	Females				0.1098	0.1814	0.2143	0.2286	0.2979	0.25	0.28966	0.16285	0.161	0.2424	0.131	0.2167**	0.1429	0.333**	0.1993	0.286	0.1194
	Males					0.1092	0.0784	0.141	0.114	0.13276	0.01855	0.161	0.0855	0.1289	0.0938	0.1429	0.1765	0.1825	0.1291	0.08775	0.10203
10/09/199	Females						0.1428	0.1558	0.2232	0.12292	0.10878	0.1728	0.119	0.2381	0.0973	0.1786	0.2857**	0.2609	0.143	0.19615	0.15177
	Males							0.0797	0.0804	0.07393	0.09014	0.161	0.1126	0.1905	0.0956	0.1429	0.1464	0.2609**	0.1431	0.14179	0.09826
11/09/199	Females								0.1037	0.1368	0.2232	0.12292	0.10878	0.1479	0.1117	0.1429	0.2261**	0.2183	0.1004	0.14691	0.1011
	Males									0.1306	0.11442	0.2027	0.1686	0.1905	0.1375	0.1831	0.1675	0.2609	0.2235	0.16895	0.17416
1990	Females										0.1512	0.16066	0.12832	0.19446	0.15666	0.18256	0.1931	0.24021	0.15862	0.17062	0.11398
	Males											0.15331	0.10394	0.12932	0.10253	0.1429	0.19454	0.19936	0.14754	0.09323	0.12047
10/06/199	Females												0.1134	0.0791	0.1387	0.0784	0.204	0.148	0.1957	0.04019	0.12993
	Males													0.1472	0.1094	0.1353	0.1667	0.1679	0.1193	0.123	0.03277
11/06/199	Females														0.1714	0.1429	0.2378	0.0952	0.2384	0.06716	0.16373
	Males															0.1476	0.2	0.2376	0.153	0.15718	0.12593
13/06/199	Females																0.2259	0.1695	0.1789	0.07574	0.15183
	Males																	0.2026	0.286	0.2136	0.13393
14/06/199	Females																		0.2425	0.1191	0.16269
	Males																			0.15551	0.11911
1991	Females																				0.13953

** significant difference at 95% level

Table A2iii.41 Kolmogorov-Smirnov D-statistics and test results for comparisons of size frequency distributions, Dale 1989

Sample		11/05/1989	15/06/1989		20/07/1989		20/07/198		1989	
Date	Sex	Males	Females	Males	Females	Males	Females	Males	Females	Males
11/05/1989	Females	0.5761	0.1174	0.1	0.2414	0.1014	0.0822	0.1556	0.12069	0.119
	Males		0.2083	0.567	0.2414	0.667	0.6093	0.6448	0.58941	0.6075
15/06/1989	Females			0.1083	0.1393	0.2275	0.1506	0.1861	0.09623	0.18
	Males				0.1414	0.1923	0.1723	0.1778	0.12069	0.0833
20/07/1989	Females					0.1658	0.1645	0.0866	0.1205	0.1224
	Males						0.0962	0.2025	0.13127	0.1382
20/07/1989	Females							0.1256	0.05437	0.0898
	Males								0.08663	0.0611
1989	Females									0.08827
	Males									

** significant difference at 95% level

Table A2iii.42 Kolmogorov-Smirnov D-statistics and test results for comparisons of size frequency distributions, Selsey 1989 to 1990

Sample		26/05/1989	06/07/1989		09/08/1989		07/09/1989		1989		23/05/1990		19/07/1990		1990	
Date	Sex	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males
26/05/1989	Females	0.1858	0.1618	0.10822	0.2113	0.03555	0.17917	0.1744	0.131	0.0945	0.09965	0.1577	0.19125**	0.07188	0.16117**	0.0553
	Males		0.21238**	0.07758	0.2127	0.1818	0.2091	0.2303	0.20764**	0.09105	0.2512**	0.1758	0.20564**	0.11392	0.16257	0.13034
06/07/1989	Females			0.16441**	0.07618	0.16047	0.08525	0.06025	0.05234	0.13676**	0.1225	0.04918	0.08254	0.13964	0.07776	0.11863
	Males				0.15292	0.10422	0.13152	0.20394	0.13006**	0.02765	0.17362	0.1297	0.12805	0.05578	0.13708**	0.23417**
09/08/1989	Females					0.19	0.0821	0.1062	0.0803	0.13945	0.1712	0.0964	0.07519	0.18914	0.09223	0.15316
	Males						0.1578	0.2	0.10813	0.09075	0.121	0.1364	0.16995	0.06788	0.08271	0.05146
07/09/1989	Females							0.1455	0.07864	0.11805	0.1398	0.1333	0.0658	0.15694	0.0611	0.15575
	Males								0.09187	0.17629	0.132	0.0724	0.12207	0.18849	0.11729	0.15816
1989	Females									0.11659**	0.09354	0.05466	0.06025	0.10884	0.03017	0.0773
	Males										0.16015	0.10209	0.11459	0.05889	0.12361**	0.0409
23/05/1990	Females											0.1184	0.15195	0.13728	0.12187	0.12086
	Males												0.0675	0.13554	0.07219	0.09956
19/07/1990	Females													0.16909**	0.03008	0.13311**
	Males														0.13901**	0.03598
1990	Females															0.08432
	Males															

** significant difference at 95% level

Table A2iii.43 Kolmogorov-Smirnov D-statistics and test results for comparisons of size frequency distributions for male lobsters, between sites

Sample site		Bridlington		Selsey		Dale
	Sample date	1990	1991	1989	1990	1989
Bridlington	1989	0.03824	0.091489	0.15177**	0.11248**	0.26484**
	1990		0.120469	0.14882**	0.13267**	0.24195**
	1991			0.17519**	0.1359**	0.18753**
Selsey	1989				0.03929	0.31805**
	1990					0.33766**

*** significant difference at 95% level*

Table A2iii.44 Kolmogorov-Smirnov D-statistics and test results for comparisons of size frequency distributions for female lobsters, between sites

Sample site		Yorkshire		Bridlington			South coast		Selsey		Pembrokeshire		Dale
	Sample date	1973	1974	1989	1990	1991	1972	1973	1989	1990	1972	1973	1989
Yorkshire	1972	0.04548**	0.06799**	0.08487**	0.0949**	0.14572**	0.1916**	0.09106**	0.11015**	0.11911**	0.23808**	0.21749**	0.33116**
	1973		0.022513	0.10281**	0.1371**	0.17477**	0.14613**	0.11989**	0.15235**	0.14529**	0.1926**	0.17201**	0.28568**
	1974			0.11108**	0.14537**	0.18304**	0.12518**	0.12421**	0.16062**	0.15356**	0.17009**	0.16319**	0.13054**
Bridlington	1989				0.035746	0.109446	0.10673**	0.07539**	0.059409	0.055236	0.15321**	0.132621	0.24629**
	1990					0.07282	0.11562**	0.053242	0.05967	0.0352	0.1621**	0.14155**	0.25518**
	1991						0.12437**	0.067267	0.07963	0.05421	0.17095**	0.17922**	0.26403**
South coast	1972							0.12793**	0.10266**	0.02447	0.07401**	0.06557**	0.13956**
	1973								0.044847	0.10417**	0.1744**	0.15381**	0.26748**
Selsey	1989									0.03058	0.14914**	0.1568**	0.24222**
	1990										0.1582**	0.14974**	0.21205**
Pembrokeshir	1972											0.049555	0.13418
	1973												0.113268

*** significant difference at 95% level*

Table A2iii.45 ANCOVA results for log book CPUE comparisons between sites

Source of Variation	SSQ	df.	MSQ	Fs	Signif.
Covariates	399.042	2	199.521	7.048	0.0014
Month	343.8528	1	343.8528	12.147	0.0008
Year	13.19145	1	13.19145	0.466	0.5038
Effects	1431.282	3	477.094	16.853	0
Data type	1422.398	2	711.1991	25.123	0
Site	37.4332	1	37.43321	1.322	0.2531
Data type and site interactions	134.7951	2	67.39754	2.381	0.0981
Residual	2632.685	93	28.30844		
Total	4597.804	100			

Table A2iii.46 ANCOVA results for CPUE weight with CPUE lobster number between sites

Source of Variation	SSQ	df.	MSQ	Fs	Signif.
Covariates	1108.686	3	369.562	47.421	0
Number	774.923	1	774.923	99.436	0
Month	8.7345	1	8.73447	1.121	0.3018
Year	5.5025	1	5.50252	0.706	0.4191
Effects	165.4354	2	82.71767	10.614	0.0007
Site	165.4354	2	82.71767	10.614	0.0007
Residual	163.6569	21	7.793184		
Total	1437.778	26			

Table A2iii.47 ANCOVA results for CPUE lobster number with CPUE weight between sites

Source of Variation	SSQ	df.	MSQ	Fs	Signif.
Covariates	1704.14	3	568.0465	36.961	0
Weight	1231.326	1	1231.326	80.118	0
Month	1.2707	1	1.2707	0.083	0.7796
Year	4.7663	1	4.7663	0.31	0.5894
Effects	200.1682	2	100.0841	6.512	0.0063
Site	200.1682	2	100.0841	6.512	0.0063
Residual	322.7481	21	15.36896		
Total	2227.056	26			

Appendix Table A3i.1 Ovary staging of *Homarus spp.* according to Aiken and Waddy (1980)

Ovary Stage	Description	Ovary colour	Oocyte diameter	Ovary factor
1	Immature	White	<0.5 mm	<100
2	Immature/ developing	Yellow, beige, or pale green	<0.8 mm	<100
3	Developing	Light to medium green	<1.0 mm	<200
4	Developing	Medium to dark green	0.1 to 1.6 mm	<325
5	Developing	Dark green	1.0 to 1.6 mm	>325
6	Ripe	Dark green	1.4 to 1.6 mm	>400
6A	Oocytes free			
Spent/Reabsorbing		White or yellow with residual ova		

Appendix A3ii.1 Female internal condition indices

Ovary Factor (Aiken and Waddy, 1980)

$$\text{Ovf} = \frac{\text{Ovary weight (mg)}}{\text{Carapace Length}^3\ \text{(mm)}} \times 10$$

Relative ovary weight (Gonado-somatic index)

$$\text{ROW} = \frac{\text{Ovary wet weight (g)}}{\text{Total wet weight (g)}} \times 100$$

Relative hepatopancreas weight

$$\text{RHW} = \frac{\text{Hepatopancreas wet weight (g)}}{\text{Total wet weight (g)}} \times 100$$

Appendix A3iii.1.Histological methods

Buffered formalin (fixative)

1L 10% Formaldehyde
6.5g Anhydrous disodium phosphate (Na_2PO_4)
4g Sodium acid phosphate ($NaH_2PO_4.H_2O$)

Buoins Fixative

75 ml Picric Acid
25 ml Formaldehyde
5 ml Glacial acetic acid

Tissues fixed for minimum of 12 hours and then washed in several changes of 70% alcohol (Propan-2-ol).

Dehydration schedule

70% Propan-2-ol	2 hours (or more)
2x 80% Propan-2-ol	2 hours
2x 90% Propan-2-ol	2 hours
3x 100% Propan-2-ol	2 hours
2x "Histoclear"	2 hours

Appendix A3iii.2 Stains

Ehrlich's haematoxylin and eosin (Cox *et al*, 1969)

(stains nuclei blue, cytoplasm red)

A. 2g Ehrlich's acid haematoxylin
    10 ml Glacial acetic acid
    100 ml Glycerol
    100 ml Absolute alcohol
    100 ml Distilled water
    0.2g Potassium iodate
B. 1g Eosin
    100 ml Absolute alcohol

1. Clear in "Histoclear"
2. Rehydrate in 100% to 30% Propan-2-ol
3. Distilled water 5 minutes
4. Stain in A, 10 minutes
5. Rinse to blue in tap water (approximately 10 to 15 minutes)
6. Stain in B, 10 minutes
7. Rinse in water and dehydrate in 90% then 100% Propan-2-ol
8. Rinse in "Histoclear", dry and mount in DPX

Appendix Table A3iv.1 Oocyte size frequency distributions by ovary stage

Oocyte	Ovary stage 1		Ovary stage 2		Ovary stage 3		Ovary stage 4		Ovary stage 5		Ovary stage 6	
diameter (mm)	Avg	Std. Dev.	Avg	Std. Dev.	Avg	Std. Dev.	Avg	Std. Dev.	Avg	Std. Dev.	Avg	Std. Dev.
0.05	14.5	7.5	7.333	7.71722	3.2	4.48999	0	0	0	0	0	0
0.15	15.5	4.5	9.667	3.68179	7.2	3.18748	0	0	0	0	0	0
0.25	3	3	2.667	1.69967	2.8	1.6	0	0	0	0	0	0
0.35	0	0	1.333	1.24722	2.4	1.0198	0	0	0	0	0	0
0.45	0	0	1.667	2.35702	2.2	1.6	0	0	0	0	0	0
0.55	0	0	0	0	1	0.89443	0	0	0	0	0	0
0.65	0	0	0	0	1	0.63246	0	0	0	0	0	0
0.75	0	0	0.333	0.4714	1.2	1.16619	2.5	1.5	0	0	0	0
0.85	0	0	0	0	0	0	4	0	0	0	0	0
0.95	0	0	0	0	0	0	6.5	2.5	1.5	0.5	0	0
1.05	0	0	0	0	0	0	3	2	1	0	0	0
1.15	0	0	0	0	0.2	0.4	1	0	2.5	1.5	2	0
1.25	0	0	0	0	0	0	1	0	2	1	2	0
1.35	0	0	0	0	0	0	1	0	2	2	3	0
1.45	0	0	0	0	0	0	0	0	0	0	3	0
1.55	0	0	0	0	0	0	0	0	0	0	3	0
1.65	0	0	0	0	0	0	0	0	1	0	0	0
1.75	0	0	0	0	0	0	0	0	0	0	0	0

Appendix Table A3iv.2 Oocyte size frequency distributions by ovary stage (spent ovaries)

Oocyte	Ovary stage 2s		Ovary stage 3s		Ovary stage 4s	
diameter (mm)	Avg	Std. Dev.	Avg	Std. Dev.	Avg	Std. Dev.
0.05	3	0	2.5	2.5	0	0
0.15	8	0	8.5	8.5	1	0
0.25	4	0	0.5	0.5	2	0
0.35	1	0	2	0	0	0
0.45	1	0	1.5	1.5	0	0
0.55	3	0	1	0	1	0
0.65	0	0	0	0	1	0
0.75	0	0	1	1	1	0
0.85	0	0	0.5	0.5	3	0
0.95	0	0	1	1	1	0
1.05	0	0	0	0	0	0
1.15	0	0	0	0	0	0
1.25	0	0	0	0	0	0
1.35	0	0	0	0	0	0
1.45	0	0	0	0	0	0
1.55	0	0	0	0	0	0
1.65	0	0	0	0	0	0
1.75	0	0	0	0	0	0

Appendix Table A3iv.3 Average oocyte diameters by ovary stage

		Avg diameter (mm)	Std Dev. (mm)
Ovary stage	1	0.1	0.034448
	2	0.2	0.126836
	3	0.3	0.267413
	4	1	0.119191
	5	1.2	0.168238
	6	1.4	0.130293
Ovary stage (spent)	2S	0.2	0.149896
	3S	0.7	0.237852
	4S	0.6	0.274789

Appendix Tàble A3v.1 Female internal condition indices, Bridlington

CL (mm)	Wet Weight (g)	Hepatopancreas Weight (g)	Ovary Weight (g)	Ovary Factor	Relative Hep. Weight	Relative Ovary Weight	Ovary Stage
73	259.32	8.05	0.75	19.2794	3.10427271	0.28921795	1
68	231.11	11.17	1.36	43.252	4.8332	0.58846437	2
82	391.94	13.71	4.45	80.7083	3.49798439	1.13537786	3
85	317.55	13.2	4.47	72.79	4.1568	1.40765234	3
83	365.6	13.84	4.97	86.92	3.786	1.35940919	3
90	466.02	18.92	5.47	75.0343	4.06	1.17376937	3
79	386.4	17.76	3.49	70.79	4.596	0.90320911	3
79	330.27	13.34	3.37	68.35	4.039	1.02037727	3
93	509.2	16.62	4.07	50.5994	3.264	0.79929301	3
88	435.56	16.6	4.17	61.1911	3.811	0.95738819	3
87	456.62	18.8	6.03	91.5713	4.117	1.32057291	3
87	442.46	19.07	7.12	108.124	4.31	1.60918501	3
89	480.18	23.56	12.52	177.596	4.9065	2.60735557	4
83	414.78	22.63	6.98	122.073	5.4559	1.68281981	4
86	425.6	16.2	6.59	103.607	3.806	1.54840226	4
93	569.5	23.75	10.49	130.415	4.17	1.84196664	4
90	530	27.06	13.63	186.968	5.1057	2.57169811	4
87	462.38	20.05	12.31	186.939	4.336	2.66231238	4
86	405.96	15.71	6.4	100.62	3.86983939	1.57651	4
80	366.33	16.55	5.26	102.734	4.51778451	1.43586384	4
90	510.78	17.55	10.54	144.582	3.463	2.06351071	4
86	423.04	15.54	10.54	165.709	3.673	2.49149017	4
84	424.68	19.08	10.34	174.454	4.4928	2.43477442	4
85	446.26	20.08	8.25	134.337	4.5	1.84869807	4
83	426.38	19.12	10.18	178.038	4.48426286	2.38754163	4
86	416.16	14.86	10.51	165.237	3.57074202	2.52547097	4
81	357.23	14.59	8.93	168.033	4.0842	2.49979005	4
88	399.29	16.51	8.55	125.464	4.135	2.14130081	4
98	634.12		25.93	275.502		4.08913139	4
87	488.86	16.44	18.25	277.144	3.363	3.73317514	4
96	596.44	26.73	24.67	278.84	4.482	4.13620817	4
96	566.54	22.17	22.5	254.313	3.913	3.97147598	5
94	567.1	20.71	26.28	316.404	3.562	4.63410333	5
90	501.7	20.92	26.99	370.233	4.1698	5.37970899	5
75	310.94	12.41	14.04	332.8	3.991	4.51534058	5
90	474.88	21.74	28.2	386.831	4.578	5.93834232	5
98	642.24	21.52	36.09	383.45	3.352	5.61939462	5
92	524.94	22.58	23.83	306.03	4.3014	4.53956643	5
92	529.82	20.55	19.17	246.183	3.879	3.61820996	5
98	549.68	19.51	28.54	303.232	3.549	5.19211177	5
110	894.6	32.34	32.86	246.882	3.61502347	3.67315001	5
111	901.9	35.19	33.73	246.63	3.9018	3.73988247	5
90	505.6	23.94	25.36	347.874	4.735	5.01582278	5
103	784.32	36.24	43.5	398.087	4.621	5.54620563	5
112	882.3	32.55	36.15	257.309	3.68922135	4.09724583	5
90	464.58	19.13	27.65	379.286	4.1177	5.95161221	5
96	556.96	24.32	34.83	393.677	4.367	6.25359092	5
91	504.68	17.9	29.69	393.991	3.547	5.88293572	5
105	719.98	26.59	42.02	362.985	3.693	5.83627323	5
100	624.6	23.45	35.04	350.4	3.754	5.60999039	5
97	593.12	18.19	50.14	549.375	3.067	8.45360129	6
99	637.8	20.68	48.74	502.319	3.242	7.64189401	6
92	432.5	16.5	32.54	417.882	3.815	7.52369942	6
100	670.06	26.75	46.17	461.7	3.992	6.89042772	6
95	584.42	18.38	42.52	495.932	3.145	7.27558947	6
97	634	18.47	40.91	448.244	2.913	6.45268139	6

Appendix Table A3v.2 Female internal condition indices, Bridlington (spent ovaries)

CL (mm	Wet Weight (g)	Hepatopancreas Weight (g)	Ovary Weight (g)	Ovary Factor	Relative Hep. Weight	Relative Ovary Weight	Ovary Stage
93	511.44	16.38	4.76	59.1777	3.203	0.930705459	2s
109	809.75	26.66	8.57	66.1761	3.29237419	1.058351343	2s
90	427.94	20	3.89	53.3608	4.673552367	0.909005935	2s
94	527.28	21.04	5.01	60.319	3.990289789	0.950159308	2s
73	366.64	16.71	1.82	46.784	4.5576	0.496399738	2s
96	592.96	23.04	6.68	75.5027	3.886	1.126551538	2s
124	1108	51.68	15.48	81.1906	4.664	1.397111913	3s
111	859.68	41.36	13.96	102.074	4.769	1.623860041	3s
84	380.2	15.84	6.33	106.8	4.525	1.664913204	3s
100	629.14	30.62	9.66	96.6	4.867	1.535429316	3s
89	419.94	21.33	12.87	182.561	5.079297042	3.064723532	4s
128	1525.2	65.71	36.71	175.047	4.308287438	2.406897456	4s
87	521.58	20.45	10.98	166.742	3.920779171	2.105142068	4s
92	595.5	25.85	15.03	193.017	4.340890008	2.523929471	4s
93	647.48	28.58	15.04	186.982	4.414035955	2.322851671	4s
103	791	32.77	20.37	186.414	4.142857143	2.575221239	4s
84	464.2	21.07	9.64	162.644	4.538991814	2.076691081	4s
86	433.12	20.51	9.1	143.069	4.6523	2.101034355	4s
118	1002.45	49.08	23.42	142.541	4.896004788	2.336276123	4s
103	853.15	34.7	21.94	200.782	4.06728008	2.571646252	4s
130	1388.9	65.66	34.67	157.806	4.72748218	2.49622003	4s
97	631.52	25.84	14.27	156.354	4.091715227	2.259627565	4s
129	1330.98	58.29	32.05	149.3	4.379479782	2.40800012	4s
103	750.72	30.79	23.5	215.058	4.101395993	3.130328218	4s
98	637.64	29.56	20.12	213.771	4.635844677	3.155385484	4s
96	454.3	33.77	18.85	213.057	7.4334	4.14924059	4s
107	836.55	40.61	29.1	237.543	4.854461778	3.478572709	4s
107	815.95	44.09	28.71	234.359	5.403517372	3.518597953	4s
84	350.39	0	12.75	215.115	0	3.638802477	4s
113	1095.55	40.07	27.95	193.708	3.657523618	2.551229976	4s
102	716.08	31.93	20.69	194.966	4.458998995	2.889341973	4s
123	1190.05	54.84	37.25	200.176	4.608209739	3.130120583	4s
93	547.18	27.63	14.72	183.003	5.049526664	2.690156804	4s
107	849.15	27.73	24.37	198.932	3.6158	2.869928752	4s
94	607.3	22.77	16.44	197.933	4.21261	2.707064054	4s
88	516.06	20.81	13.34	195.753	4.72998	2.58497074	4s
117	1236.9	45.56	45.66	285.088	3.683402054	3.691486781	4s
88	506.58	12.9	20.34	298.471	2.5465	4.015160488	4s
120	1317.8	58.31	44.9	259.838	4.424798907	3.407193808	4s
125	1458.6	56.97	40.85	209.152	3.905800082	2.800630742	4s
117	1071	48.73	40.17	250.81	4.549953315	3.75070028	4s
109	1002.15	48.78	40.15	310.032	4.706	4.00638627	5s
98	649.08	32.45	18.7	339.156	4.9994	2.881000801	5s
102	1129.8	47.58	30.41	286.56	4.8378	2.691626837	5s
113	1002.95	50.62	43.48	301.338	5.047111022	4.335211127	5s

Appendix Table A3v.3 Female internal condition indices, Dale

CL (mm)	Wet Weight (g)	Hepatopancreas Weight (g)	Ovary Weight (g)	Ovary Factor	Relative Hep Weight	Relative Ovary Weight	Ovary Stage
81	253.84	14.98	2.3	43.278	5.9014	0.906082572	1
86	377.12	16.74	2.48	38.99	4.4389	0.657615613	2
98	515.53		4.03	42.818		0.781719784	2
92	516.66						3
83	395.73						3
95	488.24	16.15	5.04	58.784	3.308	1.032279207	2s
120	1133.25	45.17	13.18	76.273	3.989	1.163026693	2s
99	408.52	18.7	7.45	76.78	4.5775	1.823656125	3s
99	733.86	26.78	10.53	108.523	3.649	1.434878587	3s
115	840.8	43.64	18.2	119.667	5.19	2.164605138	3s
107	837.28	30.65	17.82	145.4643	3.6606631	2.128320275	3s
109	999.33	42.45	19.04	147.0237	4.24784606	1.905276535	3s
105	826.93	35.09	18.18	157.0457	4.24340633	2.198493222	3s
112	995.23	39.81	25.21	179.4398	4.00008038	2.533082805	3s
89	512.76	21.78	9.2	130.502	4.248	1.794211717	4s
126	935.5	56.9	26.53	132.62	6.082	2.835916622	4s
120	1066.45	48.56	25	144.675	4.5534	2.344226171	4s
106	737.46	32.45	19.49	163.641	4.4002	2.642855206	4s
112	907.77	36.69	27.86	198.302	4.0417727	3.069059343	4s
101	692.85	27.04	23.32	226.3416	3.90272065	3.365807895	4s
139	1837.85	87.11	61.6	229.3698	4.73977746	3.351742525	4s
106	832.82		27.68	232.4066	0	3.323647367	4s
108	822.05	31.52	25.97	206.158	3.83	3.159175233	4s
104	768.66	32.89	24.84	220.826	4.2789	3.231597846	4s
102	701.48	27.83	25.29	238.313	3.9673	3.605234647	4s
104	768.96	32.53	27.77	246.874	4.2301	3.611371203	4s
128	1342.55	59.84	53.72	256.156	4.4572	4.001340732	4s

Appendix Table A3v.4 Female internal condition indices, Selsey

CL (mm)	Wet Weight (g	Hepatopacreas Weight (g)	Ovary Weight (g)	Ovary Factor	Relative Hep. Weight	Relative Ovary Weight	Ovary Stage
85	419	17.07	1.06	17.26	4.074	0.252983294	1
65	199.72	6.61	0.061	22.212	3.31	0.03054276	1
73	262.6	10.41	1.3	33.417	3.964	0.495049505	1
64	167.03	6.01	0.58	22.125	3.598	0.34724301	1
75	280.13	12.67	1.07	25.362	4.523	0.381965516	1
73	261	10.66	0.96	24.67	4.084	0.367816092	1
66	202.3	8.61	0.83	28.87	4.262	0.41028176	1
85	448.92	16.28	3.02	49.1	3.626	0.672725653	2
72	240.53	12.64	1.13	30.274	5.255	0.469795867	2
91	551.74	23.25	7.94	105.365	4.214	1.439083626	3
85	425.4	16.54	4.17	67.9015	3.888	0.980253879	3
86	372.27	12.11	6.34	99.6768	3.253	1.70306498	3
89	505.06	18.68	5.13	72.7692	3.699	1.015720904	3
85	443.24	19.89	2.94	47.873	4.487	0.663297536	3
90	470.68	18.88	7.96	109	4.0112	1.691170222	3
85	389.69	20.23	3.66	59.6	5.191	0.939208088	3
85	339.86	18.36	7.86	127.987		2.312717001	3
86	440.1	22.45	3.1	48.737	5.10111338	0.704385367	3
90	432.7	17.89	5.63	77.229	4.135	1.301132424	3
82	377.1	19.07	3.95	71.639	5.057	1.047467515	3
88	400.56	18.28	10.67	93.7	4.564	2.663770721	4
85	405.66	12.87	8.71	141.8	3.173	2.147118276	4
89	415.76	12.51	12.2	173	3.009	2.934385222	4
89	511.68	12.94	6.48	91.9189	2.529	1.26641651	4
100	675.99	24.18	18.78	187.8	3.577	2.778147606	4
86	448.68	15.36	10.43	163.979	3.423	2.324596594	4
91	502.72	17.33	13.04	173.043	3.447	2.593889243	4
92	551.24	17.5	9.2	118.147	3.175	1.668964516	4
90	545.26	20.95	14.3	196.159	3.842	2.622602061	4
86	443.26	14.23	8.239	129.533	3.21	1.858728511	4
85	442	19.62	6.79	110.564	4.439	1.536199095	4
82	405.08	19.13	6.99	126.78	5.23	1.72558507	4
87	451.56	17.5	7.59	115.26	3.875	1.680839756	4
86	421.28	14.26	10.84	170.425	3.385	2.57311052	4
88	472.6	17.49	4.5	222	3.701	0.952179433	4
84	367.78	20.34	10.39	175.3	5.53	2.825058459	4
90	515.36	20.14	7.29	100	3.908	1.414545172	4
86	435.7	19.05	10.29	161.78	4.372	2.361716778	4
87		15.85	11.51	174.79			4
93	503.34	20.22	12.41	154.285	4.017	2.465530258	4
92	538.66	30.15	14.85	190.705	3·27717391	2.75684105	4
87	427.9	16.88	9.58	145.481	3.9448	2.238840851	4
81	369.19	15.31	7.52	141.502	4.147	2.036891573	4
87	388.99	15.94	14.48	219.892	4.098	3.722460732	4
91	454.86	17.56	7.47	99.128	3.861	1.642263554	4
98	716.18	29.66	10.4	110.498	4.141	1.452148901	4
91	429.74	22.39	8.3	110.142	5.21	1.931400382	4
91	570.98	21.51	12.12	160.834	3.767	2.122666293	4
90	517.76	21.6	10.89	149.383	4.172	2.1032911	4
81	342.44	17	6.63	124.755	4.964	1.936105595	4
88	502.86	20.01	14.55	213.5	3.9792	2.893449469	4
85	323.66	17.92	10.56	171.952	5.537	3.262683062	4
94	603.24	24.22	16.82	202.508	4.015	2.788276639	5
85	411.55	16.31	13.12	213.637	3.963	3.187948001	5
85	416	16.9	12.6	205.169	4.06210941	3.028846154	5
92	512.4	21.44	17.01	218.444	4.184	3.319672131	5
103	742.2	26.5	25.98	237.754	3.57	3.500404204	5
85	366.04	14.98	25.42	413.922	4.092	6.944596219	5
87	498.1	21.38	20.95	318.146	4.292	4.205982734	5
91	519.96	16.58	15.39	204.228	3.189	2.959843065	5
87	514.12	21.81	15.5	235.382	4.242	3.014860344	5
92	522.28	16.77	22.37	287.278	3.211	4.283143142	5
95	616.52	17.01	25.94	302.56	2.759	4.207487186	5
85	453.48	20.55	15.34	250	4.523	3.382729117	5
93	575.96	22.98	23.73	295.018	2·47096774	4.120077783	5
100	684.72	23.3	23.12	231.2	3.403	3.376562683	5
90	508.52	18.09	19.86	265.569	3.557	3.905451113	5
96	523.98	19.22	26.63	300.994	3.668	5.082255048	5
87	423.44	19.55	13.64	207.136	4.617	3.221235594	5
91	565.28	21.72	23.22	308.133	3.842	4.10769884	5
86	447.4	20.93	16.08	252.808	4.678	3.59409924	5
97	521.26	17.35	53.36	584.65	3.328	10.23673407	6
93	568.34	17.55	37.16	461.984	3.08794032	6.538339726	6
114	1007.35	26.52	84.3	569.001	2.633	8.368491587	6
94	622.9	21.89	38.94	468.826	3.514	6.25140472	6

Appendix Table A3v.5 Female internal condition indices, Selsey (spent ovaries)

CL (mm)	Wet Weight (g)	Hepatopacreas Weight (g)	Ovary Weight (g)	Ovary Factor	Relative Hep. Weight	Relative Ovary Weight	Ovary Stage
101	695.26	32.05	7.12	69.106	4.61	1.024077324	1s
97	523.48	26.29	10.08	110.44	5.022	1.925574998	1s
87	474	22.53	8.15	123.77	4.753	1.719409283	1s
88	477.58	20.53	3.85	56.495	4.299	0.806147661	1s
90	337.49	18.69	3.79	51.989	5.538	1.122996237	1s
106	822.15	33.79	8.45	70.9	4.1	1.027792982	1s
89	1423.2		5.41	76.74		0.380129286	1s
76	431.49	18.32	4.28	97.499	4.246	0.991911748	1s
89	385.16		4.5	63.833		1.168345623	1s
89	473.4	22.58	3.15	44.68	2·537078652	0.66539924	2s
91	527.6	23.41	7.52	99.792	4.437	1.425322214	2s
86	384.76	27.25	7.09	111.47	7.082337	1.842707142	2s
85	387.68	20.37	3.29	53.572	5.254	0.848638052	2s
117	1061.7	34.87	13.8	86.163	3.284	1.299802204	2s
90	561.3	25.48	5.5	75.446	4.539	0.979868163	2s
94	559.56	25.01	6.2	74.646	4.47	1.108013439	2s
91	540.62	22.05	4.77	63.299	4.078650438	0.882320299	3s
87	493.54	17.78	5.66	85.953	3.603	1.146816874	3s
93	637.46	26.52	11.62	144.46	4.16	1.822859474	3s
110	820	38.71	9.96	74.831	4.721	1.214634146	3s
87	486.7	20.76	4.38	66.515	4.2655	0.89993836	3s
91	531.34	25.57	9.57	127	4.812	1.801106636	3s
88	431.56	23.33	8.7	127.66	2·651136364	2.015942163	3s
86	446.16		7.18	112.88		1.609288148	3s
89	508.88	21.9	4.55	64.542	4.3036	0.894120421	3s
87	345.89	18.14	4.27	64.844		1.234496516	3s
84	435.46	19.1	5.71	96.338	4.386	1.311257061	3s
84	446.78	17.89	3.73	62.932	4.004	0.834862796	3s
90	489.6	23.21	7.82	107.3	4.741	1.597222222	3s
92	578.74	24.64	7.87	101.07	4.258	1.35985071	3s
86	471.52	21.09	4.65	73.107	4.473	0.986172379	3s
87	508.7	20.65	4.36	66.211	4.059	0.857086692	3s
97	623.26	29.75	15.55	170.38	4.773	2.494945929	4s
99	669.86	25.27	19.04	196.23	3.77243006	2.842384976	4s
126	1390.15	47.84	20.69	103.43	3.441355249	1.488328598	4s
88	457.32	18.26	7.45	109.32	3.993	1.629056241	4s
91	520.26	20.6	13.69	181.67	3.96	2.631376619	4s
90	514.3	22.2	12.97	177.91	4.316546763	2.521874392	4s
104	783.64	32.84	21.84	194.16	4.190699811	2.786994028	4s
85	437.02	17.59	10.23	166.58	4.024	2.340853965	4s
91	522.76	26.85	9.98	132.44	5.136200168	1.909097865	4s
90	476.36	23.11	13.61	186.69	4.851372911	2.857082878	4s
97	621.02	28.68	16.52	181.01	4.618208753	2.66013977	4s
90	507.86	21.55	13.57	186.15	4.243295396	2.671996219	4s
90	574.78	24.92	14.18	194.51	4.335571871	2.467030864	4s
90	504.54	27.25	15.24	209.05	5.40095929	3.020573195	4s
90	465.04	21.52	14.47	198.49	4.628	3.111560296	4s
92	499.84	25.61	9.46	121.49	5.124	1.892605634	4s
85	443.96	18.97	9.32	151.76	4.273	2.099288224	4s
88	504.64	16.21	8.6	126.2	3.212	1.704185162	4s
87	488.12	21.27	6.48	98.405	4.358	1.327542408	4s
88	464.56	18.67	12.45	182.69	21.21590909	2.679955226	4s
101	711.02	36.67	15.73	152.67	5.157	2.212314703	4s
90	519.46	18.14	11.46	157.2	3.492	2.206137142	4s
92	587.77	26.39	13.26	170.29	4.49	2.255984484	4s
88	452	17.3	10.46	153.5	3.827	2.314159292	4s
86	431.4	15.61	11.91	187.25	3.618451553	2.76077886	4s
79	307.29	15.68	6.26	126.96	5.103	2.037163591	4s
108	807.45	31.4	19.61	155.67	3.888785683	2.428633352	4s
108	883.15	39.53	37.99	301.58	4.476023326	4.301647512	5s
95	619.68	21.42	20.21	235.72	3.456622773	3.261360702	5s
104	811.5	31.82	27.43	243.85	3.921133703	3.380160197	5s
85	405.26	20.56	18.97	308.9	5.073	4.680945566	5s
93	576.26	18.4	24.66	306.58	3.193003158	4.279318363	5s
96	677.92	29.22	19.42	219.5	4.310243097	2.864644796	5s
88	480.66	19.37	19.36	284.09	4.03	4.027795115	5s
99	670	28.26	31.18	321.34	4.217910448	4.653731343	5s
89	463.74	14.16	16.9	239.73	3.053	3.644283435	5s
84	365.68	17.44	25.2	425.17	4.769	6.891271057	5s
100	663.9	32.76	25.36	253.6	4.934	3.819852387	5s
104	746.86	31.81	29.42	261.54	4.259165038	3.939158611	5s
121	1160.05	51.42	43.73	246.84	4.432567562	3.769665101	5s
111	1092.4	44.01	38.34	280.34	4.02874405	3.509703405	5s
92	547.9	16.76	29.33	376.66	3.058952364	5.353166636	5s
93	579.32	18.25	33.68	418.72	3.150245115	5.813712629	5s
92	582.98	18.25	33.68	432.52	3.130467598	5.777213627	6s

Appendix Table A3v.6 Linear regression statistics for Ovf-ovary development stage relationships

Site	N	R-square	r	Sy/x	F(df,df	P(F)		Coeff.	Std. Error	t-statistic	P
Bridlington	56	0.817	0.904	60.4587	1,54	<0.001	a	-277.57	34.03244	-8.156	<0.001
Non-berried							b	119.678	7.7139	15.515	<0.001
Selsey	75	0.685	0.828	67.1833	1,73	<0.001	a	-131.67	25.42353	-5.179	<0.001
Non-berried							b	78.5865	6.23996	12.594	<0.001
Bridlington	45	0.776	0.881	35.2816	1,43	<0.001	a	-117.61	25.10137	-4.686	<0.001
Berried							b	80.2244	6.57433	12.203	<0.001
Dale	22	0.586	0.766	39.2316	1,20	<0.001	a	-69.129	45.32784	-1.525	0.143
Berried							b	67.7406	12.72841	5.322	<0.001
Selsey	76	0.628	0.792	57.4177	1,74	<0.001	a	-39.176	19.0807	-2.053	0.044
Berried							b	57.4023	5.13587	11.177	<0.001

Appendix Table A3v.7 Polynomial regression statistics for Ovf-ovary development stage relationships

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff.	P
Bridlington	56	0.874	0.9349	50.5875	2,54	<0.001	a	33.84	<0.001
Non-berried							b	-47.02	
							c	20.7	
Selsey	75	0.863	0.929	44.559	2,73	<0.001	a	97.17	<0.001
Non-berried							b	-84.69	
							c	24.38	
Bridlington	45	0.802	0.8955	33.521	2,43	<0.001	a	37.72	<0.001
Berried							b	-21.01	
							c	15.27	
Dale	22	0.586	0.7655	40.2466	2,20	<0.001	a	-56.15	0.002
Berried							b	59.14	
							c	1.351	
Selsey	76	0.834	0.9132	38.6536	2,74	<0.001	a	152.9	<0.001
Berried							b	-92.11	
							c	23.86	

Appendix Table A3v.8 Linear regression statistics for ROW-ovary development stage relationships

Site	N	R-square	r	Sy/x	F(df,df	P(F)		Coeff.	Std. Error	t-statistic	P
Bridlington	56	0.816	0.903	0.9337	1,54	<0.001	a	-4.3576	0.52558	-8.291	<0.001
Non-berried							b	1.84217	0.11913	15.463	<0.001
Selsey	74	0.635	0.797	1.1202	1,72	<0.001	a	-1.9623	0.42404	-4.628	<0.001
Non-berried							b	1.16569	0.10405	11.203	<0.001
Bridlington	45	0.662	0.814	0.5566	1,43	<0.001	a	-0.9987	0.396	-2.522	0.015
Berried							b	0.95212	0.10372	9.18	<0.001
Dale	22	0.675	0.822	0.49187	1,20	<0.001	a	-1.0254	0.5683	-1.804	0.086
Berried							b	1.02958	0.15958	6.452	<0.001
Selsey	76	0.611	0.782	0.85269	1,74	<0.001	a	-0.551	0.28336	-1.944	0.056
Berried							b	0.82263	0.07627	10.786	<0.001

Appendix Table A3v.9 Polynomial regression statistics for ROW-ovary development stage relationships

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff.	P
Bridlington	56	0.882	0.939	0.75448	2,54	<0.001	a	0.795	<0.001
Non-berried							b	-0.9161	
							c	0.3426	
Selsey	74	0.801	0.895	0.83339	2,72	<0.001	a	1.438	<0.001
Non-berried							b	-1.264	
							c	0.3627	
Bridlington	45	0.667	0.8167	0.55944	2,43	<0.001	a	-1.819	<0.001
Berried							b	1.487	
							c	-0.081	
Dale	22	0.677	0.8228	0.50367	2,20	<0.001	a	-0.321	<0.001
Berried							b	0.5627	
							c	0.073	
Selsey	76	0.797	0.8927	0.62014	2,74	<0.001	a	2.101	<0.001
Berried							b	-1.242	
							c	0.3295	

Appendix Table A3v.10 Linear regression statistics for RHW-ovary development stage relationships

Site	N	R-square	r	Sy/x	F(df,df	P(F)		Coeff.	Std. Error	t-statistic	P
Bridlington	55	0.047	0.218	0.53344	1,53	0.11	a	4.46572	0.30096	14.838	<0.001
Non-berried							b	-0.1107	0.06811	-1.625	0.11
Selsey	73	0.00112	0.033	4.2053	1,71	0.779	a	4.2264	1.60226	2.638	0.01
Non-berried							b	0.11036	0.39194	0.282	0.779
Bridlington	45	0.027	0.164	0.97356	1,43	0.283	a	3.60709	0.69265	5.208	<0.001
Berried							b	0.1972	0.18141	1.087	0.283
Dale	22	0.00176	0.042	1.10045	1,20	0.853	a	3.83829	1.27145	3.019	0.007
Berried							b	0.06694	0.35703	0.187	0.853
Selsey	72	0.026	0.161	4.09323	1,70	0.178	a	7.02588	1.46444	4.798	<0.001
Berried							b	-0.5274	0.38737	-1.362	0.178

Appendix Table A3v.11 Polynomial regression statistics for RHW-ovary development stage relationships

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff.	P
Bridlington	55	0.227	0.4765	0.48508	2,53	0.001	a	2.348	0.008
Non-berried							b	1.026	
							c	-0.1412	
Selsey	73	0.007	0.0836	4.22175	2,71	0.769	a	2.732	0.61
Non-berried							b	1.185	
							c	-0.1607	
Bridlington	45	0.029	0.1703	0.98391	2,43	0.538	a	4.215	0.432
Berried							b	-0.1991	
							c	0.06	
Dale	22	0.022	0.1483	1.11777	2,20	0.813	a	0.267	0.652
Berried							b	2.434	
							c	-0.3717	
Selsey	72	0.044	0.2098	4.084	2,70	0.212	a	4.32	0.212
Berried							b	1.51	
							c	-0.3194	

Appendix Table A3v.12 Linear regression statistics for Ovf-ROW relationships

Site	N	R-square	r	Sy/x	F(df,df	P(F)		Coeff.	Std. Error	t-statistic	P
Bridlington	56	0.985	0.992	17.2812	1,54	<0.001	a	7.39239	4.46729	1.655	0.104
Non-berried							b	64.4386	1.08105	59.608	<0.001
Selsey	74	0.943	0.971	28657	1,72	<0.001	a	11.8163	5.7264	2.063	0.043
Non-berried							b	63.0822	1.82032	34.655	<0.001
Bridlington	45	0.813	0.901	32.2666	1,43	<0.001	a	2.55936	13.98662	0.183	0.856
Berried							b	70.1645	5.13858	13.654	<0.001
Dale	22	0.904	0.951	18.935	1,20	<0.001	a	-5.1343	13.27189	-0.387	0.703
Berried							b	67.1395	4.90387	13.691	<0.001
Selsey	76	0.977	0.988	14.3639	1,74	<0.001	a	3.3137	3.2744	1.012	0.315
Berried							b	68.0341	1.22104	55.718	<0.001

Appendix Table A3v.13 Polynomial regression statistics for Ovf-ROW relationships

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff.	P
Bridlington	56	0.986	0.993	16.7923	2,54	<0.001	a	-4.618	<0.001
Non-berried							b	73.04	
							c	-1.078	
Selsey	74	0.946	0.9726	28.2833	2,72	<0.001	a	1.6	<0.001
Non-berried							b	70.68	
							c	-0.9329	
Bridlington	45	0.822	0.9066	31.833	2,43	<0.001	a	-31.48	<0.001
Berried							b	102.9	
							c	-6.709	
Dale	22	0.905	0.9513	19.3274	2,20	<0.001	a	10.11	<0.001
Berried							b	53.42	
							c	2.747	
Selsey	76	0.977	0.9884	14.4488	2,74	<0.001	a	1.557	<0.001
Berried							b	69.56	
							c	-0.2479	

Appendix Table A3v.14 Linear regression statistics for RHW-Ovf relationships

Site	N	R-square	r	Sy/x	F(df,df	P(F)		Coeff.	Std. Error	t-statistic	P
Bridlington	55	0.088	0.297	0.52192	1,53	0.028	a	4.25177	0.13503	31.489	<0.001
Non-berried							b	-0.074	0.03267	-2.264	0.028
Selsey	73	0.0008	0.028	4.20596	1,71	0.812	a	4.4849	0.86877	5.162	<0.001
Non-berried							b	0.00098	0.00412	0.239	0.812
Bridlington	45	0.003	0.051	0.98557	1,43	0.74	a	4.22087	0.39511	10.683	<0.001
Berried							b	0.00067	0.00202	0.334	0.74
Dale	22	0.038	0.196	1.08015	1,20	0.383	a	4.66593	0.70398	6.628	<0.001
Berried							b	-0.0035	0.00396	-0.892	0.383
Selsey	72	0.019	0.137	4.10821	1,70	0.253	a	6.12973	0.98267	6.238	<0.001
Berried							b	-0.4136	0.35852	-1.154	0.253

Appendix Table A3v.15 Polynomial regression statistics for RHW-Ovf relationships

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff.	P
Bridlington	55	0.183	0.4278	0.49888	2,53	0.005	a	3.786	0.02
Non-berried							b	0.004	
							c	-9.6E-06	
Selsey	73	0.021	0.1449	4.19359	2,71	0.482	a	3.33	0.393
Non-berried							b	0.014	
							c	-2.6E-05	
Bridlington	45	0.004	0.0633	0.9966	2,43	0.924	a	4.084	0.78
Berried							b	0.002	
							c	-5.1E-06	
Dale	22	0.085	0.2915	1.08085	2,20	1.08085	a	3.019	0.359
Berried							b	0.02	
							c	-7.2E-05	
Selsey	72	0.026	0.1613	4.122	2,70	0.401	a	6.623	0.339
Berried							b	-0.011	
							c	9.16E-06	

Appendix Table A3v.16 Linear regression statistics for RHW-ROW relationships

Site	N	R-square	r	Sy/x	F(df,df	P(F)		Coeff.	Std. Error	t-statistic	P
Bridlington	55	0.079	0.281	0.52452	1,53	0.038	a	4.24396	0.13813	30.723	<0.001
Non-berried							b	-0.0011	0.00051	-2.132	0.038
Selsey	73	0.00042	0.02	4.20677	1,71	0.864	a	4.53814	0.84336	5.381	<0.001
Non-berried							b	0.04591	0.26725	0.172	0.864
Bridlington	43	0.006	0.077	0.98392	1,43	0.615	a	414.036	0.4265	9.708	<0.001
Berried							b	0.07941	0.15669	0.507	0.615
Dale	22	0.00194	0.044	1.10035	1,20	0.846	a	4.21726	0.77126	5.468	<0.001
Berried							b	-0.0561	0.28498	-0.197	0.846
Selsey							a				
Berried							b				

Appendix Table A3v.17 Polynomial regression statistics for RHW-ROW relationships

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff.	P
Bridlington	55	0.162	0.4025	0.50515	2,53	0.01	a	3.872	0.029
Non-berried							b	0.1998	
							c	-0.034	
Selsey	73	0.019	0.1378	4.19795	2,71	0.518	a	3.529	0.418
Non-berried							b	0.7993	
							c	-0.093	
Bridlington	45	0.006	0.0775	0.99556	2,43	0.882	a	4.137	0.725
Berried							b	0.082	
							c	-0.0006	
Dale	22	0.041	0.2025	1.10635	2,20	0.669	a	2.471	0.529
Berried							b	1.515	
							c	-0.3145	
Selsey	72	0.019	0.1378	4.1375	2,70	0.519	a	6.294	0.419
Berried							b	-0.5524	
							c	0.022	

Appendix Table A3v.18 ANCOVA results for Ovf with ovary development stage at Bridlington, between berried and non-berried females

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (ovary stage)	1105197	1	1105197	384.85	0
Berried/non-berried effect	748.5166	1	748.5166	0.261	0.6163
Residual	281430.9	98	2871.744		
Total	1387377	100			

Appendix Table A3v.19 ANCOVA results for Ovf with ovary development stage at Dale, between berried and non-berried females

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (ovary stage)	82470.04	1	82470.04	53.596	0
Berried/non-berried effect	155.5842	1	155.5842	0.101	0.7569
Residual	33852.15	22	1538.734		
Total	116477	24			

Appendix Table A3v.20 ANCOVA results for Ovf with ovary development stage at Selsey, between berried and non-berried females

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (ovary stage)	1098886	1	1098886	270.86	0
Berried/non-berried effect	7543.919	1	7543.919	1.859	0.1748
Residual	600444.9	148	4057.06		
Total	1706875	150			

Appendix Table A3v.21 ANCOVA results for RHW with ovary development stage at Bridlington, between berried and non-berried females

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (ovary stage)	242.7387	1	242.7387	313.29	0
Berried/non-berried effect	0.3362928	1	0.3362928	0.434	0.5186
Residual	75.9315	98	0.7748112		
Total	319.0065	100			

Appendix Table A3v.22 ANCOVA results for RHW with ovary development stage at Dale, between berried and non-berried females

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (ovary stage)	0.9791583	1	0.9791583	0.812	0.3873
Berried/non-berried effect	1.2302738	1	1.2302783	1.02	0.324
Residual	25.331103	21	1.20624		
Total	27.540535	23			

Appendix Table A3v.23 ANCOVA results for RHW with ovary development stage at Selsey, between berried and non-berried females

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (ovary stage)	5.676839	1	5.67684	11.29	0.001
Berried/non-berried effect	1.9854877	1	1.98548	3.949	0.0488
Residual	71.40162	142	0.502828		
Total	79.0639	144			

Appendix Table A3v.24 ANCOVA results for ROW with ovary development stage at Bridlington, between berried and non-berried females

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (ovary stage)	0.364447	1	0.36445	0.613	0.444
Berried/non-berried effect	2.722617	1	2.72262	4.577	0.0349
Residual	57.69563	97	0.5948		
Total	60.78269	99			

Appendix Table A3v.25 ANCOVA results for ROW with ovary development stage at Dale, between berried and non-berried females

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (ovary stage)	17.68716	1	17.6872	67.467	0
Berried/non-berried effect	0.004263	1	0.00426	0.016	0.901
Residual	5.767492	22	0.26216		
Total	23.45891	24			

Appendix Table A3v.26 ANCOVA results for ROW with ovary development stage at Selsey, between berried and non-berried females

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (ovary stage)	236.4064	1	236.406	229.792	0
Berried/non-berried effect	0.774453	1	0.77445	0.753	0.3963
Residual	151.231	147	1.02878		
Total	388.4118	149			

Appendix Table A3v.27 ANCOVA results for Ovf with ovary development stage for non-berried females, between sites

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (ovary stage)	1688050	1	1688050	365.319	0
Site	30789.359	2	15394.68	3.332	0.0388
Residual	600699.08	130	4620.7621		
Total	2319538.4	133			

Appendix Table A3v.28 ANCOVA results for RHW with ovary development stage for non-berried females, between sites

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (ovary stage)	4.0934344	1	4.0934344	10.671	0.0014
Site	1.7398808	2	0.8699404	2.268	0.1077
Residual	48.332731	126	0.3835931		
Total	54.166046	129			

Appendix Table A3v.29 ANCOVA results for ROW with ovary development stage for non-berried females, between sites

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (ovary stage)	381.55355	1	381.55355	312.551	0
Site	9.0878606	2	4.5439303	3.722	0.0268
Residual	157.47983	129	1.2207739		
Total	548.12124	132			

Appendix Table A3v.30 ANCOVA results for Ovf with ovary development stage for berried females, between sites

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (ovary stage)	639439.89	1	639439.89	260.811	0
Site	1196.7727	2	598.38634	0.244	0.7838
Residual	340791.76	139	2451.7393		
Total	981428.42	142			

Appendix Table A3v.31 ANCOVA results for RHW with ovary development stage for berried females, between sites

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (ovary stage)	0.710785	1	0.710785	0.896	0.3557
Site	1.2556395	2	0.6278198	0.791	0.4553
Residual	107.10017	135	0.7933346		
Total	109.06659	138			

Appendix Table A3v.32 ANCOVA results for ROW with ovary development stage for berried females, between sites

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (ovary stage)	121.13825	1	121.13825	231.756	0
Site	1.0874706	2	0.5437353	1.04	0.3561
Residual	72.654892	139	0.5226971		
Total	194.88061	142			

Appendix Table A3vi.1 Cement gland development stage and female internal condition indices, Bridlington and Selsey 1990

Cement gland development

Site	Date	CL (mm)	Cement gland stage	Ovary stage	Ovary factor	Relative ovary weight	Moult stage
Bridlington	17/9/1990	98	3	4	275.5017	4.08913139	C1
		110	3	4	246.88204	3.67315001	C1
		112	4	4	257.30856	4.09724583	C4
	16/08/1990	85	3	4	134.33747	1.84894666	C4
		86	3	6	511.74739	-	C4
		86	2	4	165.70868	2.49149017	C4
		86	3	3	103.60723	1.54840226	C4
		87	3	4	277.14376	3.73317514	C4
		88	3	4	125.4637	2.14130081	C4
		90	1	2	75.034294	1.17376937	C4
		90	4	5	347.8738	5.01582278	C4
		90	2	4	144.58162	2.06351071	C4
		91	3	5	393.99075	5.88293572	C4
		92	4	6	417.88239	7.52369942	C4
		93	3	4	130.41473	1.84196664	C4
		93	2	3	50.599423	0.79929301	C4
		95	4	5	495.93235	7.27558947	C4
		96	4	5	393.67676	6.25359092	C4
		96	4	4	254.31315	3.97147598	C4
		98	2	5	303.2325	5.19211177	C2
		99	4	6	502.31939	7.64189401	C4
		100	3	5	461.7	6.88939955	C4
		105	3	5	362.98456	5.83627323	C3
		97	4	5	448.243	6.452681	C4
		94	3	5	316.4	4.6341033	C4
		87	0	3	108.12	1.609185	C4
		92	3	4	246.18	3.61821	C4
		88	0	3	61.19	0.957388	C2
		98	3	5	383.44	5.6193946	C4
Selsey	07/11/1990	100	1	4	187.8	3.3503407	C4
		85	1	4	141.8	2.1548323	C4
		88	1	3	93.7	2.66377	C4
		90	0	3	107.3	1.59722	C4
		100	2	4	231.2	3.376562	C4
		89	0	4	173	2.93439	C4
		85	0	3	49.1	0.6727256	C4
		95	1	4	302.56	4.21104	C4
		88	2	4	222	0.952179	C4
	19/07/1990	91	3	5	308	4.10769884	C4
		86	2	4	252	3.59409924	C4
		96	3	5	301	5.08225505	C4
		87	2	4	207	3.22123559	C4
		89	3	5	350	3.64428343	C4
		87	2	4	175	-	C4
		92	3	4	218	3.31967213	C4
		103	2	4	238	3.5004042	C4
		85	2	4	214	3.187948	C4
		86	2	4	187	2.76077886	C4
	27/09/1990	87	3	4	235.38	3.01486	C4
		91	3	4	204.22	2.9598	C4
		91	1	4	181.66	2.63138	C4
		87	2	5	318.14	4.2059827	C4
		86	1	4	129.53	1.858729	C4
		84	2	5	425.17	6.8969	C4
		92	1	4	287.27	4.283143	C4
	7/11/1990	90	1	4	157.2	2.206137	C4
		85	1	4	110.56	1.536	C4
		85	2	4	47.87	0.6632975	C4
		94	3	5	202.5	2.78828	C4

Appendix Table A3vi.2 Linear regression statistics for ovary development stage-cement gland development stage relationships

Site	N	R-square	r	Sx/y	F(df,df)	P(F)		Coeff.	Std. Error	t-statistic	P
Bridlington	29	0.423	0.65	0.846	1,27	<0.001	a	-0.3091	0.73005	-0.423	0.675
							b	0.7299	0.16409	4.448	<0.001
Selsey	30	0.427	0.653	0.728	1,28	<0.001	a	-2.8851	1.02022	-2.828	0.009
							b	1.1264	0.24672	4.566	<0.001

Appendix Table A3vi.3 Polynomial regression statistics for ovary development stage-cement gland development stage relationships

Site	N	R-square	r	Sx/y	F(df,df)	P(F)		Coeff.	P
Bridlington	29	0.473	0.68775	0.82346	2,27	<0.001	a	-3.683	0.002
							b	2.417	
							c	-0.2	
Selsey	30	0.433	0.658	0.73703	2,28	<0.001	a	-5.667	0.003
							b	2.5	
							c	-0.1667	

Appendix Table A3vi.4 Linear regression statistics for Ovf-cement gland development stage relationships

Site	N	R-square	r	Sx/y	F(df,df)	P(F)		Coeff.	Std. Error	t-statistic	P
Bridlington	29	0.429	0.655	0.841	1,27	<0.001	a	1.4961	0.34096	4.388	<0.001
							b	0.005	0.0011	4.506	<0.001
Selsey	30	0.271	0.52	0.821	1,28	0.003	a	0.5518	0.3958	1.394	0.174
							b	0.0057	0.00176	3.225	0.003

Appendix Table A3vi.5 Polynomial regression statistics for Ovf-cement gland development stage relationships

Site	N	R-square	r	Sx/y	F(df,df)	P(F)		Coeff.	P
Bridlington	29	0.503	0.70922	0.79945	2,27	<0.001	a	0.551	0.001
							b	0.014	
							c	-2E-05	
Selsey	30	0.31	0.55678	0.81321	2,28	0.007	a	-0.183	0.021
							b	0.014	
							c	-2E-05	

Appendix Table A3vi.6 Linear regression statistics for ROW-cement gland development stage relationships

Site	N	R-square	r	Sx/y	F(df,df)	P(F)		Coeff.	Std. Error	t-statistic	P
Bridlington	28	0.456	0.675	0.836	1,26	<0.001	a	1.4449	0.34126	4.234	<0.001
							b	0.3472	0.07437	4.669	<0.001
Selsey	30	0.149	0.386	0.902	1,27	0.039	a	0.8801	0.4228	2.082	0.047
							b	0.2801	0.12885	2.174	0.039

Appendix Table A3vi.7 Polynomial regression statistics for ROW-cement gland development stage relationships

Site	N	R-square	r	Sx/y	F(df,df)	P(F)		Coeff.	P
Bridlington	29	0.503	0.70922	0.815	2,27	<0.001	a	0.666	0.002
							b	0.8546	
							c	-0.061	
Selsey	30	0.174	0.417	0.90498	2,28	0.083	a	0.394	0.109
							b	0.6279	
							c	-0.052	

Appendix Table A3vi.8 ANCOVA results for ovary development stage with CG development stage between sites

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (cg stage)	14.159031	1	14.159031	37.943	0
Site effect	1.0792677	1	1.0792677	2.892	0.0946
Residual	20.897295	56	0.373166		
Total	36.135593	58			

Appendix Table A3vi.9 ANCOVA results for Ovf with CG development stage between sites

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (cg stage)	353233.33	1	353233.33	38.402	0
Site effect	1500.1837	1	1500.1837	0.163	0.6922
Residual	515109.46	56	9198.3832		
Total	869842.97	58			

Appendix Table A3vi.10 ANCOVA results for ROW with CG development stage between sites

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (cg stage)	71.867292	1	71.867292	32.518	0
Site effect	0.0255072	1	0.0255072	0.012	0.916
Residual	119.34293	54	2.2100543		
Total	191.23573	56			

Appendix Table A3vii.1 Average calorific values, % water and % ash (wet weight) for ovary development stages

Ovary Stage	Average Cal/g dry weight	Std. Dev. Cal/g dry weight	Average % water	Std. Dev. % water	Average % ash	Std. Dev. % ash
1	-	-	74.51957	0.992672	0	0
2	-	-	66.02453	10.20219	4.889191	2.123596
3	-	-	62.64004	5.700273	4.531874	1.060298
4	6201.16666667	41.3578556289	55.79834	4.651364	3.589001	1.009272
5	6218.58333333	99.7757555165	52.7173	3.55184	3.379968	0.579077
6	6327	32	51.3415	0.7635	2.730008	0.336804
1s	5358	0	73.941	0	-	-
2s	-	-	69.58905	11.54321	6.179835	1.101972
3s	6126.5	379.5422	58.03604	8.371595	4.295993	1.665695
4s	6390.75	123.2282	54.07714	3.541217	3.606768	0.950489
5s	6394	137.4348	53.96581	2.163589	3.142659	0.794781

Appendix Table A3vii.2 Linear regression statistics for Calorific value-ovary development stage relationships

Reproductive state	N	R-square	r	Sx/y	F(df,df)	P(F)		Coeff.	Std. Error	t-statistic	P
Non-ovigerous	14	0.189	0.435	80.753	1,12	0.121	a	5984	146.9729	40.712	<0.001
							b	51.54	30.83811	1.671	0.121
Ovigerous	39	0.347	0.589	230.22	1,37	<0.001	a	5474	192.0743	28.5	<0.001
(spent)							b	216.1	48.68636	4.438	<0.001

Appendix Table A3vii.3 Polynomial regression statistics for Calorific value-ovary development stage relationships

Reproductive state	N	R-square	r	Sx/y	F(df,df)	P(F)		Coeff.	P
Non-ovigerous	14	0.253	0.503	80.9276	2,12	0.201	a	7041	0.199
							b	-392.1	
							c	45.5	
Ovigerous	39	0.447	0.6686	214.78	2,27	<0.001	a	4638	<0.001
(spent)							b	740.1	
							c	-76.67	

Appendix Table A3vii.4 Linear regression statistics for % water-ovary development stage relationships

Reproductive state	N	R-square	r	Sx/y	F(df,df)	P(F)		Coeff.	Std. Error	t-statistic	P
Non-ovigerous	50	0.472	0.687	5.757	1,48	<0.001	a	76.03	2.86115	26.572	<0.001
							b	-4.8	0.73339	-6.55	<0.001
Ovigerous	60	0.386	0.621	6.5779	1,58	<0.001	a	77.39	3.47183	22.292	<0.001
(spent)							b	-5.55	0.9181	-6.042	<0.001

Appendix Table A3vii.5 Polynomial regression statistics for % water-ovary development stage relationships

Reproductive state	N	R-square	r	Sx/y	F(df,df)	P(F)		Coeff.	P
Non-ovigerous	50	0.493	0.7021	5.70116	2,48	<0.001	a	83	<0.001
							b	-9.352	
							c	0.6597	
Ovigerous	60	0.452	0.6723	6.271	2,58	<0.001	a	97.07	<0.001
(spent)							b	-18.71	
							c	1.999	

Appendix Table A3vii.6 Linear regression statistics for % ash-ovary development stage relationships

Reproductive state	N	R-square	r	Sx/y	F(df,df)	P(F)		Coeff.	Std. Error	t-statistic	P
Non-ovigerous	28	0.027	0.164	1.6021	1,28	0.405	a	4.562	0.96656	4.72	<0.001
							b	-0.22	0.25702	-0.846	0.405
Ovigerous	55	0.358	0.598	1.161	1,53	<0.001	a	7.656	0.69444	11.024	<0.001
(spent)							b	-0.99	0.18152	-5.433	<0.001

Appendix Table A3vii.7 Polynomial regression statistics for % ash-ovary development stage relationships

Reproductive state	N	R-square	r	Sx/y	F(df,df)	P(F)		Coeff.	P
Non-ovigerous	28	0.12	0.3464	1.55378	2,26	0.203	a	1.72	0.204
							b	1.538	
							c	-0.2538	
Ovigerous	55	0.396	0.6293	1.13624	2,53	<0.001	a	11.16	<0.001
(spent)							b	-3.164	
							c	0.3154	

Appendix Table A3vii.8 ANCOVA results for calorific value with ovary development stage between non-berried and berried females

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (ovary stage)	47.4293	1	47.4293	31.921	0
Berried/non-berried effect	0.1927293	1	0.1927293	0.13	0.7235
Residual	117.38003	79	1.4858232		
Total	165.00206	81			

Appendix Table A3vii.9 ANCOVA results for water content with ovary development stage between non-berried and berried females

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (ovary stage)	543470.89	1	543470.89	12.458	0.0009
Berried/non-berried effect	449062.97	1	449062.97	10.294	0.0023
Residual	2181242.5	50	43624.849		
Total	3173776.3	52			

Appendix Table A3vii.10 ANCOVA results for ash content with ovary development stage between non-berried and berried females

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (ovary stage)	2961.2591	1	2961.2591	76.982	0
Berried/non-berried effect	52.059677	1	52.059677	1.353	0.2473
Residual	4115.937	107	38.466701		
Total	7129.2558	109			

Appendix Table A4ii.1 Female abdomen width and relative abdomen width, Bridlington 1989

CL (mm)	Average AW (mm)	Std. Dev AW (mm)	Average RAW	Std. Dev. RAW
62.5	30	0	46.88	0
67.5	36	1.095445	53.0982	1.501827
72.5	38.71429	1.516351	53.75552	1.440874
77.5	43.08108	1.977965	55.94146	2.167174
82.5	47.60465	2.950282	58.13966	3.096274
87.5	51.97778	2.489881	59.83629	2.473085
92.5	56.23913	3.072917	61.40307	3.135988
97.5	60.88889	2.377882	62.93478	2.716517
102.5	64.75	1.47902	63.97375	2.066505
112.5	72	0	64.86	0
122.5	84	0	67.472	0
127.5	85	0	67.46	0

Appendix Table A4ii.2 Male abdomen width and relative abdomen width, Bridlington 1989

CL (mm)	Average AW (mm)	Std. Dev AW (mm)	Average RAW	Std. Dev. RAW
62.5	32.5	0.5	50.397	0.397
67.5	33.5	0.5	48.914	1.086001
72.5	35.88235	1.131493	49.75288	1.258319
77.5	38	0.825723	49.09575	1.036041
82.5	40.54545	1.634679	49.49545	1.1833
87.5	42.7	0.971253	49.27243	0.984517
92.5	45	1.626395	48.89077	1.442709
97.5	47.11111	1.409842	49.1795	1.132964
102.5	54	6.557439	58.14425	8.230886
107.5	49	3.559026	46.05433	2.937596

Appendix Table A4ii.3 Female abdomen width and relative abdomen width, Bridlington 1990

CL (mm)	Average AW (mm)	Std. Dev. AW (mm)	Average RAW	Std. Dev. RAW
57.5	38	0	67.857143	0
67.5	34.5	1.5	51.855204	1.0859729
72.5	38.6	2.1540659	53.444586	2.3992766
77.5	43.25	2.1650635	55.970106	2.2911838
82.5	46.952381	1.914262	57.561286	2.1517437
87.5	51.764706	2.6240833	59.786349	2.9954108
92.5	55.521739	2.8109965	60.568235	2.6978307
97.5	58.571429	6.1494981	60.353404	6.0551811
102.5	64.8	1.9390719	63.770341	1.3181426
107.5	68.5	2.5	63.997379	1.1402359
112.5	72.333333	0.4714045	65.165994	0.2409003
122.5	77	0	62.601626	0
132.5	87	0	64.925373	0
152.5	105	0	70	0

Appendix Table A4ii.4 Male abdomen width and relative abdomen width, Bridlington 1990

CL (mm)	Average AW (mm)	Std. Dev. AW (mm)	Average RAW	Std. Dev. RAW
62.5	31	0	48.4375	0
72.5	36	0.8164966	49.092929	1.1617697
77.5	37.666667	0.8164966	48.99326	0.8598104
82.5	40.642857	1.7971065	49.853945	1.5948755
87.5	43.333333	0.4714045	49.067975	1.0654241
92.5	44.5	1.2583057	48.191938	0.9788291
97.5	47.75	0.4330127	49.232064	0.7644335
102.5	50	0	49.019608	0
137.5	65.333333	3.0912062	47.553995	1.7314299
142.5	67	0	46.853147	0
147.5	67	0	45.578231	0

Appendix Table A4ii.5 Female abdomen width and relative abdomen width, Dale 1989

CL (mm)	Average AW (mm)	Std. Dev. AW (mm)	Average RAW	Std. Dev. RAW
72.5	38	0	51.351	0
82.5	44.25	1.47902	54.11775	1.365929
87.5	48.16667	3.236081	54.898	2.844664
92.5	53.375	2.912795	57.8565	2.908029
97.5	58.38462	3.563457	60.19338	3.59356
102.5	61.07692	3.911748	59.48508	3.849064
107.5	66.33333	5.537749	61.79222	5.070011
112.5	70	5.05682	62.42007	4.393824
117.5	74	3.535534	63.0935	2.435393
122.5	79.5	2.718981	65.31207	1.973495
127.5	83.25	2.106537	65.68769	1.777985
132.5	88.6	4.079216	67.2256	3.031502
137.5	92.4	2.57682	66.77	2.044449
142.5	92.66667	0.471405	65.87567	0.11715
147.5	97	0	65.541	0

Appendix Table A4ii.6 Male abdomen width and relative abdomen width, Dale 1989

CL (mm)	Average AW (mm)	Std. Dev. AW (mm)	Average RAW	Std. Dev. RAW
72.5	36	0	50.70423	0
82.5	41	0	49.39759	0
87.5	43.66667	1.598611	50.08688	1.389243
92.5	45.1	1.3	49.28686	1.204777
97.5	48.5	0.5	48.9899	0.505051
102.5	51.09091	1.378705	49.86494	1.180257
107.5	52	1.264911	48.69303	1.038606
112.5	55.28571	0.880631	49.24247	0.843312
117.5	56.75	0.433013	48.82102	0.551736
122.5	59.3	1.486607	48.6476	1.072917
127.5	61.36364	1.226431	48.49105	0.871448
132.5	62.5	0.5	47.44213	0.471726
137.5	65.5	0.866025	42.74145	13.93746
142.5	60	0	42.85714	0
147.5	70	0	47.78658	0.489282
152.5	72	0	48	0

Appendix Table A4ii.7 Female abdomen width and relative abdomen width, Selsey 1989

CL (mm)	Average AW (mm)	Std. Dev. AW (mm)	Average RAW	Std. Dev. RAW
62.5	33.2	1.32665	53.12	2.12264
67.5	35.29412	2.269094	52.28758	3.361621
72.5	39.0566	2.505956	53.87118	3.456491
77.5	43.04819	2.389251	55.54606	3.082905
82.5	46.85088	3.393059	56.78894	4.112799
87.5	51.12195	2.847293	58.42509	3.254049
92.5	55.12245	2.335464	59.59184	2.524826
97.5	61.16667	1.462494	62.73504	1.499994
102.5	63.5	1.5	61.95122	1.463415

Appendix Table A4ii.8 Male abdomen width and relative abdomen width, Selsey 1989

CL (mm)	Average AW (mm)	Std. Dev. AW (mm)	Average RAW	Std. Dev. RAW
62.5	31.4	1.496663	50.1392	1.528087
67.5	33.11765	1.231085	49.1252	1.577876
72.5	35.66667	1.086534	49.37342	1.421842
77.5	38.09009	1.255973	49.30387	1.321196
82.5	40.29825	1.317426	49.42817	467.4061
87.5	42.64444	1.675385	49.27835	1.672021
92.5	45.6	3.929377	49.7162	4.166901
97.5	47.33333	0.942809	48.96667	0.731087

Appendix Table A4ii.9 Female abdomen width and relative abdomen width, Selsey 1990

CL (mm)	Average AW (mm)	Std. Dev. AW (mm)	Average RAW	Std. Dev. RAW
67.5	35.33333	0.471405	52.34568	0.698377
72.5	40	2.44949	55.17241	3.378607
77.5	44.5	2.101587	57.41935	2.711725
82.5	46.95455	2.946142	56.9146	3.571081
87.5	52.29412	3.267752	59.76471	3.734573
92.5	55.45455	2.675262	59.95086	2.892175
97.5	63.66667	1.490712	65.29915	1.528935
102.5	63.5	1.118034	61.95122	1.090765
107.5	66	0	61.39535	0

Appendix Table A4ii.10 Male abdomen width and relative abdomen width, Selsey 1990

CL (mm)	Average AW (mm)	Std. Dev. AW (mm)	Average RAW	Std. Dev. RAW
62.5	31.5	0.5	49.60317	0.396825
72	35	2.160247	48.64943	3.511453
77.5	40	3.435113	51.89834	4.613969
82.5	40.30769	0.991085	48.92826	1.067863
87.5	42.3	5.2886	48.77967	7.001753
92.5	44.5	8.890875	48.63799	10.67712
122.5	55.5	3.5	45.65041	2.317073

Appendix Table A4ii.11 Female abdomen width and relative abdomen width, Whitby 1973

CL (mm)	Average AW (mm)	Std. Dev. AW (mm)	Average RAW	Std. Dev. RAW
57.5	28	0	47.45763	0
62.5	31.5	1.5	50.42243	2.803379
67.5	34.44444	2.21666	50.71743	2.831868
72.5	37.375	4.451708	51.95796	6.378357
77.5	39.78125	3.314121	51.77722	4.038177
82.5	43.84615	4.347345	53.73634	4.838283
87.5	49.5	1.627882	56.96526	1.731173
92.5	53.5	2.5	58.1295	2.085549
102.5	69	0	66.34615	0
112.5	71	0	64.54545	0

Appendix Table A4ii.12 Male abdomen width and relative abdomen width, Whitby 1973

CL (mm)	Average AW (mm)	Std. Dev. AW (mm)	Average RAW	Std. Dev. RAW
57.5	28	0	47.45763	0
62.5	30	0	47.61905	0
67.5	31.61538	1.273303	46.60991	1.891113
72.5	33.8	1.375984	46.98474	1.540074
77.5	36.42857	1.613084	47.32585	1.741951
82.5	39.33333	1.563472	47.97691	1.965988
87.5	41.4	1.2	47.7082	1.588004
92.5	43.8	0.979796	47.30192	0.903827
97.5	45.75	1.299038	47.77409	1.00786
107.5	49.5	1.5	47.18182	0.818182
122.5	59	0	47.58065	0

Appendix Table A4ii.13 Female abdomen width and relative abdomen width, Staithes 1980 to 1981

CL (mm)	Average AW (mm)	Std. Dev. AW (mm)	Average RAW	Std. Dev. RAW
62.5	31.67615	0.857703	50.84615	1.349995
67.5	34.13769	1.106826	50.69231	1.407923
72.5	38.97385	2.915214	52.76923	2.495756
82.5	45.56949	2.414641	55.4359	2.478574
87.5	51.47875	2.472925	59.15	2.632014
92.5	54.55158	2.571948	59.52632	2.54162
97.5	59.27737	1.861295	60.94737	1.82017
102.5	62.87286	2.737272	61.95238	2.399924
107.5	66.89667	3.355985	62.46667	2.704728
112.5	70.16	4.284789	62.63636	3.674797
117.5	71.71714	3.150736	62.14286	2.948538
122.5	82.17429	2.340401	65	2.165064
127.5	86.43	0	67	0
137.5	87.725	1.325	64.5	0.5

Appendix Table A4ii.14 Female abdomen width and relative abdomen width, Pembrokeshire 1973

CL (mm)	Average AW (mm)	Std. Dev. AW (mm)	Average RAW	Std. Dev. RAW
67.5	34	0	50.51226	0.929241
72.5	35.66667	0.471405	50.23474	0.331975
77.5	42	0	53.84615	0
82.5	45.66667	0.471405	55.24638	0.346909
87.5	50	2.160247	56.8015	1.974148
92.5	51.5	0.5	57.22222	0.555556
97.5	57	0	60	0
102.5	62.5	0.5	61.89216	1.107843
117.5	82	0	69.49153	0
127.5	83	0	64.34109	0
137.5	87.5	1.5	64.81481	1.111111

Appendix Table A4ii.15 Male abdomen width and relative abdomen width, Pembrokeshire 1973

CL (mm)	Average AW (mm)	Std. Dev. AW (mm)	Average RAW	Std. Dev. RAW
62.5	31	0	48.4375	0
72.5	36.33333	0.471405	50.23474	0.650355
77.5	35.5	0.5	47.01754	0.350877
82.5	41	0	49.39759	0
87.5	42	0	49.41176	0
92.5	44	0	47.82609	0
97.5	46	0	47.91667	0
102.5	49.25	0.433013	48.40322	0.405399
112.5	56	0	49.12281	0
117.5	55	3	46.99006	2.162478
142.5	64	0	45.71429	0

Appendix Table A4ii.16 Female abdomen width and relative abdomen width, St. Davids 1980 to 1981

CL (mm)	Average AW (mm)	Std. Dev. AW (mm)	Average RAW	Std. Dev. RAW
62.5	33.28	0	52	0
72.5	36.4325	1.13427	50.25	1.089725
77.75	40.75167	0.938996	52.41667	1.114924
82.5	43.79533	2.030802	53.13333	1.927578
87.5	48.39455	2.011695	55.86364	2.242066
92.5	53.39389	3.32279	57.94444	3.099681
97.5	57.42625	3.13475	59.58333	3.094574
102.5	63.12458	2.65811	61.625	2.21383
107.5	67.14889	2.740813	63.05556	2.59213
112.5	71.03381	3.214428	63.61905	2.90281
117.5	75.32294	2.671474	64.52941	1.752902
122.5	79.11111	3.101804	64.77778	2.199888
127.5	84.1675	3.832258	66.58333	3.067527
132.5	89.445	1.789211	67.5	0.866025
137.5	94.97667	0.315841	69.66667	0.471405
147.5	98.1975	3.879274	67.25	2.692582
152.5	96.64	3.839872	64	2.384848
157.5	104.94	0	66	0
162.5	102.69	0	63	0

Appendix Table A4ii.17 Female abdomen width and relative abdomen width, Selsey 1973

CL (mm)	Average AW (mm)	Std. Dev. AW (mm)	Average RAW	Std. Dev. RAW
62.5	31.91667	1.656217	51.12328	1.832398
67.5	33.76923	2.043897	49.75379	2.590694
72.5	36.83019	2.098839	51.23031	2.369155
77.5	39.89362	2.299251	52.08506	2.607471
82.5	44.67442	2.899246	54.52624	3.160088
87.5	48.58333	3.161179	56.10181	3.389191
92.5	55.14286	2.2315	59.39322	2.530306
112.5	73	0	64.60177	0
117.5	75	0	64.10256	0

Appendix Table A4ii.18 Male abdomen width and relative abdomen width, Selsey 1973

CL (mm)	Average AW (mm)	Std. Dev. AW (mm)	Average RAW	Std. Dev. RAW
57.5	28	0	48.27586	0
62.5	30.25	1.089725	48.59831	1.83158
67.5	33.1	0.7	48.54223	1.30475
72.5	34.45238	1.276199	48.10473	1.561384
77.5	37.14286	1.505093	48.57771	1.711627
82.5	40.10909	1.723345	48.82924	1.732704
87.5	42.83333	1.984663	49.01136	1.575366
102.5	49	0	48.51485	0
112.5	55	0	48.24561	0
127.5	61	0	48.0315	0

Appendix Table A4ii.33 AW-CL linear regression intersections

Site	Individual		5 mm CL groups	
	CL (mm)	AW (mm)	CL (mm)	AW (mm)
Bridlington, 1989	61.156	30.268	47.704	17.897
Bridlington, 1990	62.8564	31.6018	64.8254	32.7769
Dale, 1989	74.671	38.173	73.1281	37.603
Selsey, 1989	63.624	30.9257	60.564	30.1335
Selsey, 1990	64.319	33.524	63.78465	32.7842
Whitby, 1973	56.4774	26.3514	61.267	28.918
Pembrokeshire, 1973	56.79	25.4267	68.422	33.924
Selsey, 1973	64.551	31.1186	62.922	30.5079

Appendix Table A4ii.34 AW-CL log-linear regression intersections

Site	Individual		5 mm CL groups	
	CL (mm)	AW (mm)	CL (mm)	AW (mm)
Bridlington, 1989	54.191	26.914	63.135	31.297
Bridlington, 1990	58.0636	29.2895	58.435	29.4967
Dale, 1989	68.984	35.281	67.6458	34.61
Selsey, 1989	56.082	26.0668	57.0765	28.4236
Selsey, 1990	61.116	31.739	59.488	30.365
Whitby, 1973	48.2504	21.8667	58.668	27.921
Pembrokeshire, 1973	64.457	31.9458	64.986	32.148
Selsey, 1973	61.585	29.642	62.276	30.1524

Appendix Table A4ii.35 AW-CL second order polynomial regression intersections

Site	Individual		5 mm CL groups	
	CL (mm)	AW (mm)	CL (mm)	AW (mm)
Bridlington, 1989	65.389	32.226	65.226	32.8892
Bridlington, 1990	62.5036	30.578	62.0748	30.4945
Dale, 1989	74.96085	37.3328	72.3117	36.1349
Selsey, 1989	54.28821	26.91059	53.2714	27.1446
Selsey, 1990	63.78465	32.7842	65.2385	32.4697
Whitby, 1973	-	-	66.989	31.6671
Pembrokeshire, 1973	67.794	33.1855	69.529	33.846
Selsey, 1973	69.395	33.447	66.2495	32.0898

Appendix Table A4ii.36 RAW-CL linear regression intersections

Site	Individual		5 mm CL groups	
	CL (mm)	RAW (mm)	CL (mm)	RAW (mm)
Bridlington, 1989	43.138	48.813	55.123	49.1042
Bridlington, 1990	49.4151	50.3539	45.823	50.239
Dale, 1989	66.591	52.179	63.601	51.377
Selsey, 1989	63.007	49.8718	55.046	49.737
Selsey, 1990	58.082	51.854	56.199	48.981
Whitby, 1973	50.603	46.618	58.1373	47.2987
Pembrokeshire, 1973	61.021	49.6052	59.669	49.4996
Selsey, 1973	61.225	52.703	53.927	46.6559

Appendix Table A4ii.37 RAW-CL log-linear regression intersections

Site	Individual		5 mm CL groups	
	CL (mm)	RAW (mm)	CL (mm)	RAW (mm)
Bridlington, 1989	53.131	49.192	60.34	49.259
Bridlington, 1990	58.0636	50.4353	56.101	50.2056
Dale, 1989	76.524	53.324	69.873	51.546
Selsey, 1989	46.14785	48.78	62.502	51.534
Selsey, 1990	61.116	51.979	59.71	51.1068
Whitby, 1973	52.0035	46.38	58.878	47.261
Pembrokeshire, 1973	64.457	49.553	63.998	49.477
Selsey, 1973	61.585	48.124	62.0061	48.636

Appendix Table A4ii.38 RAW-CL second order polynomial regression intersections

Site	Individual		5 mm CL groups	
	CL (mm)	RAW (mm)	CL (mm)	RAW (mm)
Bridlington, 1989	61.22889	49.2273	63.6789	49.5243
Bridlington, 1990	62.03977	49.1024	54.64151	48.1224
Dale, 1989	73.29529	49.1275	76.5003	50.48567
Selsey, 1989	46.14785	48.78024	51.4035	50.3351
Selsey, 1990	65.2695	50.9642	63.9337	49.8225
Whitby, 1973	-	-	54.9294	47.2166
Pembrokeshire, 1973	64.4152	49.058	69.4529	48.7556
Selsey, 1973	56.78929	47.40058	58.2685	48.3238

Appendix Table A4ii.39 AW-CL third order polynomial regression inflexions

Site	CL (mm) Minimum	AW (mm) Minimum	CL (mm) Maximum	AW (mm) Maximum
Bridlington 1989	-	-	-	-
Bridlington 1990	-	-	-	-
Dale 1989	41.7522	26.65	171.7446	105.531
Selsey 1989	35.2873	25.2651	155.5049	106.285
Selsey 1990	56.475	32.5356	111.52016	64.9669
Whitby 1973	-	-	-	-
Staithes 1980 to 1981	-	-	-	-
Pembrokeshire 1973	56.424	31.857	138.0857	89.717
St. Davids 1980 to 1981	31.6095	18.0832216	168.0543	98.6589041
Selsey, 1973	-	-	-	-

Appendix Table A4ii.40 RAW-CL third order polynomial regression inflexions

Site	CL (mm) Minimum	RAW (mm) Minimum	CL (mm) Maximum	RAW (mm) Maximum
Bridlington 1989	-	-	-	-
Bridlington 1990	-	-	-	-
Dale 1989	20.39004	41.4265	152.6577	77.08511
Selsey 1989	62.1805	50.203	107.0242	59.08554
Selsey 1990	64.7646	52.974	98.487	60.64772
Whitby 1973	-	-	-	-
Staithes 1980 to 1981	14.7763	39.4786	131.8871	72.331
Pembrokeshire 1973	62.318	51.098	123.4989	71.2276
St. Davids 1980 to 1981	2.287559	31.649	137.03672	66.7714632
Selsey, 1973	65.3506	50.477	112.2402	65.183

Appendix Table A4ii.41 AW-CL inflexions

Site	AW CL (mm)
Bridlington, 1989	-
Bridlington, 1990	-
Dale, 1989	-
Selsey, 1989	-
Selsey, 1990	-
Whitby, 1973	76.5
Staithes, 1980 to 1981	-
Pembrokeshire, 1973	-
St. Davids, 1980 to 1981	-
Selsey, 1973	78

Appendix Table A4ii.42 RAW-CL inflexions

Site	RAW CL (mm) First inflexion	Second inflexion	ln(RAW) CL (mm) First inflexion	Second inflexion
Bridlington, 1989	79	87	-	-
Bridlington, 1990	-	-	-	-
Dale, 1989	-	102	-	-
Selsey, 1989	-	-	-	-
Selsey, 1990	-	-	-	-
Whitby, 1973	-	-	-	-
Staithes, 1980 to 1981	81.5	88	82.7	86.6
Pembrokeshire, 1973	-	-	-	-
St. Davids, 1980 to 1981	86.5	99	86	101
Selsey, 1973	-	-	-	-

Appendix Table A4ii.19 Linear regressions statistics for lobster AW-CL relationships

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Bridlington	258	0.993	0.996	2.324	1,256	<0.001	a	-21.042	0.404	-52.136	<0.001
Females 1989							b	0.839	0.004	99.999	<0.001
Bridlington	219	0.854	0.924	1.625	1,217	<0.001	a	0.485	1.153	0.42	0.675
Males 1989							b	0.487	0.014	35.561	<0.001
Bridlington	102	0.953	0.976	2.318	1,100	<0.001	a	-20.569	1.67	-12.318	<0.001
Females 1990							b	0.83	0.018	44.905	<0.001
Bridlington	46	0.978	0.989	1.318	1,44	<0.001	a	3.945	0.92	4.289	<0.001
Males 1990							b	0.444	0.01	44.338	<0.001
Dale	116	0.937	0.968	3.613	1,114	<0.001	a	-25.82	2.336	-11.054	<0.001
Females 1989							b	0.857	0.021	41.311	<0.001
Dale	84	0.971	0.985	1.371	1,82	<0.001	a	5.318	0.971	5.475	<0.001
Males 1989							b	0.44	0.008	51.976	<0.001
Selsey	412	0.952	0.976	4.216	1,410	<0.001	a	-25.699	0.829	-31.015	<0.001
Females 1989							b	0.89	0.01	90.138	<0.001
Selsey	373	0.856	0.925	4.904	1,371	<0.001	a	-2.667	0.929	-2.871	0.004
Males 1989							b	0.528	0.011	46.882	<0.001
Selsey	74	0.854	0.924	2.696	1,72	<0.001	a	-18.897	3.358	-5.627	<0.001
Females 1990							b	0.815	0.04	20.501	<0.001
Selsey	42	0.767	0.876	2.37	1,40	<0.001	a	8.249	2.863	2.881	0.006
Males 1990							b	0.393	0.034	11.474	<0.001
Whitby	84	0.549	0.741	3.587	1,82	<0.001	a	-12.618	5.176	-2.438	0.017
Females 1973							b	0.69	0.069	9.989	<0.001
Whitby	83	0.925	0.962	1.3	1,81	<0.001	a	-1.379	1.216	-1.135	0.26
Males 1973							b	0.491	0.015	31.659	<0.001
Staithes	256	0.968	0.984	2.335	1,254	<0.001	a	-20.321	0.827	-24.578	<0.001
Females 1980 to 1981							b	0.813	0.009	87.328	<0.001
Pembrokeshire	22	0.988	0.994	2.033	1,20	<0.001	a	-22.36	1.938	-11.536	<0.001
Females 1973							b	0.828	0.021	39.818	<0.001
Pembrokeshire	19	0.978	0.989	1.352	1,17	<0.001	a	3.822	1.526	2.504	0.023
Males 1973							b	0.441	0.016	27.483	<0.001
St. Davids	215	0.966	0.983	2.936	1,213	<0.001	a	-24.811	1.146	-21.653	<0.001
Females 1980 to 1981							b	0.852	0.011	78.295	<0.001
Selsey	201	0.893	0.945	2.248	1,199	<0.001	a	-20.07	1.511	-13.281	<0.001
Females 1973							b	0.793	0.019	40.732	<0.001
Selsey	245	0.902	0.95	1.313	1,243	<0.001	a	-1.544	0.854	-1.808	0.072
Males 1973							b	0.506	0.011	47.306	<0.001

Appendix Table A4ii.20 Second order polynomial regressions statistics for lobster AW-CL relationships

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff.	P
Bridlington	258	0.911	0.954	2.298	2,256	<0.001	a	-31.81	<0.001
Females 1989							b	1.049	
							c	-0.00096	
Bridlington	219	0.854	0.924	1.626	2,217	<0.001	a	8.922	<0.001
Males 1989							b	0.2868	
							c	0.001174	
Bridlington	102	0.953	0.97622	2.319	2,100	<0.001	a	-26.79	<0.001
Females 1990							b	0.9579	
							c	-0.00064	
Bridlington	46	0.98	0.99	1.284	2,44	<0.001	a	-5.402	<0.001
Males 1990							b	0.6294	
							c	-0.00086	
Dale	116	0.938	0.969	3.618	2,114	<0.001	a	-37.95	<0.001
Females 1989							b	1.08	
							c	-0.001	
Dale	84	0.972	0.986	1.347	2,82	<0.001	a	-5.547	<0.001
Males 1989							b	0.6384	
							c	-0.00088	
Selsey	412	0.846	0.92	2.58	2,410	<0.001	a	2.022	<0.001
Females 1989							b	0.2413	
							c	0.004	
Selsey	373	0.846	0.92	1.333	2,31	<0.001	a	2.076	<0.001
Males 1989							b	0.4352	
							c	0.000409	
Selsey	74	0.854	0.924	2.713	2,72	<0.001	a	-24.9	<0.001
Females 1990							b	0.9573	
							c	-0.00083	
Selsey	42	0.769	0.877	2.39	2,40	<0.001	a	0.618	<0.001
Males 1990							b	0.5617	
							c	-0.0009	
Whitby	84	0.557	0.746	3.576	2,82	<0.001	a	37.78	<0.001
Females 1973							b	-0.6819	
							c	0.009	
Whitby	83	0.926	0.962	1.298	2,81	<0.001	a	-9.863	<0.001
Males 1973							b	0.7004	
							c	-0.00128	
Staithes	256	0.968	0.984	2.333	2,254	<0.001	a	-24.99	<0.001
Females 1980 to 1981							b	0.9192	
							c	-0.00058	
Pembrokeshire	22	0.988	0.994	2.032	2,20	<0.001	a	-32.09	<0.001
Females 1973							b	1.032	
							c	-0.00102	
Pembrokeshire	19	0.981	0.99	1.298	2,17	<0.001	a	-5.987	<0.001
Males 1973							b	0.649	
							c	-0.00105	
St. Davids	215	0.97	0.985	2.777	2,213	<0.001	a	-49.51	<0.001
Females 1980 to 1981							b	1.32	
							c	-0.002	
Selsey	201	0.901	0.949	2.168	2,199	<0.001	a	8.147	<0.001
Females 1973							b	0.087	
							c	0.004	
Selsey	245	0.903	0.95	1.309	2,243	<0.001	a	-7.595	<0.001
Males 1973							b	0.6518	
							c	-0.00087	

Appendix Table A4ii.21 Third order polynomial regressions statistics for lobster AW-CL relationships

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff.	P
Bridlington 1989	258	0.53	0.728011	2.678	3,255	<0.001	a	-23.33	<0.001
							b	1.794	
							c	-0.012	
							d	2.774E-05	
Bridlington 1990	103	0.453	0.673053	3.249	3,100	<0.001	a	-34.5	<0.001
							b	2.249	
							c	-0.018	
							d	4.884E-05	
Dale 1989	116	0.556	0.74565	3.328	3,113	<0.001	a	44.23	<0.001
							b	-0.2878	
							c	0.008	
							d	-3.082E-05	
Selsey 1989	412	0.326	0.570964	3.511	3,409	<0.001	a	148.8	<0.001
							b	-3.933	
							c	0.05	
							d	-0.000197	
Selsey 1990	74	0.338	0.5813777	3.162	3,71	<0.001	a	246.6	<0.001
							b	-7.568	
							c	0.098	
							d	-0.0004002	
Whitby 1973	84	0.088	0.296648	4.384	3,81	0.061	a	-420.2	0.114
							b	19.59	
							c	-0.2719	
							d	0.001262	
Staithes 1980 to 1981	256	0.746	0.863713	2.525	3,253	<0.001	a	41.18	<0.001
							b	-2.392	
							c	0.009	
							d	-4.091E-05	
Pembrokeshire 1973	22	0.946	0.97263	1.437	3,19	<0.001	a	156.3	<0.001
							b	-4.059	
							c	0.049	
							d	-0.0001758	
St. Davids 1980 to 1981	215	0.773	0.879204	2.538	3,212	<0.001	a	31.68	<0.001
							b	-0.027	
							c	0.006	
							d	-2.871E-05	
Selsey, 1973	201	0.48	0.69282	2.696	3,198	<0.001	a	215.8	<0.001
							b	-6.278	
							c	0.076	
							d	-0.0002853	

Appendix Table A4ii.22 Log-linear regressions statistics for lobster AW-CL relationships (5 mm CL groups)

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Bridlington	258	0.989	0.995	0.049	1,256	<0.001	a	-2.213	0.04	-55.698	<0.001
Females 1989							b	1.379	0.009	99.999	<0.001
Bridlington	219	0.87	0.933	0.036	1,217	<0.001	a	-0.612	0.114	-5.383	<0.001
Males 1989							b	0.978	0.026	38.075	<0.001
Bridlington	102	0.943	0.971	0.045	1,100	<0.001	a	-2.248	0.153	-14.667	<0.001
Females 1990							b	1.385	0.034	40.555	<0.001
Bridlington	46	0.976	0.988	0.028	1,44	<0.001	a	-4	0.099	-4.048	<0.001
Males 1990							b	0.93	0.022	42.19	<0.001
Dale	116	0.931	0.965	0.057	1,114	<0.001	a	-2.381	0.168	-14.134	<0.001
Females 1989							b	1.404	0.036	39.217	<0.001
Dale	84	0.973	0.987	0.024	1,82	<0.001	a	-0.281	0.079	-3.581	<0.001
Males 1989							b	0.908	0.017	54.553	<0.001
Selsey	412	0.954	0.977	0.087	1,410	<0.001	a	-2.997	0.074	-40.542	<0.001
Females 1989							b	1.554	0.017	92.529	<0.001
Selsey	373	0.826	0.909	0.081	1,371	<0.001	a	-1.495	0.126	-11.902	<0.001
Males 1989							b	1.181	0.029	41.086	<0.001
Selsey	74	0.858	0.926	0.054	1,72	<0.001	a	-2.255	0.295	-7.639	<0.001
Females 1990							b	1.389	0.067	20.841	<0.001
Selsey	42	0.759	0.871	0.057	1,40	<0.001	a	0.044	0.326	0.136	0.892
Males 1990							b	0.83	0.074	11.217	<0.001
Whitby	84	0.585	0.765	0.086	1,82	<0.001	a	-1.997	0.526	-3.799	<0.001
Females 1973							b	1.311	0.122	10.749	<0.001
Whitby	83	0.919	0.959	0.036	1,81	<0.001	a	-0.942	0.15	-6.298	<0.001
Males 1973							b	1.044	0.034	30.372	<0.001
Staithes	256	0.969	0.985	0.045	1,254	<0.001	a	-2.43	0.071	-34.406	<0.001
Females 1980 to 1981							b	1.42	0.016	89.618	<0.001
Pembrokeshire	22	0.988	0.994	0.035	1,20	0.988	a	-2.46	0.155	-15.879	<0.001
Females 1973							b	1.422	0.035	41.214	<0.001
Pembrokeshire	19	0.98	0.99	0.028	1,17	<0.001	a	-0.402	0.145	-2.774	0.013
Males 1973							b	0.928	0.032	28.907	<0.001
St. Davids	215	0.966	0.983	0.047	1,213	<0.001	a	-2.498	0.085	-29.218	<0.001
Females 1980 to 1981							b	1.431	0.018	77.457	<0.001
Selsey	201	0.884	0.94	0.054	1,199	<0.001	a	-2.503	0.159	-15.695	<0.001
Females 1973							b	1.43	0.037	38.939	<0.001
Selsey	245	0.897	0.947	0.034	1,243	<0.001	a	-0.929	0.099	-9.351	<0.001
Males 1973							b	1.048	0.023	46.085	<0.001

Appendix Table A4ii.23 Linear regressions statistics for lobster AW-CL relationships (5 mm CL groups)

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Bridlington	12	0.997	0.999	0.983	1,10	<0.001	a	-22.889	1.322	-17.319	<0.001
Females 1989							b	0.855	0.014	61.007	<0.001
Bridlington	10	0.936	0.967	1.89	1,8	<0.001	a	3.569	3.588	0.995	0.349
Males 1989							b	0.45	0.042	10.814	<0.001
Bridlington	13	0.997	0.999	1.115	1,11	<0.001	a	-19.991	1.341	-14.903	<0.001
Females 1990							b	0.814	0.013	62.683	<0.001
Bridlington	11	0.996	0.998	0.88	1,9	<0.001	a	4.513	0.984	4.589	0.001
Males 1990							b	0.436	0.009	46.131	<0.001
Dale	15	0.996	0.998	1.312	1,13	<0.001	a	-22.728	1.748	-13.006	<0.001
Females 1989							b	0.825	0.015	53.973	<0.001
Dale	16	0.965	0.982	2.003	1,14	<0.001	a	6.962	2.487	2.8	0.0014
Males 1989							b	0.419	0.021	19.725	<0.001
Selsey	9	0.993	0.996	0.98	1,7	<0.001	a	-18.136	2.112	-8.585	<0.001
Females 1989							b	0.797	0.025	90.138	<0.001
Selsey	8	0.998	0.999	0.285	1,7	<0.001	a	1.729	0.71	2.435	0.051
Males 1989							b	0.469	0.009	53.434	<0.001
Selsey	9	0.98	0.99	1.684	1,7	<0.001	a	-18.033	3.846	-4.688	0.002
Females 1990							b	0.8	0.043	18.397	<0.001
Selsey	7	0.981	0.991	1.151	1,5	<0.001	a	6.701	2.189	3.062	0.028
Males 1990							b	0.407	0.025	16.131	<0.001
Whitby	10	0.549	0.741	3.587	1,8	<0.001	a	-22.301	4.308	-5.177	<0.001
Females 1973							b	0.836	0.052	16.136	<0.001
Whitby	11	0.997	0.999	0.503	1,9	<0.001	a	0.184	0.695	0.264	0.797
Males 1973							b	0.469	0.008	58.478	<0.001
Staithes	16	0.991	0.995	1.761	1,17	<0.001	a	-18.657	2.116	-8.816	<0.001
Females 1980 to 1981							b	0.794	0.02	38.866	<0.001
Pembrokeshire	11	0.979	0.989	0.296	1,9	<0.001	a	-23.071	4.064	-5.676	<0.001
Females 1973							b	0.833	0.041	20.281	<0.001
Pembrokeshire	11	0.979	0.989	1.516	1,9	<0.001	a	4.503	2.049	2.197	0.056
Males 1973							b	0.43	0.021	20.501	<0.001
St. Davids	19	0.984	0.992	3.098	1,17	<0.001	a	-17.972	2.845	-6.318	<0.001
Females 1980 to 1981							b	0.784	0.024	32.136	<0.001
Selsey	9	0.99	0.995	1.692	1,7	<0.001	a	-22.284	2.756	-8.449	<0.001
Females 1973							b	0.839	0.031	26.708	<0.001
Selsey	10	0.998	0.999	0.503	1,8	<0.001	a	0.431	0.646	0.667	0.524
Males 1973							b	0.478	0.007	64.945	<0.001

Appendix Table A4ii.24 Second order polynomial regressions statistics for lobster AW-CL relationships (5 mm CL groups)

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff.	P
Bridlington	12	0.997	0.9985	1.037	2,10	<0.001	a	-22.86	<0.001
Females 1989							b	0.8545	
							c	3.2E-06	
Bridlington	10	0.936	30.594	2.02	2,8	<0.001	a	2.532	<0.001
Males 1989							b	0.4752	
							c	-0.00015	
Bridlington	13	0.997	0.9985	1.169	2,11	<0.001	a	-20.07	<0.001
Females 1990							b	0.815	
							c	-6.9E-06	
Bridlington	11	0.998	0.999	0.707	2,9	<0.001	a	-4.729	<0.001
Males 1990							b	0.6202	
							c	-0.00085	
Dale	15	0.996	0.998	1.308	2,13	<0.001	a	-31.74	<0.001
Females 1989							b	0.9936	
							c	-0.00076	
Dale	16	0.968	0.984	2.003	2,14	<0.001	a	-4.944	<0.001
Males 1989							b	0.6375	
							c	-0.00096	
Selsey	9	0.996	0.998	0.785	2,7	<0.001	a	8.159	<0.001
Females 1989							b	0.1433	
							c	0.004	
Selsey	8	0.998	0.999	0.294	2,6	<0.001	a	6.17	<0.001
Males 1989							b	0.3559	
							c	0.000709	
Selsey	9	0.983	0.991	1.679	2,7	<0.001	a	-47.32	<0.001
Females 1990							b	1.484	
							c	-0.004	
Selsey	7	0.989	0.994	0.994	2,5	<0.001	a	-8.98	<0.001
Males 1990							b	0.7567	
							c	-0.00186	
Whitby	10	0.978	0.9889	2.524	2,8	<0.001	a	8.224	<0.001
Females 1973							b	0.082	
							c	0.004	
Whitby	11	0.998	0.999	0.511	2,9	<0.001	a	2.763	<0.001
Males 1973							b	0.4087	
							c	0.000335	
Staithes	16	0.991	0.995	1.823	2,14	<0.001	a	-21.1	<0.001
Females 1980 to 1981							b	0.8466	
							c	-0.00027	
Pembrokeshire	11	0.98	0.99	3.017	2,9	<0.001	a	-39.98	<0.001
Females 1973							b	1.18	
							c	-0.0017	
Pembrokeshire	11	0.983	0.991	1.446	2,9	<0.001	a	-5.883	<0.001
Males 1973							b	0.6451	
							c	-0.00106	
St. Davids	19	0.99	0.995	2.508	2,17	<0.001	a	-45.64	<0.001
Females 1980 to 1981							b	1.301	
							c	-0.002	
Selsey	9	0.994	0.997	1.435	2,7	<0.001	a	2.367	<0.001
Females 1973							b	0.2499	
							c	0.003	
Selsey	10	0.998	0.999	0.531	2,8	<0.001	a	-0.905	<0.001
Males 1973							b	0.5093	
							c	-0.00017	

Appendix Table A4ii.25 Log-linear regressions statistics for lobster AW-CL relationships (5 mm CL groups)

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Bridlington	12	0.995	0.998	0.024	1,10	<0.001	a	-2.514	0.141	-17.81	<0.001
Females 1989							b	1.442	0.031	46.018	<0.001
Bridlington	10	0.955	0.977	0.038	1,8	<0.001	a	-0.288	0.308	-0.935	0.377
Males 1989							b	0.905	0.07	13.009	<0.001
Bridlington	13	0.995	0.998	0.024	1,11	<0.001	a	-2.083	0.131	-15.927	<0.001
Females 1990							b	1.344	0.028	47.153	<0.001
Bridlington	11	0.997	0.999	0.015	1,9	<0.001	a	-0.346	0.074	-4.672	0.001
Males 1990							b	0.917	0.016	56.678	<0.001
Dale	15	0.995	0.998	0.021	1,13	<0.001	a	-2.221	0.122	-18.198	<0.001
Females 1989							b	1.368	0.026	52.723	<0.001
Dale	16	0.975	0.988	0.032	1,14	<0.001	a	-0.156	0.176	-0.885	0.391
Males 1989							b	0.878	0.037	23.516	<0.001
Selsey	9	0.995	0.997	0.018	1,7	<0.001	a	-2.23	0.163	-13.663	<0.001
Females 1989							b	1.379	0.037	37.205	<0.001
Selsey	8	0.998	0.999	0.008	1,7	<0.001	a	-0.499	0.082	-6.065	<0.001
Males 1989							b	0.951	0.019	50.626	<0.001
Selsey	9	0.984	0.992	0.03	1,7	<0.001	a	-2.221	0.301	-7.375	<0.001
Females 1990							b	1.379	0.067	20.435	<0.001
Selsey	7	0.98	0.99	0.028	1,5	<0.001	a	-0.125	0.245	-0.513	0.63
Males 1990							b	0.866	0.055	15.676	<0.001
Whitby	10	0.982	0.991	0.044	1,8	<0.001	a	-2.583	0.302	-8.565	<0.001
Females 1973							b	1.452	0.069	21.119	<0.001
Whitby	11	0.998	0.999	0.011	1,9	<0.001	a	-0.714	0.067	-10.606	<0.001
Males 1973							b	0.991	0.015	65.057	<0.001
Staithes	16	0.993	0.996	0.028	1,17	<0.001	a	-2.146	0.144	-14.95	<0.001
Females 1980 to 1981							b	1.355	0.031	43.419	<0.001
Pembrokeshire	11	0.984	0.992	0.044	1,9	<0.001	a	-2.482	0.277	-8.949	<0.001
Females 1973							b	1.426	0.061	23.397	<0.001
Pembrokeshire	11	0.981	0.99	0.032	1,9	<0.001	a	-0.349	0.193	-1.813	0.103
Males 1973							b	0.915	0.042	21.551	<0.001
St. Davids	19	0.985	0.993	0.046	1,17	<0.001	a	-2.023	0.183	-11.037	<0.001
Females 1980 to 1981							b	1.326	0.039	33.982	<0.001
Selsey	9	0.992	0.996	0.031	1,7	<0.001	a	-2.568	0.224	-11.474	<0.001
Females 1973							b	1.446	0.05	28.673	<0.001
Selsey	10	0.998	0.999	0.012	1,8	<0.001	a	-0.684	0.067	-10.186	<0.001
Males 1973							b	0.99	0.015	65.155	<0.001

Appendix Table A4ii.26 Linear regressions statistics for lobster RAW-CL relationships

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Bridlington	258	0.88	0.938	2.856	1,256	<0.001	a	38.503	0.496	77.64	<0.001
Females 1989							b	0.239	0.006	43.48	<0.001
Bridlington	219	0.003	0.057	2.082	1,217	0.402	a	48.166	1.477	32.613	<0.001
Males 1989							b	0.015	0.018	0.84	0.402
Bridlington	102	0.528	0.727	2.74	1,100	<0.001	a	38.939	1.974	19.73	<0.001
Females 1990							b	0.231	0.022	10.574	<0.001
Bridlington	46	0.196	0.442	1.379	1,44	0.002	a	52.034	0.963	54.059	<0.001
Males 1990							b	-0.034	0.01	-3.271	0.002
Dale	116	0.528	0.727	3.401	1,114	<0.001	a	37.462	2.198	17.041	<0.001
Females 1989							b	0.221	0.02	11.298	<0.001
Dale	84	0.089	0.298	4.964	1,82	0.006	a	57.639	3.326	17.33	<0.001
Males 1989							b	-0.082	0.029	-2.826	0.006
Selsey	412	0.708	0.842	5.337	1,410	<0.001	a	24.984	1.049	23.819	<0.001
Females 1989							b	0.395	0.013	31.564	<0.001
Selsey	356	0.035	0.186	2.113	1,354	<0.001	a	52.014	0.759	68.493	<0.001
Males 1989							b	-0.034	0.009	-3.568	<0.001
Selsey	74	0.316	0.562	3.17	1,72	<0.001	a	36.172	3.95	9.158	<0.001
Females 1990							b	0.27	0.047	5.764	<0.001
Selsey	42	0.111	0.333	2.984	1,40	0.031	a	57.43	3.606	15.925	<0.001
Males 1990							b	-0.096	0.043	-2.233	0.031
Whitby	84	0.066	0.256	4.832	1,82	0.019	a	35.334	6.972	5.068	<0.001
Females 1973							b	0.223	0.093	2.399	0.019
Whitby	83	0.017	0.13	1.698	1,81	0.241	a	45.404	1.588	25.597	<0.001
Males 1973							b	0.024	0.02	1.182	0.241
Staithes	256	0.708	0.841	2.698	1,254	<0.001	a	33.981	0.955	35.576	<0.001
Females 1980 to 1981							b	0.267	0.011	24.813	<0.001
Pembrokeshire	22	0.844	0.919	2.323	1,20	<0.001	a	34.533	2.215	15.591	<0.001
Females 1973							b	0.247	0.024	10.406	<0.001
Pembrokeshire	19	0.25	0.5	1.341	1,17	0.029	a	51.924	1.514	34.286	<0.001
Males 1973							b	-0.038	0.016	-2.377	0.029
St. Davids	215	0.672	0.82	3.034	1,213	<0.001	a	36.144	1.184	30.519	<0.001
Females 1980 to 1981							b	0.235	0.011	20.909	<0.001
Selsey	201	0.442	0.665	2.779	1,199	<0.001	a	29.71	1.868	15.903	<0.001
Females 1973							b	0.302	0.024	12.551	<0.001
Selsey	245	0.016	0.125	1.654	1,243	0.05	a	46.547	1.075	43.305	<0.001
Males 1973							b	0.027	0.013	1.969	0.05

Appendix Table A4ii.27 Second order polynomial regressions statistics for lobster RAW-CL relationships

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff.	P
Bridlington	258	0.53	0.728	2.674	2,256	<0.001	a	-1.904	<0.001
Females 1989							b	1.08	
							c	-0.004	
Bridlington	219	0.024	0.1549	2.065	2,217	0.07	a	72.74	0.102
Males 1989							b	-5.677	
							c	0.003	
Bridlington	102	0.585	0.7649	2.582	2,100	<0.001	a	12.01	<0.001
Females 1990							b	0.7848	
							c	-0.003	
Bridlington	46	0.221	0.47	1.373	2,44	0.005	a	45.58	0.018
Males 1990							b	0.094	
							c	-0.0006	
Dale	116	0.555	0.745	3.319	2,114	<0.001	a	3.786	<0.001
Females 1989							b	0.8385	
							c	-0.003	
Dale	84	0.107	0.327	4.675	2,82	0.01	a	33.19	0.031
Males 1989							b	0.3633	
							c	-0.00199	
Selsey	412	0.325	0.57	3.509	2,410	<0.001	a	46.96	<0.001
Females 1989							b	0.099	
							c	0.003	
Selsey	373	0.003	0.0548	1.451	2,31	0.561	a	44.71	0.447
Males 1989							b	0.12881	
							c	-0.00088	
Selsey	74	0.325	0.5701	3.171	2,72	<0.001	a	9.98	<0.001
Females 1990							b	0.889	
							c	-0.004	
Selsey	42	0.111	0.333	3.022	2,40	0.1	a	55.27	<0.001
Males 1990							b	-0.049	
							c	-0.00026	
Whitby	84	0.073	0.27	4.843	2,82	0.047	a	79.02	0.079
Females 1973							b	-0.9659	
							c	0.008	
Whitby	83	0.029	0.17	1.698	2,81	0.309	a	35.37	0.278
Males 1973							b	0.2721	
							c	-0.00151	
Staithes	256	0.743	0.862	2.535	2,254	<0.001	a	9.65	<0.001
Females 1980 to 1981							b	0.8198	
							c	-0.003	
Pembrokeshire	22	0.907	0.952	1.841	2,20	<0.001	a	3.294	<0.001
Females 1973							b	0.9037	
							c	-0.003	
Pembrokeshire	19	0.282	0.531	1.352	2,17	0.7	a	46.33	0.095
Males 1973							b	0.081	
							c	-0.0006	
St. Davids	215	0.769	0.877	2.554	2,213	<0.001	a	-5.692	<0.001
Females 1980 to 1981							b	1.027	
							c	-0.004	
Selsey	201	0.449	0.67	2.769	2,199	<0.001	a	43.79	<0.001
Females 1973							b	-0.05	
							c	0.002	
Selsey	245	0.024	0.1549	1.65	2,243	0.052	a	39.79	0.085
Males 1973							b	-1891	
							c	-0.00097	

Appendix Table A4ii.28 Third order polynomial regressions statistics for lobster RAW-CL relationships

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff.	P
Bridlington 1989	258	0.911	0.95446	2.303	3,255	<0.001	a	-22.34	<0.001
							b	0.7335	
							c	0.002	
							d	-1.226E-05	
Bridlington 1990	103	0.923	0.96073	3.001	3,100	<0.001	a	-55.16	<0.001
							b	1.868	
							c	-0.01	
							d	3.131E-05	
Dale 1989	116	0.939	0.96902	3.608	3,113	<0.001	a	56.29	<0.001
							b	-1.545	
							c	0.023	
							d	-7.182E-05	
Selsey 1989	412	0.846	0.919783	2.583	3,409	<0.001	a	43.56	<0.001
							b	-1.323	
							c	0.023	
							d	-8.036E-05	
Selsey 1990	74	0.858	0.926283	2.698	3,71	<0.001	a	205	<0.001
							b	-7.348	
							c	0.098	
							d	-0.0003889	
Whitby 1973	84	0.565	0.75166482	3.567	3,81	<0.001	a	-340.9	<0.001
							b	14.91	
							c	-0.2031	
							d	0.0009574	
Staithes 1980 to 1981	256	0.969	0.984378	2.309	3,253	<0.001	a	16.73	<0.001
							b	-0.4818	
							c	0.015	
							d	-5.412E-05	
Pembrokeshire 1973	22	0.994	0.996995	1.465	3,19	<0.001	a	152.9	<0.001
							b	-4.967	
							c	0.062	
							d	-0.0002125	
St. Davids 1980 to 1981	215	0.972	0.985901	2.682	3,212	<0.001	a	33.06	<0.001
							b	-1.011	
							c	0.019	
							d	-6.344E-05	
Selsey, 1973	201	0.906	0.9518403	2.118	3,198	<0.001	a	134.4	<0.001
							b	-4.483	
							c	0.059	
							d	-0.0002094	

Appendix Table A4ii.29 Log-linear regressions statistics for lobster RAW-CL relationships

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Bridlington	258	0.875	0.935	0.049	1,256	<0.001	a	2.398	0.04	60.586	<0.001
Females 1989							b	0.377	0.009	42.328	<0.001
Bridlington	219	0.000587	0.024	0.039	1,217	0.721	a	3.856	0.122	31.567	<0.001
Males 1989							b	0.01	0.028	0.357	0.721
Bridlington	102	0.56	0.748	0.045	1,100	<0.001	a	2.357	0.153	15.375	<0.001
Females 1990							b	0.385	0.034	11.282	<0.001
Bridlington	46	0.188	0.434	0.028	1,44	0.003	a	4.205	0.099	42.586	<0.001
Males 1990							b	-0.07	0.022	-3.192	0.003
Dale	116	0.528	0.726	0.057	1,114	<0.001	a	2.224	0.168	13.207	<0.001
Females 1989							b	0.404	0.036	11.287	<0.001
Dale	84	0.043	0.206	0.229	1,82	0.059	a	5.269	0.736	7.16	<0.001
Males 1989							b	-0.298	0.156	-1.911	0.059
Selsey	412	0.702	0.838	0.097	1,410	<0.001	a	1.49	0.082	18.143	<0.001
Females 1989							b	0.58	0.019	31.102	<0.001
Selsey	356	0.033	0.182	0.043	1,354	<0.001	a	4.128	0.066	62.308	<0.001
Males 1989							b	-0.053	0.015	-3.478	<0.001
Selsey	74	0.321	0.567	0.312	1,72	<0.001	a	2.351	0.295	7.964	<0.001
Females 1990							b	0.389	0.067	5.836	<0.001
Selsey	42	0.117	0.342	0.057	1,40	0.027	a	4.65	0.326	14.25	<0.001
Males 1990							b	-0.17	0.074	-2.301	0.027
Whitby	84	0.073	0.271	0.086	1,82	0.013	a	2.608	0.526	4.96	<0.001
Females 1973							b	0.311	0.122	2.548	0.013
Whitby	83	0.02	0.141	0.036	1,81	0.203	a	3.663	0.15	24.494	<0.001
Males 1973							b	0.044	0.034	1.284	0.203
Staithes	256	0.734	0.857	0.045	1,254	<0.001	a	2.175	0.071	30.803	<0.001
Females 1980 to 1981							b	0.42	0.016	26.49	<0.001
Pembrokeshire	22	0.882	0.939	0.035	1,20	<0.001	a	2.145	0.155	13.841	<0.001
Females 1973							b	0.422	0.035	12.235	<0.001
Pembrokeshire	19	0.227	0.477	0.028	1,17	0.039	a	4.203	0.145	28.977	<0.001
Males 1973							b	-0.072	0.032	-2.235	0.039
St. Davids	215	0.718	0.848	0.047	1,213	<0.001	a	2.107	0.085	24.645	<0.001
Females 1980 to 1981							b	0.431	0.018	23.317	<0.001
Selsey	201	0.408	0.639	0.054	1,199	<0.001	a	2.102	0.159	13.186	<0.001
Females 1973							b	0.43	0.037	11.706	<0.001
Selsey	245	0.018	0.133	0.034	1,243	0.037	a	3.676	0.099	36.997	<0.001
Males 1973							b	0.048	0.023	2.095	0.037

Appendix Table A4ii.30 Linear regressions statistics for lobster RAW-CL relationships (5 mm CL groups)

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Bridlington	12	0.916	0.957	1.921	1,10	<0.001	a	33.339	2.581	12.918	<0.001
Females 1989							b	0.286	0.027	10.437	<0.001
Bridlington	10	0.017	0.129	3.265	1,8	0.722	a	47.671	6.198	7.692	<0.001
Males 1989							b	0.026	0.072	0.368	0.722
Bridlington	13	0.873	0.934	1.901	1,11	<0.001	a	41.441	2.288	18.112	<0.001
Females 1990							b	0.192	0.022	8.681	<0.001
Bridlington	11	0.658	0.811	0.769	1,9	0.002	a	51.797	0.859	60.279	<0.001
Males 1990							b	-0.034	0.008	-4.164	0.002
Dale	15	0.904	0.951	1.609	1,13	<0.001	a	38.148	2.143	17.804	<0.001
Females 1989							b	0.208	0.019	11.081	<0.001
Dale	16	0.455	0.674	1.731	1,14	0.004	a	55.384	2.149	25.771	<0.001
Males 1989							b	-0.063	0.018	-3.417	0.004
Selsey	9	0.949	0.974	0.914	1,7	<0.001	a	34.875	1.972	17.688	<0.001
Females 1989							b	0.27	0.024	11.433	<0.001
Selsey	8	0.192	0.438	0.355	1,7	0.278	a	50.453	0.886	56.935	<0.001
Males 1989							b	-0.013	0.011	-1.194	0.278
Selsey	9	0.78	0.883	1.955	1,7	0.002	a	36.941	4.464	8.276	<0.001
Females 1990							b	0.251	0.05	4.975	0.002
Selsey	7	0.581	0.762	1.3	1,5	0.046	a	55.262	2.473	22.349	<0.001
Males 1990							b	-0.075	0.029	-2.634	0.046
Whitby	10	0.918	0.958	1.898	1,8	<0.001	a	27.532	2.99	9.208	<0.001
Females 1973							b	0.34	0.036	9.448	<0.001
Whitby	11	0.059	0.243	0.397	1,9	0.472	a	47.008	0.55	85.523	<0.001
Males 1973							b	0.005	0.006	0.751	0.472
Staithes	16	0.869	0.932	1.916	1,17	<0.001	a	38.342	2.303	16.649	<0.001
Females 1980 to 1981							b	0.214	0.022	9.626	<0.001
Pembrokeshire	11	0.832	0.912	2.651	1,9	<0.001	a	34.821	3.643	9.559	<0.001
Females 1973							b	0.246	0.037	6.686	<0.001
Pembrokeshire	11	0.378	0.614	1.092	1,9	0.044	a	51.588	1.477	34.929	<0.001
Males 1973							b	-0.035	0.015	-2.336	0.044
St. Davids	19	0.725	0.851	3.199	1,17	<0.001	a	42.157	2.937	14.352	<0.001
Females 1980 to 1981							b	0.169	0.025	6.695	<0.001
Selsey	9	0.953	0.976	1.299	1,7	<0.001	a	31.071	2.116	14.684	<0.001
Females 1973							b	0.289	0.024	11.978	<0.001
Selsey	10	0.085	0.292	0.316	1,8	0.413	a	48.813	0.405	120.431	<0.001
Males 1973							b	-0.004	0.005	-0.864	0.413

Appendix Table A4ii.31 Second order polynomial regressions statistics for lobster RAW-CL relationships (5 mm CL groups)

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff.	P
Bridlington	12	0.982	0.991	0.938	2,10	<0.001	a	-1.819	<0.001
Females 1989							b	1.061	
							c	-0.004	
Bridlington	10	0.019	0.1378	3.487	2,8	0.936	a	52.84	<0.001
Males 1989							b	-0.099	
							c	0.000737	
Bridlington	13	0.922	0.96021	1.562	2,11	<0.001	a	22.37	<0.001
Females 1990							b	0.5661	
							c	-0.00174	
Bridlington	11	0.865	0.93	0.513	2,9	<0.001	a	42.19	<0.001
Males 1990							b	0.1572	
							c	-0.00089	
Dale	15	0.973	0.986	0.897	2,13	<0.001	a	5.756	<0.001
Females 1989							b	0.8142	
							c	-0.003	
Dale	16	0.456	0.675	1.795	2,14	0.019	a	53.6	0.036
Males 1989							b	-0.03	
							c	-0.00014	
Selsey	9	0.956	0.9778	0.921	2,7	<0.001	a	48.14	<0.001
Females 1989							b	-0.06	
							c	0.001998	
Selsey	8	0.265	0.5148	0.371	2,6	0.463	a	55.52	<0.001
Males 1989							b	-0.1424	
							c	0.000808	
Selsey	9	0.855	0.9247	1.713	2,7	0.003	a	-14.66	0.006
Females 1990							b	1.457	
							c	-0.007	
Selsey	7	0.658	0.8112	1.313	2,5	0.117	a	43.31	0.121
Males 1990							b	0.1911	
							c	-0.00142	
Whitby	10	0.925	0.962	1.943	2,8	<0.001	a	39.63	<0.001
Females 1973							b	0.041	
							c	0.001768	
Whitby	11	0.071	0.2665	0.419	2,9	0.746	a	46.2	0.596
Males 1973							b	0.024	
							c	-0.0001	
Staithes	16	0.914	0.956	1.61	2,14	<0.001	a	16.48	<0.001
Females 1980 to 1981							b	0.6815	
							c	-0.002	
Pembrokeshire	11	0.91	0.954	2.061	2,9	<0.001	a	-2.861	<0.001
Females 1973							b	1.021	
							c	-0.004	
Pembrokeshire	11	0.474	0.6885	1.065	2,9	0.077	a	44.84	0.094
Males 1973							b	0.1043	
							c	-0.00069	
St. Davids	19	0.915	0.957	1.834	2,17	<0.001	a	3.81	<0.001
Females 1980 to 1981							b	0.8851	
							c	0.003	
Selsey	9	0.954	0.977	1.389	2,7	<0.001	a	35.62	<0.001
Females 1973							b	0.1845	
							c	0.000575	
Selsey	10	0.498	0.7057	0.25	2,8	0.09	a	45.33	0.105
Males 1973							b	0.077	
							c	-0.00044	

Appendix Table A4ii.32 Log-linear regressions statistics for lobster RAW-CL relationships (5 mm CL groups)

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Bridlington	12	0.935	0.967	0.029	1,10	<0.001	a	2.007	0.173	11.628	<0.001
Females 1989							b	0.461	0.038	12.037	<0.001
Bridlington	10	0.009	0.096	0.062	1,8	0.792	a	3.77	0.507	7.437	<0.001
Males 1989							b	0.031	0.114	0.273	0.792
Bridlington	13	0.908	0.953	0.027	1,11	<0.001	a	2.563	0.148	17.347	<0.001
Females 1990							b	0.336	0.032	10.446	<0.001
Bridlington	11	0.568	0.754	0.018	1,9	0.007	a	4.194	0.092	45.674	<0.001
Males 1990							b	-0.069	0.02	-3.443	0.007
Dale	15	0.938	0.968	0.022	1,13	<0.001	a	2.316	0.129	18.014	<0.001
Females 1989							b	0.383	0.027	13.999	<0.001
Dale	16	0.424	0.651	0.038	1,14	0.006	a	4.554	0.212	21.481	<0.001
Males 1989							b	-0.144	0.045	-3.209	0.006
Selsey	9	0.937	0.968	0.018	1,7	<0.001	a	2.375	0.163	14.551	<0.001
Females 1989							b	0.379	0.037	10.229	<0.001
Selsey	8	0.211	0.46	0.007	1,7	0.252	a	3.996	0.076	52.834	<0.001
Males 1989							b	-0.022	0.017	-1.268	0.252
Selsey	9	0.818	0.905	0.03	1,7	<0.001	a	2.384	0.301	7.918	<0.001
Females 1990							b	0.379	0.067	5.614	<0.001
Selsey	7	0.543	0.737	0.028	1,5	0.059	a	4.486	0.245	18.288	<0.001
Males 1990							b	-0.135	0.055	-2.437	0.059
Whitby	10	0.911	0.954	0.035	1,8	<0.001	a	1.875	0.236	7.951	<0.001
Females 1973							b	0.486	0.054	9.04	<0.001
Whitby	11	0.063	0.251	0.008	1,9	0.456	a	3.819	0.051	74.812	<0.001
Males 1973							b	0.009	0.012	0.779	0.456
Staithes	16	0.903	0.95	0.028	1,17	<0.001	a	2.458	0.144	17.117	<0.001
Females 1980 to 1981							b	0.356	0.031	11.389	<0.001
Pembrokeshire	11	0.882	0.939	0.038	1,9	<0.001	a	2.134	0.236	9.03	<0.001
Females 1973							b	0.425	0.052	8.184	<0.001
Pembrokeshire	11	0.327	0.572	0.024	1,9	0.066	a	4.176	0.144	29.012	<0.001
Males 1973							b	-0.066	0.032	-2.093	0.066
St. Davids	19	0.804	0.897	0.046	1,17	<0.001	a	2.581	0.183	14.081	<0.001
Females 1980 to 1981							b	0.326	0.039	8.348	<0.001
Selsey	9	0.939	0.969	0.026	1,7	<0.001	a	2.056	0.19	10.812	<0.001
Females 1973							b	0.443	0.043	10.337	<0.001
Selsey	10	0.048	0.22	0.007	1,8	0.542	a	3.905	0.038	103.522	<0.001
Males 1973							b	-0.005	0.009	-0.637	0.542

Appendix Table A4ii.43 ANCOVA results for female AW with CL between-years (1989 and 1990) at Bridlington

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	25734.606	1	25734.606	1000	0
Year effect	11.422119	1	11.422119	1.681	0.1957
Residual	2439.643	359	6.795663		
Total	28185.671	361			

Appendix Table A4ii.44 ANCOVA results for female RAW with CL between-years (1989 and 1990) at Bridlington

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	2451.2584	1	2451.2584	254.79	0
Year effect	13.57544	1	13.57544	1.411	0.2357
Residual	3453.8714	359	9.6208116		
Total	5918.7052	361			

Appendix Table A4ii.45 ANCOVA results for male AW with CL between-years (1989 and 1990) at Bridlington

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	6976.4241	1	6976.4241	1000	0
Year effect	1.8543585	1	1.8543585	0.732	0.4021
Residual	663.69894	262	2.5332021		
Total	7641.9774	264			

Appendix Table A4ii.46 ANCOVA results for male RAW with CL between-years (1989 and 1990) at Bridlington

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	7.1950696	1	7.1950696	1.807	0.18
Year effect	5.0575233	1	5.0575233	1.27	0.2607
Residual	1043.0001	262	3.9809164		
Total	1055.2527	264			

Appendix Table A4ii.47 ANCOVA results for AW with CL between-sexes at Bridlington, 1989

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	16237.948	1	16237.948	1000	0
Sex effect	7617.2891	1	7617.2891	1000	0
Residual	3138.2891	474	6.6204301		
Total	26993.321	476			

Appendix Table A4ii.48 ANCOVA results for RAW with CL between-sexes at Bridlington, 1989

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	1244.1601	1	1244.1601	161.457	0
Sex effect	9915.3197	1	9915.3197	1000	0
Residual	3652.555	474	7.7058123		
Total	14812.035	476			

Appendix Table A4ii.49 ANCOVA results for AW with CL between-sexes at Bridlington, 1990

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	12916.546	1	12916.546	870.862	0
Sex effect	3142.5571	1	3142.5571	211.878	0
Residual	2180.2903	147	14.831907		
Total	18239.393	149			

Appendix Table A4ii.50 ANCOVA results for RAW with CL between-sexes at Bridlington, 1990

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	179.41643	1	179.41643	14.042	0.0003
Sex effect	3580.8314	1	3580.8314	280.259	0
Residual	1878.1965	147	12.776847		
Total	5638.4443	149			

Appendix Table A4ii.51 ANCOVA results for AW with CL between-years (1989 and 1990) and sexes at Bridlington

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	31447.43	1	31447.43	1000	0
Effects	10844.03	2	5422.013	619.504	0
Year	1.572	1	1.572	0.18	0.6764
Sex	10697.8	1	10697.8	1000	0
Site and year interactions	92.6826	1	92.6826	10.59	0.0012
Residual	5443.859	622	8.752184		
Total	47827.99	626			

Appendix Table A4ii.52 ANCOVA results for RAW with CL between-years (1989 and 1990) and sexes at Bridlington

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	1430.025	1	1430.025	154.861	0
Effects	13638.37	2	6819.186	738.468	0
Year	6.948	1	6.948	0.752	0.3953
Sex	13486.12	1	13486.12	1000	0
Site and year interactions	53.85953	1	53.85953	5.833	0.016
Residual	5743.694	622	9.234234		
Total	20865.95	626			

Appendix Table A4ii.53 ANCOVA results for female AW with CL between-years (1989 and 1990) at Selsey

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	18512.277	1	18512.277	1000	0
Year effect	24.599974	1	24.599974	3.626	0.0575
Residual	3277.0165	483	6.7847132		
Total	21813.893	485			

Appendix Table A4ii.54 ANCOVA results for female RAW with CL between-years (1989 and 1990) at Selsey

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	2883.4642	1	2883.4642	240.379	0
Year effect	45.976061	1	45.976061	3.833	0.0508
Residual	5793.8107	483	11.995467		
Total	8723.251	485			

Appendix Table A4ii.55 ANCOVA results for male AW with CL between-years (1989 and 1990) at Selsey

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	4132.6988	1	4132.6988	1000	0
Year effect	0.0044622	1	0.0044622	0.002	0.9655
Residual	917.85813	396	2.3178236		
Total	5050.5614	398			

Appendix Table A4ii.56 ANCOVA results for male RAW with CL between-years (1989 and 1990) at Selsey

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	7.8980449	1	7.8980449	2.287	0.1313
Year effect	0.7691234	1	0.7691234	0.223	0.6423
Residual	1367.5956	396	3.4535242		
Total	1376.2628	398			

Appendix Table A4ii.57 ANCOVA results for AW with CL between-sexes at Selsey, 1989

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	21235.663	1	21235.663	1000	0
Sex effect	6786.4871	1	6786.4871	1000	0
Residual	4376.0811	766	5.7128996		
Total	32398.231	768			

Appendix Table A4ii.58 ANCOVA results for RAW with CL between-sexes at Selsey, 1989

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	2973.5825	1	2973.5825	328.362	0
Sex effect	9743.3171	1	9743.3171	1000	0
Residual	6936.7516	766	9.0558115		
Total	19653.651	768			

Appendix Table A4ii.59 ANCOVA results for AW with CL between-sexes at Selsey, 1990

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	3733.2581	1	3733.2581	362.409	0
Sex effect	1725.4873	1	1725.4873	167.503	0
Residual	1164.0392	113	10.301231		
Total	6622.7845	115			

Appendix Table A4ii.60 ANCOVA results for RAW with CL between-sexes at Selsey, 1990

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	6.26031	1	6.26031	0.692	0.416
Sex effect	29.802687	1	29.802687	3.295	0.0722
Residual	1022.1296	113	9.0453949		
Total	1058.1943	115			

Appendix Table A4ii.61 ANCOVA results for AW with CL between-years (1989 and 1990) and sexes at Selsey

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	25853.81	1	25853.81	1000	0
Effects	8575.839	2	4287.92	669.709	0
Year	8509.71	1	8509.71	1000	0
Sex	14.3366	1	14.3366	2.239	0.1349
Site and year interactions	80.48853	1	80.48853	12.571	0.0004
Residual	5634.341	880	6.40266		
Total	40144.48	884			

Appendix Table A4ii.62 ANCOVA results for RAW with CL between-years (1989 and 1990) and sexes at Selsey

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	3141.326	1	3141.326	327.167	0
Effects	12190.56	2	6095.281	634.82	0
Year	12071.55	1	12071.55	1000	
Sex	32.86	1	32.86	3.422	0.0647
Site and year interactions	83.27226	1	83.27226	8.673	0.0033
Residual	8449.405	880	9.601596		
Total	23864.57	884			

Appendix Table A4ii.63 ANCOVA results for AW with CL between-sexes at Dale, 1989

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	23116.258	1	23116.258	1000	0
Sex effect	12000.573	1	12000.573	578.962	0
Residual	4083.3637	197	20.727734		
Total	39200.195	199			

Appendix Table A4ii.64 ANCOVA results for RAW with CL between-sexes at Dale, 1989

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	191.0614	1	191.0614	8.532	0.0039
Sex effect	9306.4024	1	9306.4024	415.595	0
Residual	4411.4083	197	22.392935		
Total	13908.872	199			

Appendix Table A4ii.65 ANCOVA results for AW with CL between-sexes at Whitby, 1973

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	2496.5134	1	2496.5134	322.563	0
Sex effect	587.45809	1	587.45809	75.903	0
Residual	1269.298	164	7.739622		
Total	4353.2695	166			

Appendix Table A4ii.66 ANCOVA results for RAW with CL between-sexes at Whitby, 1973

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	1.9442067	1	1.9442067	0.143	0.7096
Sex effect	999.95869	1	999.95869	73.701	0
Residual	2225.1202	164	13.567806		
Total	3227.0231	166			

Appendix Table A4ii.67 ANCOVA results for AW with CL between-sexes at Pembrokeshire, 1973

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	7071.8498	1	7071.8498	372.341	0
Sex effect	902.22308	1	902.22308	47.503	0
Residual	721.73195	38	18.992946		
Total	8695.8049	40			

Appendix Table A4ii.68 ANCOVA results for RAW with CL between-sexes at Pembrokeshire, 1973

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	217.04052	1	217.04052	17.57	0.0002
Sex effect	800.40601	1	800.40601	64.794	0
Residual	469.41675	38	12.353072		
Total	1486.8633	40			

Appendix Table A4ii.69 ANCOVA results for AW with CL between-sexes at Selsey, 1973

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	10704.856	1	10704.856	1000	0
Sex effect	1649.4018	1	1649.4018	364.175	0
Residual	2006.4143	443	4.529152		
Total	14360.673	445			

Appendix Table A4ii.70 ANCOVA results for RAW with CL between-sexes at Selsey, 1973

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	392.6536	1	392.88126	63.549	0
Sex effect	2412.6536	1	2412.6536	390.247	0
Residual	2738.7957	443	6.1823831		
Total	554.3306	445			

Appendix Table A4ii.71 ANCOVA results for female AW with CL between-sites at Bridlington 1989, 1990, Whitby 1973 and Staithes 1980

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	78054.479	1	78054.479	1000	0
Site effect	644.91808	3	214.97269	30.321	0
Residual	4941.618	697	7.0898394		
Total	83641.015	701			

Appendix Table A4ii.72 ANCOVA results for female RAW with CL between-sites at Bridlington 1989, 1990, Whitby 1973 and Staithes 1980

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	8936.9452	1	8936.9452	862.577	0
Site effect	1336.2116	3	445.40385	42.99	0
Residual	7221.4464	697	10.360755		
Total	17494.603	701			

Appendix Table A4ii.73 ANCOVA results for male AW with CL between-sites at Bridlington 1989, 1990, Whitby 1973 and Staithes 1980

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	8076.7442	1	8076.7442	1000	0
Site effect	25.783732	2	25.783732	13.926	0.0003
Residual	185.14201	345	1.8514201		
Total	8287.6699	348			

Appendix Table A4ii.74 ANCOVA results for male RAW with CL between-sites at Bridlington 1989, 1990, Whitby 1973 and Staithes 1980

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	149.13044	1	149.13044	8.07	0.0055
Site effect	26.201368	2	26.201368	1.418	0.2366
Residual	1847.8528	345	18.478525		
Total	2023.1843	348			

Appendix Table A4ii.75 ANCOVA results for female AW with CL between-sites at Dale 1989, Pembrokeshire 1973 and St. Davids 1980

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	87880.27	1	87880.27	1000	0
Site effect	16.002108	2	8.0010539	0.818	0.4421
Residual	3413.2317	349	9.7800337		
Total	91309.504	352			

Appendix Table A4ii.76 ANCOVA results for female RAW with CL between-sites at Dale 1989, Pembrokeshire 1973 and St. Davids 1980

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	6581.4334	1	6581.4334	676.756	0
Site effect	10.312556	2	5.156278	0.53	0.589
Residual	3394.0159	349	9.7249738		
Total	9985.7618	352			

Appendix Table A4ii.77 ANCOVA results for male AW with CL between-sites at Dale 1989, Pembrokeshire 1973 and St. Davids 1980

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	10018.539	1	10018.539	1000	0
Site effect	160.03846	2	80.019231	34.199	0
Residual	804.90213	344	2.3398318		
Total	10983.48	347			

Appendix Table A4ii.78 ANCOVA results for male RAW with CL between-sites at Dale 1989, Pembrokeshire 1973 and St. Davids 1980

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	8.0728812	1	8.0728812	2.163	0.1423
Site effect	268.04088	2	134.02044	35.905	0
Residual	1284.0426	344	3.732682		
Total	1560.1564	347			

Appendix Table A4ii.79 ANCOVA results for female AW with CL between-sites at Selsey 1989, 1990 and Selsey 1973

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	31199.387	1	31199.387	1000	0
Site effect	686.6337	2	343.31685	54.473	0
Residual	4304.6457	638	6.302556		
Total	36190.667	686			

Appendix Table A4ii.80 ANCOVA results for female RAW with CL between-sites at Selsey 1989, 1990 and Selsey 1973

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	5627.1912	1	5627.1912	523.836	0
Site effect	1117.3698	2	558.6849	52.008	0
Residual	7336.9783	683	10.742282		
Total	14081.539	686			

Appendix Table A4ii.81 ANCOVA results for male AW with CL between-sites at Selsey 1989, 1990 and Selsey 1973

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	7997.7069	1	7997.7069	1000	0
Site effect	48.081707	2	24.040854	11.429	0
Residual	1346.2409	640	2.1035015		
Total	9392.0295	643			

Appendix Table A4ii.82 ANCOVA results for male RAW with CL between-sites at Selsey 1989, 1990 and Selsey 1973

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	0.0350949	1	0.0350949	0.011	0.9178
Site effect	81.11776	2	40.55888	12.654	0
Residual	2051.3252	640	3.2051956		
Total	2132.478	643			

Appendix Table A4ii.83 ANCOVA results for female AW with CL between-sites and years, Bridlington 1989, 1990, Dale 1989, Selsey 1989 and 1990

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	114119.59	1	114119.59	1000	0
Effects	417.20642	3	139.06881	18.477	0
Site	379.89998	2	189.94999	25.237	0
Year	0.3488	1	0.3488	0.046	0.8319
Site and year interactions	38.199616	1	38.199616	5.075	0.0245
Residual	7210.5712	958	7.5266923		
Total	121785.56	963			

Appendix Table A4ii.84 ANCOVA results for female RAW with CL between-sites and years, Bridlington 1989, 1990, Dale 1989, Selsey 1989 and 1990

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	8063.8402	1	8063.8402	720.166	0
Effects	755.91301	3	251.971	22.503	0
Site	652.60361	2	326.30181	29.141	0
Year	7.16439	1	7.16439	0.64	0.4325
Site and year interactions	76.703708	1	76.703708	6.85	0.009
Residual	10726.917	958	11.197199		
Total	19623.374	963			

Appendix Table A4ii.85 ANCOVA results for male AW with CL between-sites and years, Bridlington 1989, 1990, Dale 1989, Selsey 1989 and 1990

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	33770.315	1	33770.315	1000	0
Effects	10.019155	3	3.3397184	1.417	0.2364
Site	8.666335	2	4.3331677	1.839	0.1597
Year	0.293485	1	0.2934846	0.125	0.728
Site and year interactions	1.2596012	1	1.2596012	0.535	0.4727
Residual	1748.4528	742	2.3564054		
Total	35530.047	747			

Appendix Table A4ii.86 ANCOVA results for male RAW with CL between-sites and years, Bridlington 1989, 1990, Dale 1989, Selsey 1989 and 1990

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	189.42901	1	189.42901	32.739	0
Effects	4.4490334	3	1.4830111	0.256	0.8569
Site	4.4244751	2	2.2122376	0.382	0.6824
Year	0.0018232	1	0.0018232	0	0.986
Site and year interactions	3.3832377	1	3.3832377	0.585	0.4529
Residual	4293.1741	742	5.7869489		
Total	4490.4354	747			

Appendix Table A4ii.87 ANCOVA results for female AW with CL between-sites and years, Whitby 1973, Pembrokeshire 1973, Selsey 1973, Staithes 1980 and St. Davids 1980

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	175755.07	1	175755.07	1000	0
Site effect	185.77043	4	46.44207	6.532	0
Residual	5488.9038	772	7.109979		
Total	181429.74	777			

Appendix Table A4ii.88 ANCOVA results for female RAW with CL between-sites and years, Whitby 1973, Pembrokeshire 1973, Selsey 1973, Staithes 1980 and St. Davids 1980

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	17720.166	1	17720.166	1000	0
Site effect	417.63989	4	104.40997	10.837	0
Residual	7438.2092	772	9.634986		
Total	25576.015	777			

Appendix Table A4ii.89 ANCOVA results for male AW with CL between-sites and years, Whitby 1973, Pembrokeshire 1973, Selsey 1973, Staithes 1980 and St. Davids 1980

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	7852.2453	1	7852.2453	1000	0
Site effect	71.812803	2	35.906401	20.27	0
Residual	607.5961	343	1.7714172		
Total	8531.6542	346			

Appendix Table A4ii.90 ANCOVA results for male RAW with CL between-sites and years, Whitby 1973, Pembrokeshire 1973, Selsey 1973, Staithes 1980 and St. Davids 1980

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	6.2133539	1	6.2133539	2.42	0.1352
Site effect	116.05293	2	58.026463	20.941	0
Residual	950.45559	343	2.7710075		
Total	1072.7219	346			

Appendix Table A4iv.1 Linear regression statistics for CG stage and CL relationships

Site	N	R-square	r	Sx/y	F(df,df)	P(F)		Coeff.	Std. Error	t-statistic	P
Bridlington	31	0.125	0.354	1.098	1,29	0.051	a	-2.755	2.707	-1.018	0.317
1989 to 1991							b	0.059	0.029	2.036	0.051
Selsey	28	0.036	0.189	4.649	1,26	0.336	a	-1.696	3.559	-0.477	0.638
1989 to 1991							b	0.039	0.04	0.98	0.336

Appendix Table A4iv.2 Polynomial regression statistics for CG stage and CL relationships

Site	N	R-square	r	Sx/y	F(df,df)	P(F)		Coeff.	P
Bridlington	31	0.149	0.386005	1.102	2,29	0.104	a	-30.3	0.128
1989 to 1991							b	0.6313	
							c	-0.003	
Selsey	28	0.039	0.197484	0.975	2,26	0.606	a	-20.09	0.481
1989 to 1991							b	0.4383	
							c	-0.002	

Appendix Table A4iv.3 ANCOVA results for CG stage with CL between-sites (Bridlington and Selsey 1990)

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	12.091392	1	12.091392	12.414	0.0009
Site effect	11.465769	1	11.465769	11.772	0.001
Residual	54.544534	56	0.9740095		
Total	78.101695	58			

Appendix Table A4v.1 Linear regression statistics for ovary weight and CL, Bridlington, Dale and Selsey, 1989 to 1991

Site	N	R-square	r	Sx/y	F(df,df)	P(F)		Coeff.	Std. Error	t-statistic	P
Bridlington	101	0.458	0.677	9.921	1,99	<0.001	a	-47.034	7.418	-6.34	<0.001
1989 to 1991							b	0.702	0.077	9.148	<0.001
Dale	25	0.668	0.817	8.272	1,23	<0.001	a	-72.39	13.8	-5.246	<0.001
1989							b	0.873	0.128	6.807	<0.001
Selsey	150	0.362	0.602	8.894	1,148	<0.001	a	-54.565	7.418	-7.356	<0.001
1989 to 1991							b	0.753	0.082	9.202	<0.001

Appendix Table A4v.2 Polynomial regression statistics for ovary weight and CL, Bridlington, Dale and Selsey, 1989 to 1991

Site	N	R-square	r	Sx/y	F(df,df)	P(F)		Coeff.	P
Bridlington	101	0.495	0.70356	9.626	2,99	<0.001	a	-163.6	<0.001
1989 to 1991							b	3.067	
							c	-0.012	
Dale	25	0.691	0.83126	8.161	2,23	<0.001	a	28.98	<0.001
1989							b	-1.011	
							c	0.009	
Selsey	150	0.363	0.6025	8.92	2,148	<0.001	a	-41.62	<0.001
1989 to 1991							b	0.4734	
							c	0.001494	

Appendix Table A4v.3 Linear regression statistics for relative ovary weight and CL, Bridlington, Dale and Selsey, 1989 to 1991

Site	N	R-square	r	Sx/y	F(df,df)	P(F)		Coeff.	Std. Error	t-statistic	P
Bridlington	101	0.043	0.207	1.756	1,99	0.038	a	0.363	1.313	0.276	0.783
1989 to 1991							b	0.029	0.014	2.103	0.038
Dale	25	0.29	0.538	0.851	1,23	0.005	a	-1.957	1.42	-1.378	0.181
1989							b	0.04	0.013	3.065	0.005
Selsey	150	0.093	0.305	1.4537	1,148	<0.001	a	-2.28427	1.21255	-1.884	0.062
1989 to 1991							b	0.05207	0.01337	3.895	<0.001

Appendix Table A4v.4 Polynomial regression statistics for relative ovary weight and CL, Bridlington, Dale and Selsey, 1989 to 1991

Site	N	R-square	r	Sx/y	F(df,df)	P(F)		Coeff.	P
Bridlington	101	0.201	0.44833	1.613	2,99	<0.001	a	-31.74	<0.001
1989 to 1991							b	0.6799	
							c	-0.003	
Dale	25	0.337	0.58052	0.841	2,23	0.011	a	-12.22	0.027
1989							b	0.2311	
							c	-0.00087	
Selsey	150	0.125	0.35355	1.4327	2,148	<0.001	a	-15.92	0.002
1989 to 1991							b	0.3466	
							c	-0.00157	

Appendix Table A4v.5 Linear regression statistics for ovary factor and CL, Bridlington, Dale and Selsey, 1989 to 1991

Site	N	R-square	r	Sx/y	F(df,df)	P(F)		Coeff.	Std. Error	t-statistic	P
Bridlington	101	0.046	0.214	115.636	1,99	0.032	a	24.655	86.471	0.285	0.776
1989 to 1991							b	1.949	0.894	2.18	0.032
Dale	25	0.229	0.479	62.479	1,23	0.015	a	-117.786	104.231	-1.13	0.27
1989							b	2.533	0.969	2.615	0.015
Selsey	150	0.123	0.351	100.22	1,148	<0.001	a	-213.584	83.586	-2.555	0.012
1989 to 1991							b	4.219	0.922	4.576	<0.001

Appendix Table A4v.6 Polynomial regression statistics for ovary factor and CL, Bridlington, Dale and Selsey, 1989 to 1991

Site	N	R-square	r	Sx/y	F(df,df)	P(F)		Coeff.	P
Bridlington	101	0.208	0.45607	105.897	2,99	<0.001	a	-212.1	<0.001
1989 to 1991							b	45.49	
							c	-0.2167	
Dale	25	0.287	0.53572	61.435	2,23	0.024	a	-917.2	0.047
1989							b	17.39	
							c	-0.068	
Selsey	150	0.159	0.39875	98.469	2,148	<0.001	a	-123.8	<0.001
1989 to 1991							b	26.34	
							c	-0.1182	

Appendix Table A4iii.1 Percentage of berried females, Bridlington, Dale and Selsey 1989 to 1991

	Bridlington			Dale	Selsey	
CL (mm)	% berried 1989	% berried 1990	% berried 1991	% berried 1989	% berried 1989	% berried 1990
52.5				-	-	-
57.5	0	0	0	-	0	-
62.5	0	0	0	-	0	0
67.5	0	0	0	-	0	0
72.5	0	0	0	-	0	0
77.5	1.923077	0	0	0	27.02703	3.571429
82.5	13.69863	0	3.846154	0	22.41379	4.225352
87.5	16.87764	7.692308	10	0	32	4
92.5	36.70213	29.41176	0	0	20	2.564103
97.5	36.11111	50	33.33333	0	33.33333	0
102.5	0	66.66667	100	27.27273	100	14.28571
107.5	66.66667	0	0	16.66667	-	-
112.5	0	0	0	25	-	-
117.5	0	0	-	25	-	-
122.5	100	0	-	28.57143	-	-
127.5	100	0	-	40	-	-
132.5	-	0	-	46.15385	-	-
137.5	-	-	-	33.33333	-	-
142.5	-	-	-	11.11111	-	-
147.5	-	-	-	0	-	-
152.5	-	-	-	0	-	-

Appendix Table A4iii.2 Percentage of berried females, Yorkshire, Pembrokeshire and Selsey 1972 to 1974

	Yorkshire			Pembrokeshire		Selsey	
CL (mm)	% berried 1972	% berried 1973	% berried 1974	% berried 1972	% berried 1973	% berried 1972	% berried 1973
52.5	-	-	-	-	-	-	-
57.5	-	-	-	-	-	-	-
62.5	-	-	-	-	-	-	-
67.5	0	0	0	0	0	0	0
72.5	0	0	0	0	0	0	0
77.5	0.877193	0	0	0	0	0	0
82.5	3.285871	3.344867	3.950104	1.234568	0	2.177858	2.045728
87.5	13.59517	14.82412	16.18257	6.086957	4.83871	6.934307	7.306889
92.5	30.87719	29.41176	28.13559	3.100775	6.382979	13.38912	20.34483
97.5	34.7561	31.37255	42.17687	5.434783	8.148148	17.92208	27.92793
102.5	33.87097	21.73913	28.40909	7.8125	18	34.29752	40
107.5	52.27273	28.30189	37.5	10.25641	19.04762	34.26966	40.59406
112.5	42.10526	29.03226	22.22222	9.52381	38.77551	41.17647	45.12195
117.5	50	35.71429	25	4.761905	34.14634	35	51.51515
122.5	66.66667	21.42857	20	5.555556	34.375	23.8806	66.66667
127.5	100	50	50	7.692308	60	32.25806	68.75
132.5	33.33333	0	50	28.57143	30.43478	58.82353	71.42857
137.5	100	100	0	0	20	62.5	33.33333
142.5	50	-	-	-	28.57143	-	25
147.5	-	100	-	-	-	-	-
152.5	-	-	-	-	-	-	-

Appendix Table A4iii.3 Size at first maturity (smallest berried females)

Site	CL (mm) SFM
Bridlington 1989	78
Bridlington 1990	89
Bridlington 1991	82
Dale 1989	95
Selsey 1989	76
Selsey 1990	78
Yorkshire 1972	75-79.9
Yorkshire 1973	80-84.9
Yorkshire 1974	80-84.9
Pembrokeshire 1972	80-84.9
Pembrokeshire 1973	85-89.9
Selsey 1972	80-84.9
Selsey 1973	80-84.9

Appendix Table A4iii.4 CL (mm) at 25 %, 50 % and 66.67% berried

Site	CL at 25 % berried	CL at 50 % berried	CL at 66.67 % berried
Bridlington 1989	90	106	107
Bridlington 1990	91	97	103
Bridlington 1991	97	99	100
Dale 1989	103	-	-
Selsey 1989	78	99	100
Selsey 1990	-	-	-
Yorkshire 1972	91	108	123
Yorkshire 1973	91	127	136
Yorkshire 1974	92	127	-
Pembrokeshire 1972	132	-	-
Pembrokeshire 1973	119	126	-
Selsey 1972	100	131	-
Selsey 1973	95	117	123

Appendix Table A4iii.5 ANCOVA results for % berried females with CL between-years at Bridlington, 1989 to 1991

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	11898.711	1	11898.711	17.878	0.0002
Year effect	221.6903	2	110.84653	0.167	0.8473
Residual	22629.19	34	665.56441		
Total	34749.594	37			

Appendix Table A4iii.6 ANCOVA results for % berried females with CL between-years at Selsey, 1989 and 1990

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	3189.7776	1	3189.7776	10.783	0.0047
Year effect	2450.3662	1	2450.3662	8.284	0.0109
Residual	4732.9394	16	295.80871		
Total	10373.083	18			

Appendix Table A4iii.7 ANCOVA results for % berried females with CL between-years at Yorkshire 1972 to 1974

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	17560.333	1	17560.333	59.261	0
Year effect	1290.0281	2	645.01407	2.177	0.1263
Residual	12149.145	41	296.3206		
Total	30999.506	44			

Appendix Table A4iii.8 ANCOVA results for % berried females with CL between-years at Pembrokeshire 1972 and 1973

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	2551.0807	1	2551.0807	26.596	0
Year effect	984.7664	1	984.7664	10.267	0.0039
Residual	2206.1288	23	95.918642		
Total	5741.9759	25			

Appendix Table A4iii.9 ANCOVA results for % berried females with CL between-years at Selsey 1972 and 1973

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	11130.221	1	11130.221	66.696	0
Year effect	191.19144	1	191.19144	1.146	0.2936
Residual	4672.6144	28	166.87908		
Total	15994.026	30			

Appendix Table A4iii.10 ANCOVA results for % berried females with CL between-years at Yorkshire and Bridlington, 1972 to 1974 and 1989 to 1991

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	31891.387	1	31891.387	69.687	0
Year effect	1656.6252	5	331.32504	0.724	0.6075
Residual	34780.29	76	457.6354		
Total	68328.302	82			

Appendix Table A4iii.11 ANCOVA results for % berried females with CL between-years at Pembrokeshire and Dale, 1972 to 1973 and 1989

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	4578.482	1	4578.482	42.73	0
Year effect	863.19714	2	431.59857	4.028	0.0264
Residual	3857.386	36	107.14961		
Total	9299.0651	39			

Appendix Table A4iii.12 ANCOVA results for % berried females with CL between-years at Selsey, 1972 to 1973 and 1989 to 1990

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	16311.708	1	16311.708	77.29	0
Year effect	2855.227	3	951.74258	4.51	0.0075
Residual	9497.0734	45	211.04608		
Total	28664.009	49			

Appendix Table A4iii.13 ANCOVA results for % berried females with CL between-sites at Bridlington, Dale, Selsey, Yorkshire and Pembrokeshire 1972 to 1974 and 1989 to 1991

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	44344.453	1	44344.453	134.26	0
Site effect	8741.4116	5	1748.2823	5.293	0.0002
Residual	54829.797	166	330.29998		
Total	107915.66	172			

Appendix Table A4iii.14 ANCOVA results for % berried females with CL between-years at Bridlington, Dale, Selsey, Yorkshire and Pembrokeshire 1972 to 1974 and 1989 to 1991

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	44344.453	1	44344.453	116.38	0
Year effect	317.74464	5	63.548928	0.167	0.9745
Residual	63253.464	166	381.04496		
Total	107915.66	172			

Appendix Table A4iii.15 ANCOVA results for % berried females with CL between-sites and between-years at Bridlington, Dale, Selsey, Yorkshire and Pembrokeshire 1972 to 1974 and 1989 to 1991

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	44344.453	1	44344.453	140.11	0
Effects	10279.612	7	1468.516	4.64	0.0001
Site	9961.867	2	4980.9337	15.737	0
Year	1765.456	5	353.0912	1.116	0.3543
Site and year interactions	2967.8865	5	593.5773	1.875	0.1015
Residual	50323.71	159	316.50132		
Total	107915.66	172			

Appendix Table A4v.7 ANCOVA results for ovary weight with CL between-sites at Bridlington, Dale and Selsey, 1989 to 1991

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	13016.081	1	13016.081	131.927	0
Site effect	353.95407	2	176.97704	1.794	0.1702
Residual	13417.893	136	98.660981		
Total	26787.929	139			

Appendix Table A4v.8 ANCOVA results for relative ovary weight with CL between-sites at Bridlington, Dale and Selsey, 1989 to 1991

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	197.43508	1	197.43508	80.502	0
Site effect	36.069913	2	18.034957	7.354	0.0009
Residual	331.09473	135	2.425536		
Total	564.59972	138			

Appendix Table A4v.9 ANCOVA results for ovary factor with CL between-sites at Bridlington, Dale and Selsey, 1989 to 1991

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	825828.36	1	825828.36	80.282	0
Site effect	156007.41	2	78003.703	7.583	0.0008
Residual	1398978.3	136	10286.605		
Total	2380814	139			

Appendix Table A4v.10 Linear regression statistics for hepatopancreas weight and CL, Bridlington, Dale and Selsey, 1989 to 1991

Site	N	R-square	r	Sx/y	F(df,df)	P(F)		Coeff.	Std. Error	t-statistic	P
Bridlington	101	0.825	0.908	5.527	1,99	<0.001	a	-61.516	4.133	-14.884	<0.001
1989 to 1991							b	0.917	0.043	21.463	<0.001
Dale	25	0.897	0.947	5.412	1,23	<0.001	a	-87.344	9.16	-9.536	<0.001
1989							b	1.149	0.085	13.556	<0.001
Selsey	150	0.723	0.85	3.675	1,148	<0.001	a	-38.266	3.069	-12.468	<0.001
1989 to 1991							b	0.661	0.034	19.527	<0.001

Appendix Table A4v.11 Polynomial regression statistics for hepatopancreas weight and CL, Bridlington, Dale and Selsey, 1989 to 1991

Site	N	R-square	r	Sx/y	F(df,df)	P(F)		Coeff.	P
Bridlington	101	0.86	0.92736	105.897	2,99	<0.001	a	50.05	<0.001
1989 to 1991							b	-1.346	
							c	0.011	
Dale	25	0.959	0.97929	3.498	2,23	<0.001	a	101.5	<0.001
1989							b	-2.366	
							c	0.016	
Selsey	150	0.737	0.85849	3.591	2,148	<0.001	a	3.264	<0.001
1989 to 1991							b	-0.2364	
							c	0.005	

Appendix Table A4v.12 Linear regression statistics for relative hepatopancreas weight and CL, Bridlington, Dale and Selsey, 1989 to 1991

Site	N	R-square	r	Sx/y	F(df,df)	P(F)		Coeff.	Std. Error	t-statistic	P
Bridlington	101	0.012	0.111	0.783	1,99	0.274	a	3.511	0.585	5.999	<0.001
1989 to 1991							b	0.007	0.006	1.101	0.274
Dale	25	0.011	0.104	1.113	1,23	0.629	a	3.249	1.882	1.727	0.098
1989							b	0.009	0.017	0.49	0.629
Selsey	150	0.0008614	0.029	4.154	1,148	0.726	a	6.114	3.48	1.757	0.081
1989 to 1991							b	-0.013	0.038	-0.351	0.726

Appendix Table A4v.13 Polynomial regression statistics for relative hepatopancreas weight and CL, Bridlington, Dale and Selsey, 1989 to 1991

Site	N	R-square	r	Sx/y	F(df,df)	P(F)		Coeff.	P
Bridlington	101	0.016	0.12649	0.785	2,99	0.453	a	5.745	0.374
1989 to 1991							b	-0.039	
							c	0.000226	
Dale	25	0.171	0.41352	1.043	2,23	0.14	a	23.69	0.156
1989							b	-0.3751	
							c	0.001741	
Selsey	150	0.009	0.09487	4.152	2,148	0.538	a	-12.06	0.432
1989 to 1991							b	0.3791	
							c	-0.002	

Appendix Table A4v.14 ANCOVA results for hepatopancreas weight with CL between-sites at Bridlington, Dale and Selsey, 1989 to 1991

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	2002.3658	1	2002.3658	93.309	0
Site effect	395.85983	2	197.92991	9.223	0.0002
Residual	2875.5768	134	21.459528		
Total	5273.8024	137			

Appendix Table A4v.15 ANCOVA results for relative weight with CL between-sites at Bridlington, Dale and Selsey, 1989 to 1991

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	0.1151085	1	0.1151085	0.012	0.9145
Site effect	13.511616	2	6.7558082	0.698	0.4994
Residual	1277.5382	132	9.67832		
Total	1291.165	135			

Appendix Table A4v.16 Linear regression statistics for ovary stage and AW, Bridlington, Dale and Selsey, 1989 to 1991

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Bridlington	55	0.311	0.558	0.77083	1,53	<0.001	a	0.61115	0.71525	0.854	0.397
1989 to 1991							b	0.06378	0.01304	4.892	<0.001
Dale	9	0.291	0.539	0.79394	1,7	0.134	a	0.08397	1.41796	0.059	0.954
1989							b	0.04062	0.02397	1.694	0.134
Selsey	75	0.543	0.737	0.72755	1,73	<0.001	a	-1.99036	0.61254	-3.249	0.002
1989 to 1991							b	0.10837	0.01172	9.25	<0.001

Appendix Table A4v.17 Polynomial regression statistics for ovary stage and AW, Bridlington, Dale and Selsey, 1989 to 1991

Site	N	R-square	r	Sx/y	F(df,df)	P(F)		Coeff.	P
Bridlington	55	0.441	0.6641	0.70083	2,53	<0.001	a	-10.51	<0.001
1989 to 1991							b	0.4725	
							c	-0.004	
Dale	9	0.342	0.5848	0.82576	2,7	0.258	a	-4.457	0.284
1989							b	0.1952	
							c	-0.00127	
Selsey	74	0.591	0.76877	0.69348	2,73	<0.001	a	-8.199	<0.001
1989 to 1991							b	0.3603	
							c	-0.003	

Appendix Table A4v.18 Linear regression statistics for ovary weight and AW, Bridlington, Dale and Selsey, 1989 to 1991

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Bridlington	55	0.571	0.755	9.51747	1,53	<0.001	a	-53.86726	8.83121	-6.1	<0.001
1989 to 1991							b	1.35131	0.16099	8.394	<0.001
Dale	9	0.755	0.869	9.0013	1,7	0.002	a	-57.39675	16.07615	-3.57	0.009
1989							b	1.26069	0.27178	4.639	0.002
Selsey	75	0.477	0.69	9.1673	1,73	<0.001	a	-49.22001	7.71827	-6.377	<0.001
1989 to 1991							b	1.20326	0.14759	8.153	<0.001

Appendix Table A4v.19 Polynomial regression statistics for ovary weight and AW, Bridlington, Dale and Selsey, 1989 to 1991

Site	N	R-square	r	Sx/y	F(df,df)	P(F)		Coeff.	P
Bridlington	55	0.571	0.7556	9.60025	2,53	<0.001	a	-67	<0.001
1989 to 1991							b	1.834	
							c	-0.004	
Dale	9	0.841	0.9171	7.825	2,7	0.004	a	55.86	0.007
1989							b	-2.594	
							c	0.032	
Selsey	74	0.622	0.7887	7.848	2,73	<0.001	a	79.13	<0.001
1989 to 1991							b	-4.005	
							c	0.052	

Appendix Table A4v.20 Linear regression statistics for relative ovary weight and AW, Bridlington, Dale and Selsey, 1989 to 1991

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Bridlington	55	0.34	0.583	1.75937	1,53	<0.001	a	-4.93293	1.63251	-3.022	0.004
1989 to 1991							b	0.15533	0.02976	5.22	<0.001
Dale	9	0.143	0.378	0.92598	1,7	0.316	a	-0.2593	1.65379	-0.157	0.88
1989							b	0.03019	0.02796	1.08	0.316
Selsey	75	0.386	0.622	1.45339	1,73	<0.001	a	-5.60104	1.22365	-4.577	<0.001
1989 to 1991							b	0.15757	0.0234	6.733	<0.001

Appendix Table A4v.21 Polynomial regression statistics for relative ovary weight and AW, Bridlington, Dale and Selsey, 1989 to 1991

Site	N	R-square	r	Sx/y	F(df,df)	P(F)		Coeff.	P
Bridlington	55	0.381	0.173	1.71882	2,53	<0.001	a	-19.66	<0.001
1989 to 1991							b	0.6964	
							c	-0.005	
Dale	9	0.182	0.4266	0.97675	2,7	0.444	a	-4.484	0.553
1989							b	0.1739	
							c	-0.00118	
Selsey	74	0.401	0.6332	1.44543	2,73	<0.001	a	0.438	<0.001
1989 to 1991							b	-0.087	
							c	0.002	

Appendix Table A4v.22 Linear regression statistics for ovary factor and AW, Bridlington, Dale and Selsey, 1989 to 1991

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Bridlington	55	0.326	0.571	115.177	1,53	<0.001	a	-302.044	106.87236	-2.826	0.007
1989 to 1991							b	9.85998	1.94827	5.061	<0.001
Dale	9	0.111	0.333	63.3496	1,7	0.381	a	-3.93144	113.4025	-0.035	0.973
1989							b	1.79076	1.91719	0.934	0.381
Selsey	75	0.416	0.645	91.461	1,73	<0.001	a	-376.6226	77.00378	-4.891	<0.001
1989 to 1991							b	10.61523	1.47251	7.209	<0.001

Appendix Table A4v.23 Polynomial regression statistics for ovary factor and AW, Bridlington, Dale and Selsey, 1989 to 1991

Site	N	R-square	r	Sx/y	F(df,df)	P(F)		Coeff.	P
Bridlington	55	0.366	0.605	112.78	2,53	<0.001	a	-1233	<0.001
1989 to 1991							b	44.07	
							c	-0.3077	
Dale	9	0.116	0.3406	68.365	2,7	0.69	a	-111.3	0.553
1989							b	5.444	
							c	-0.03	
Selsey	74	0.435	0.6595	90.584	2,73	<0.001	a	62.13	<0.001
1989 to 1991							b	-7.187	
							c	0.1786	

Appendix Table A4v.24 ANCOVA results for ovary stage with AW between-sites at Bridlington, Dale and Selsey, 1989 to 1991

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (AW)	72.415903	1	72.415903	73.847	0
Site effect	2.1494358	2	1.0747179	1.096	0.3372
Residual	132.3843	135	0.9806245		
Total	206.94964	138			

Appendix Table A4v.25 ANCOVA results for ovary weight with AW between-sites at Bridlington, Dale and Selsey, 1989 to 1991

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (AW)	12947.591	1	12947.591	132.997	0
Site effect	540.84989	2	270.42494	2.778	0.0657
Residual	13142.572	135	97.352385		
Total	26631.013	138			

Appendix Table A4v.26 ANCOVA results for relative ovary weight with AW between-sites at Bridlington, Dale and Selsey, 1989 to 1991

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (AW)	141.54654	1	141.54654	51.878	0
Site effect	47.90712	2	23.95356	8.779	0.0003
Residual	365.61216	134	2.728449		
Total	555.06582	137			

Appendix Table A4v.27 ANCOVA results for ovary factor with AW between-sites at Bridlington, Dale and Selsey, 1989 to 1991

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (AW)	599814.71	1	599814.71	52.758	0
Site effect	207923.28	2	103961.64	9.144	0.0002
Residual	1534849.6	135	11369.256		
Total	2342587.6	138			

Appendix Table A4v.28 Linear regression statistics for ovary stage and RAW, Bridlington, Dale and Selsey, 1989 to 1991

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Bridlington	55	0.222	0.471	0.81899	1,53	<0.001	a	-2.8266	1.77618	-1.591	0.117
1989 to 1991							b	0.11546	0.02967	3.892	<0.001
Dale	9	0.137	0.371	0.87562	1,7	0.326	a	0.90874	1.48308	0.613	0.559
1989							b	0.02396	0.00269	1.056	0.326
Selsey	75	0.387	0.622	0.84258	1,73	<0.001	a	-6.48468	1.50177	-4.318	<0.001
1989 to 1991							b	0.17142	0.02542	6.744	<0.001

Appendix Table A4v.29 Polynomial regression statistics for ovary stage and RAW, Bridlington, Dale and Selsey, 1989 to 1991

Site	N	R-square	r	Sx/y	F(df,df)	P(F)		Coeff.	P
Bridlington	55	0.303	0.55045	0.78287	2,53	0.001	a	-57.01	<0.001
1989 to 1991							b	1.934	
							c	-0.015	
Dale	9	0.15	0.3873	0.9389	2,7	0.494	a	-2.122	0.614
1989							b	0.1144	
							c	-0.0006	
Selsey	74	0.447	0.66858	0.8059	2,73	<0.001	a	-47.34	<0.001
1989 to 1991							b	1.584	
							c	-0.012	

Appendix Table A4v.30 Linear regression statistics for ovary weight and RAW, Bridlington, Dale and Selsey, 1989 to 1991

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Bridlington	55	0.306	0.554	12.0971	1,53	<0.001	a	-107.23457	26.23558	-4.087	<0.001
1989 to 1991							b	2.12041	0.43819	4.839	<0.001
Dale	9	0.7	0.837	9.94751	1,7	0.019	a	-50.93208	16.84852	-3.023	0.019
1989							b	1.04205	0.25771	4.043	0.005
Selsey	75	0.387	0.622	0.84258	1,73	<0.001	a	-6.48468	1.50177	-4.318	<0.001
1989 to 1991							b	0.17142	0.02542	6.744	<0.001

Appendix Table A4v.31 Polynomial regression statistics for ovary weight and RAW, Bridlington, Dale and Selsey, 1989 to 1991

Site	N	R-square	r	Sx/y	F(df,df)	P(F)		Coeff.	P
Bridlington	55	0.307	0.5541	12.212	2,53	0.001	a	-77.11	<0.001
1989 to 1991							b	1.109	
							c	0.008	
Dale	9	0.724	0.8509	10.307	2,7	0.031	a	29.79	0.021
1989							b	-1.366	
							c	0.017	
Selsey	74	0.272	0.5215	10.96216	2,73	<0.001	a	49.14	<0.001
1989 to 1991							b	-2.999	
							c	0.04	

Appendix Table A4v.32 Linear regression statistics for relative ovary weight and RAW, Bridlington, Dale and Selsey, 1989 to 1991

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Bridlington	55	0.199	0.446	1.93722	1,53	<0.001	a	-11.72923	4.20133	-2.792	0.007
1989 to 1991							b	0.25481	0.07017	3.631	<0.001
Dale	9	0.025	0.159	0.98739	1,7	0.683	a	0.79591	1.67238	0.476	0.649
1989							b	0.01091	0.02558	0.426	0.683
Selsey	75	0.386	0.622	1.45339	1,73	<0.001	a	-5.60104	1.22365	-4.577	<0.001
1989 to 1991							b	0.15757	0.0234	6.733	<0.001

Appendix Table A4v.33 Polynomial regression statistics for relative ovary weight and RAW, Bridlington, Dale and Selsey, 1989 to 1991

Site	N	R-square	r	Sx/y	F(df,df)	P(F)		Coeff.	P
Bridlington	55	0.21	0.4583	1.94239	2,53	0.002	a	-58.21	0.011
1989 to 1991							b	1.815	
							c	-0.013	
Dale	9	0.088	0.2966	1.03169	2,7	0.759	a	-6.395	0.61
1989							b	-0.2254	
							c	-0.0015	
Selsey	74	0.28	0.529	1.58545	2,73	<0.001	a	-18.52	<0.001
1989 to 1991							b	0.4682	
							c	-0.0019	

Appendix Table A4v.34 Linear regression statistics for ovary factor and RAW, Bridlington, Dale and Selsey, 1989 to 1991

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Bridlington	55	0.2	0.448	125.434	1,53	<0.001	a	-756.40261	272.03536	-2.781	0.007
1989 to 1991							b	16.55874	4.54362	3.644	<0.001
Dale	9	0.022	0.149	66.5849	1,7	0.702	a	56.04541	112.77764	0.497	0.634
1989							b	0.68779	1.72504	0.399	0.702
Selsey	75	0.306	0.553	100.392	1,73	<0.001	a	-832.46349	178.93201	-4.652	<0.001
1989 to 1991							b	17.05811	3.02852	5.632	<0.001

Appendix Table A4v.35 Polynomial regression statistics for ovary factor and RAW, Bridlington, Dale and Selsey, 1989 to 1991

Site	N	R-square	r	Sx/y	F(df,df)	P(F)		Coeff.	P
Bridlington	55	0.21	0.4583	125.867	2,53	0.011	a	-3592	0.002
1989 to 1991							b	111.7	
							c	-0.7957	
Dale	9	0.025	0.1581	71.8162	2,7	0.791	a	-46.7	0.927
1989							b	3.752	
							c	-0.022	
Selsey	74	0.306	0.5532	101.09	2,73	<0.001	a	-890.5	<0.001
1989 to 1991							b	19.06	
							c	-0.017	

Appendix Table A4v.36 ANCOVA results for ovary stage with RAW between-sites at Bridlington, Dale and Selsey, 1989 to 1991

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (RAW)	9.1797367	1	9.1797367	6.442	0.0123
Site effect	5.4356244	2	2.7178122	1.907	0.1524
Residual	193.78464	136	1.4248871		
Total	208.4	139			

Appendix Table A4v.37 ANCOVA results for ovary weight with RAW between-sites at Bridlington, Dale and Selsey, 1989 to 1991

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (RAW)	1699.1741	1	1699.1741	9.697	0.0023
Site effect	1257.0483	2	628.52417	3.587	0.0303
Residual	23831.706	136	175.23314		
Total	26787.929	139			

Appendix Table A4v.38 ANCOVA results for relative ovary weight with RAW between-sites at Bridlington, Dale and Selsey, 1989 to 1991

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (RAW)	3.1726803	1	3.1726803	0.842	0.3702
Site effect	52.766808	2	26.383404	7.002	0.0013
Residual	508.66024	135	3.7678536		
Total	564.59972	138			

Appendix Table A4v.39 ANCOVA results for ovary factor with RAW between-sites at Bridlington, Dale and Selsey, 1989 to 1991

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (RAW)	15157.705	1	15157.705	0.963	0.3386
Site effect	225406.62	2	112703.31	7.162	0.0011
Residual	2140249.9	136	15737.13		
Total	2380814	139			

Appendix Table A4vi.1 Average Ovf and % of females with ovary stages 4+ and 5+, 5 mm CL groups, Bridlington 1989 to 1991

CL (mm)	N	Average Ovf	Std. Dev Ovf	% females ovary stage 5+	% females ovary stage 4+
62.5	1	22.125	0	0	0
67.5	2	25.541	3.329	0	0
72.5	3	29.45367	3.617754	0	0
77.5	1	25.362	0	0	0
82.5	6	177.5243	114.8929	20	83.3333
87.5	43	159.6432	84.4377	35.7143	80.95238
92.5	28	208.9116	109.8131	59.25926	92.59259
97.5	5	306.8842	155.4601	80	100
102.5	4	202.357	34.51507	75	100
107.5	1	155.6705	0	100	100
112.5	1	569.6705	0	100	100

Appendix Table A4vi.2 Average Ovf and % of females with ovary stages 4+ and 5+, 5 mm CL groups, Dale 1989

CL (mm)	N	Average Ovf	Std. Dev. Ovf	% females ovary stage 5+	% females ovary stage 4+
82.5	2	71.639	28.361	0	0
87.5	2	69.495	45.756	50	50
92.5	1	99.848	0	0	0
97.5	2	59.799	16.981	50	50
102.5	1	238.313	0	100	100

Appendix Table A4vi.3 Average Ovf and % of females with ovary stages 4+ and 5+, 5 mm CL groups, Selsey 1989 to 1991

CL (mm)	N	Average Ovf	Std. Dev. Ovf	% females ovary stage 4+	% females ovary stage 5+
62.5	0				
67.5	1	43.252	0	0	0
72.5	2	33.03168	13.75232	0	0
77.5	3	157.3133	124.0918	0	0
82.5	7	130.423	39.31721	57.14286	0
87.5	12	132.7278	56.92314	58.333	0
92.5	13	274.2572	125.2972	84.6158	61.5385
97.5	10	388.4885	102.0145	100	70
102.5	4	326.6967	138.59	100	100
107.5	1	398.0866	0	100	100
112.5	3	202.0883	70.84856	100	100

Appendix Table A4vi.4 Fitted logistic curve parameters, for % females with ovary stages 4+, Bridlington, Dale and Selsey 1989 to 1991

Site		Coeff	Std. Error	% C.V.
Bridlington 1989 to 1991	a	100	6.673	6.673
	b	-0.02685	0.1912	71.2
	c	73.29	443.8	605.5
Dale 1989	a	100	16890	16890
	b	-5.1916	16500	317900
	c	102.6	1249	1217
Selsey 1989 to 1991	a	100	2.951	2.951
	b	-1.28	1.545	120.7
	c	81.25	1.601	1.97

Appendix Table A4vi.5 Fitted logistic curve parameters, for % females with ovary stages 5+, Bridlington, Dale and Selsey 1989 to 1991

Site		Coeff	Std. Error	% C.V.
Bridlington 1989 to 1991	a	100	6.857	6.857
	b	73.29	0.01296	69.05
	c	115.9	233.7	378.1
Dale 1989	a	100	16890	16890
	b	-5.91916	16500	317900
	c	102.6	1249	1217
Selsey 1989 to 1991	a	98.16	5.512	5.615
	b	-0.1893	0.03395	17.94
	c	90.67	1.192	1.314

Appendix Table A4vi.6 ANCOVA results for females with ovary stage 4+ and CL between-sites at Bridlington, Dale and Selsey, 1989 to 1991

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	35417.999	1	35417.999	98.27	0
Site effect	885.53819	2	442.76909	1.228	0.312
Residual	7929.1282	22	360.41492		
Total	44232.665	25			

Appendix Table A4vi.7 ANCOVA results for females with ovary stage 5+ and CL between-sites at Bridlington, Dale and Selsey, 1989 to 1991

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	34745.402	1	34745.402	71.595	0
Site effect	3832.158	2	1916.079	3.948	0.0343
Residual	10676.767	22	485.3076		
Total	49254.327	25			

Appendix Table A4vi.8 ANCOVA results for female ovary factor (5 mm CL groups) and CL between-sites at Bridlington, Dale and Selsey, 1989 to 1991

Source of variation	SSQ	df	MSQ	Fs	Signif.
Covariate (CL)	266849.79	1	266849.79	35.95	0
Site effect	50022.942	2	25011.471	3.37	0.0529
Residual	163302.35	22	7422.8339		
Total	480175.07	25			

Table A5ii.1 Bridlington 1989 male crusher propodite indicators (5mm CL groups).

CL (mm)	Average CPL (mm)	Std. Dev. CPL (mm)	Average A.I.	Std. Dev. A.I.	Average C.P.I.	Std. Dev. C.P.I.
62.5	83	2.727636	71.66984	11.40584	18.05741	2.239587
67.5	82.4	5.517509	77.43826	22.35566	16.72755	4.214775
72.5	91.70588	4.677163	96.47731	17.9968	18.5315	2.946794
77.5	94.07143	6.571762	107.0171	25.5089	17.86421	3.549269
82.5	102.4035	4.614252	132.9076	23.25689	19.60769	3.092454
87.5	110.8621	5.732686	162.7509	38.5329	21.67366	4.286553
92.5	119.3226	5.865859	204.1514	28.99374	24.07275	3.078778
97.5	124.9412	6.442049	216.4612	57.55737	23.57197	5.733292
102.5	131	5.715476	236.0206	55.2745	22.85987	4.246711
107.5	142	0	303.6596	0	26.75423	0

Table A5ii.2 Bridlington 1989 female crusher propodite indicators (5mm CL groups).

CL (mm)	Average CPL (mm)	Std. Dev. CPL (mm)	Average A.I.	Std. Dev. A.I.	Average C.P.I.	Std. Dev. C.P.I.
62.5	76	0	57.7125	0	14.08997	0
67.5	83.4	5.314132	71.08731	12.74958	15.40873	2.501545
72.5	86.4	2.956349	79.96836	12.09736	15.435	2.325823
77.5	93.74286	4.716796	99.26288	11.68591	16.70402	1.893626
82.5	98.97368	4.068407	111.9108	11.94223	16.70647	1.657313
87.5	103.9778	3.708782	124.2794	14.02334	16.47049	1.723036
92.5	109.5909	4.594058	140.6259	19.3551	16.75475	2.096738
97.5	117.5	5.220153	152.7424	19.76096	16.37077	2.209082
102.5	114.6667	5.906682	138.8478	33.53091	13.51934	3.602052
112.5	128	2	165.6973	24.03243	13.44836	1.950526
122.5	133	0	153.1645	0	9.961272	0
127.5	145	0	235.4524	0	14.83071	0

Table A5ii.3 Bridlington 1990 male crusher propodite indicators (5mm CL groups).

CL (mm)	Average CPL (mm)	Std. Dev. CPL (mm)	Average A.I.	Std. Dev. A.I.	Average C.P.I.	Std. Dev. C.P.I.
62.5	80	0	72	0	17.57813	0
72.5	90.5	2.5	86.44239	8.568419	15.98182	1.36858
77.5	95.25	2.537223	103.7204	14.21858	17.52961	2.596996
82.5	103.1429	5.026461	127.399	21.21076	19.16408	2.99172
87.5	113	1.632993	160.3375	12.9266	20.55093	1.630007
92.5	116.5	4.924429	186.2354	30.43183	21.92116	3.924152
97.5	124	1	221.5665	32.14411	23.54201	3.378099
102.5	135	0	277.9412	0	26.71484	0
137.5	198.6667	13.09792	640.4614	106.1556	34.04597	6.023624
142.5	216	0	752.5259	0	36.80013	0
147.5	204	0	711.9184	0	32.94546	0

Table A5ii.4 Bridlington 1990 female crusher propodite indicators (5mm CL groups).

CL (mm)	Average CPL (mm)	Std. Dev. CPL (mm)	Average A.I.	Std. Dev. A.I.	Average C.P.I.	Std. Dev. C.P.I.
57.5	70	0	48.75	0	15.54528	0
67.5	83.5	4.5	73.82538	9.774615	16.61977	1.45982
72.5	89	5.385165	78.89842	14.16374	15.2268	2.643413
77.5	96.375	3.351772	101.978	7.283478	17.08767	1.146979
82.5	99.27778	3.617942	111.0217	9.055797	16.69221	1.305502
87.5	107	2.738613	125.8249	9.318718	16.5036	0.737
92.5	109.5556	4.524283	125.5135	7.679182	15.00699	0.854305
97.5	115	0	150.5455	0	15.36021	0
102.5	122	0	115.9	0	11.13995	0
122.5	142	0	205.7268	0	13.59818	0
127.5	159	0	264.8418	0	14.74949	0
152.5	173	0	313.7067	0	13.94252	0

Table A5ii.5 Dale 1989 male crusher propodite indicators (5mm CL groups).

CL (mm)	Average CPL (mm)	Std. Dev. CPL (mm)	Average C.P.I.	Std. Dev. C.P.I.	Average A.I.	Std. Dev. A.I.
72.5	88	0	89.239	0	17.70272	0
82.5	109	0	144.457	0	20.96935	0
77.5	101	0	119.774	0	16.57773	0
87.5	112.75	3.76663	160.191	25.23021	20.68525	3.249187
92.5	113	5.612486	157.1356	16.8527	18.80436	2.30515
97.5	125	0	193.182	0	19.71042	0
102.5	130.9	4.635731	225.1053	25.35238	21.45688	2.314204
107.5	142.5	2.872281	270.0665	16.79681	23.98909	0.770457
112.5	147.8571	4.51754	310.4006	40.74006	24.59514	2.976712
117.5	147.6667	8.178563	287.9267	67.795	21.07905	4.593508
122.5	168.2857	9.837454	445.6526	80.69858	29.58351	5.2317
127.5	175.1111	7.837863	477.6048	63.904	29.67676	4.048078
132.5	168.75	9.120718	423.4633	119.9565	24.54058	7.406945
137.5	184.125	14.57256	518.5904	149.6609	27.81847	7.648926
152.5	219	0	897.608	0	39.89369	0

Table A5ii.6 Dale 1989 female crusher propodite indicators (5mm CL groups).

CL (mm)	Average CPL (mm)	Std. Dev. CPL (mm)	Average C.P.I.	Std. Dev. C.P.I.	Average A.I.	Std. Dev. A.I.
82.5	102.6667	3.399346	114.1647	13.47512	16.94434	1.662845
87.5	107	3.24037	121.8461	17.35523	15.66182	1.707969
92.5	114.8571	4.389226	145.7301	15.3193	17.1004	1.682081
97.5	117.7778	4.416579	159.3289	15.89306	14.89994	5.503332
102.5	124.4404	2.675262	171.8241	21.87383	23.62426	1.979685
107.5	127	5.830952	203.5795	24.61672	17.66167	2.496469
112.5	130.4615	18.29088	191.3491	30.10851	15.18567	2.409761
117.5	142.6667	4.784233	227.5097	20.09809	16.34821	1.541584
122.5	145.1667	4.297932	230.4852	21.6338	15.55647	1.290929
127.5	149.3333	4.229526	246.3024	27.98076	15.17658	1.646693
132.5	155.4	6.343501	269.4632	20.25001	15.51086	1.086256
137.5	158.8	4.664762	264.3376	25.85618	13.22501	2.144782
142.5	166.6667	3.299832	293.4087	30.44798	14.82032	1.460621
147.5	174	0	348	0	15.88751	0

Table A5ii.7 Selsey 1989 male crusher propodite indicators (5mm CL groups).

CL (mm)	Average CPL (mm)	Std Dev CPL (mm)	Average A.I.	Std. Dev. A.I.	Average CPI	Std. Dev CPI
62.5	76.5	3.041381	66.68687	4.042356	17.19848	0.67513
67.5	86.4117647	2.197828	91.85958	13.34342	20.2364	3.039044
72.5	92.425	4.726984	105.0873	19.83444	20.2223	3.731636
77.5	100.847619	4.651228	133.8167	21.99356	22.35925	3.37303
82.5	105.737864	5.651636	151.2583	27.35456	22.78305	3.960941
87.5	115.869565	6.777869	239.8844	327.1691	31.65029	42.12501
92.5	122.6	9.090655	223.4373	52.22082	26.94672	6.259749
97.5	127	2	215.8421	0.342105	22.72696	1.226965
102.5	132	0	268.4	0	25.79777	0

Table A5ii.8 Selsey 1989 female crusher propodite indicators (5mm CL groups).

CL (mm)	Average CPL (mm)	Std Dev CPL (mm)	Average A.I.	Std. Dev. A.I.	Average CPI	Std. Dev CPI
62.5	82	3.316625	60.7625	9.783684	14.83459	2.388595
67.5	84.0666667	4.373659	80.31353	8.819557	17.50338	1.772787
72.5	89.4038462	3.415235	90.85371	13.35666	17.47239	2.542597
77.5	97.3703704	3.95482	110.5895	13.80213	18.55357	2.215706
82.5	102.559633	3.989507	124.5983	17.6298	18.67868	2.565764
87.5	107.927711	4.306854	136.2225	13.12791	18.25228	1.587805
92.5	113.648148	4.368055	154.3351	29.28252	18.08361	1.671124
97.5	124.25	5.117372	167.8655	14.29504	17.55578	1.337747
102.5	127	4.242641	200.2257	10.07533	20.02257	1.007533

Table A5ii.9 Selsey 1990 male crusher propodite indicators (5mm CL groups).

CL (mm)	Average CPL (mm)	Std. Dev CPL (mm)	Average A.I.	Std. Dev. A.I.	Average C.P.I.	Std. Dev. C.P.I.
62.5	71	0	45.75556	0	11.52823	0
72.5	94.66667	4.229526	120.0137	19.61504	22.98837	3.956157
77.5	99.91667	5.837499	132.5341	28.562	22.49644	4.610805
82.5	109.3077	4.444264	169.7397	30.39538	25.0571	4.125557
87.5	116.0769	5.441458	188.3549	32.03799	25.24928	4.101635
92.5	123.75	3.63	235.2344	14.3297	27.65791	1.794
96	121	0	221.8333	0	26.50516	0
122.5	188	0	618.7187	0	40.89621	0

Table A5ii.10 Selsey 1990 female crusher propodite indicators (5mm CL groups).

CL (mm)	Average CPL (mm)	Std. Dev. CPL (mm)	Average A.I.	Std. Dev. A.I.	Average C.P.I.	Std. Dev. C.P.I.
67.5	83	0	33.5	0.5	18	0
72.5	96	0	39	0	29	0
77.5	98.5	2.828427	40.875	1.452369	22	0.707107
82.5	102.0476	3.945778	41.57143	4.593696	23.90476	4.936789
87.5	109.6207	4.421061	45.93103	1.638566	24.55172	1.132169
92.5	114.2778	3.708931	47.83333	2.522124	25.55556	1.116653
97.5	127	0	51	0	27	0
107.5	129	0	55	0	29	0
112.5	139	0	60	0	30	0
117.5	135	0	61	0	32	0
102.5	123.8333	1.674979	50.5	3.095696	26.83333	1.213352

Table A5ii.11 Staithes 1980 to 1981 male crusher propodite indicators (5mm CL groups).

CL (mm)	Average A.I.	Std. Dev. A.I.
57.5	37	1
62.5	58.33333	4.478343
67.5	69.6087	7.971357
72.5	84.47059	3.237967
77.5	97.47826	11.07629
82.5	119.9	18.0635
87.5	149.725	26.43387
92.5	170.8182	22.2744
97.5	213.5625	47.81209
102.5	249.8095	33.91814
107.5	276	52.23573
112.5	301	44.02878
117.5	397.25	74.49455
122.5	422.6	150.3743
127.5	530	72.0324
132.5	404	237.6163

Table A5ii.12 St. Davids 1980 to 1981 male crusher propodite indicators (5mm CL groups).

CL (mm)	Average A.I.	Std. Dev. A.I.
67.5	66	0
72.5	80.5	4.5
77.5	106.0714	8.547884
82.5	118.8261	16.29791
87.5	141.5938	19.4436
92.5	163.3571	23.4874
97.5	205.5833	28.15717
102.5	231.3077	39.75383
107.5	269.6875	46.70348
112.5	327.4	50.12026
117.5	366.8125	41.76754
122.5	425.6923	64.89919
127.5	421.375	70.41473
132.5	629.5	94.41531
137.5	576.5	2.5
142.5	594.3333	95.37412
147.5	826	0
152.5	636.4	171.6329
157.5	773	0

Table A5ii.13 Bridlington 1989 to 1990 male internal maturity indicators (5mm CL groups).

CL (mm)	Avg. hepat. weight (g)	Std. Dev.	Avg. R.H.W	Std. Dev.	Avg. vas def. weight (g)	Std. Dev.	Avg. V.D.W.	Std. Dev.	Avg. VDf	Std. Dev.
77.5	12.44	0	4.046	0	0.00029275	0	0.09	0	20.502	0
82.5	18.615	2.73013	4.338875	0.733877	0.0011419	0.000282	0.4875	0.108714	85.081	18.23782
87.5	25.06	1.76	4.7345	0.2615	0.0013005	0.000283	0.69	0.16	102.608	22.122
92.5	27.19	0.35	4.826	0.13	0.00125382	0.000214	0.7	0.09	93.355	15.015
97.5	24.175	3.175	4.02445	0.61645	0.00107085	3.2E-05	0.645	0.005	72.9685	2.8445

Table A5ii.14 Dale 1989 male internal maturity indicators (5mm CL groups).

CL (mm)	Avg. hepat. weight (g)	Std. Dev.	Avg. R.H.W	Std. Dev.	Avg. vas def. weight (g)	Std. Dev.	Avg. V.D.W.	Std. Dev.	Avg. VDf	Std. Dev.
82.5	15.15	0	4.392	0	0.000696	0	0.24	0	41.974	0
92.5	15.62	2.75	3.82965	0.14235	0.001268	0.000244	0.5	0.01	65.2595	0.2355
107.5	30.0795	0.1395	3.60375	0.19045	0.001207	0.000124	1.005	0.055	81.178	7.821
137.5	67.01	0	5.0604	0	0.001812	0	2.4	0	97.5461	0

Table A5ii.15 Selsey 1989 to 1990 male internal maturity indicators (5mm CL groups).

CL (mm)	Avg. hepat. weight (g)	Std. Dev.	Avg. R.H.W	Std. Dev.	Avg. vas def. weight (g)	Std. Dev.	Avg. V.D.W.	Std. Dev.	Avg. VDf	Std. Dev.
62.5	4.69	0	3.106	0	0.00046364	0	0.07	0	30.84	0
77.5	17.64	0	5.49	0	0.00155608	0	0.5	0	118.519	0
82.5	18.64	0	4.539	0	0.00115803	0	0.47	0	79.298	0
87.5	18.7680769	2.72223	4.561338	0.862485	0.00892818	0.026263	0.535385	0.143828	70.81192	24.35188
92.5	23.9616667	4.10097	4.657158	0.726549	0.0016637	0.000448	0.851667	0.205541	100.5828	31.97903
97.5	21.92	0	4.44	0	0.00123682	0	0.61	0	71.147	0

Table A5ii.16 Staithes 1980 to 1981 male internal maturity indicators (5mm CL groups).

CL (mm)	Avg. crusher claw weight (g)	Std. Dev.	Avg. claw weight/CL	Std. Dev.	Avg. vas def. weight (g)	Std. Dev.	Avg. VDf	Std. Dev.
62.5	11.30000	8.172936	0.29933	0.009978	0.12000	0.04918	48	18.41704
67.5	21.81538	6.587383	0.34772	0.030258	0.13231	0.06104	44.4167	19.39269
72.5	28.50000	10.87428	0.39648	0.150541	0.21625	0.09353	58.25	24.35031
77.5	40.41667	3.59301	0.52294	0.042288	0.36750	0.32052	79.9167	69.47597
82.5	51.22222	14.07344	0.61840	0.169333	0.49667	0.37418	87.1667	64.41898
87.5	61.30000	25.02619	0.70806	0.284913	0.48150	0.26854	76.15	40.8623
92.5	73.90909	25.8121	0.80625	0.279394	0.60909	0.18318	78.6364	22.01352
97.5	95.42857	47.81469	0.98069	0.483477	0.76714	0.25633	83.7143	26.29891
102.5	129.00000	14.90805	1.26832	0.136079	1.06000	0.13124	101.075	11.60127
107.5	161.70000	20.12486	1.51299	0.179048	1.35900	0.33483	110.3	28.18173
112.5	148.71429	66.29418	1.32477	0.588235	1.49071	0.45778	102.46	27.0056
117.5	281.33333	20.72572	2.38933	0.151672	2.64667	0.19067	163	13.36663
122.5	277.83333	40.58085	2.27990	0.326337	2.69000	0.85069	149.833	50.27066
127.5	347.66667	32.56105	2.73735	0.254144	3.08333	0.66123	150	29.87753
132.5	378.50000	51.5	2.88931	0.39313	3.85500	0.97500	171.5	43.5

Table A5ii.17 St. Davids 1980 to 1981 male internal maturity indicators (5mm CL groups).

CL (mm)	Avg. crusher claw weight (g)	Std. Dev	Avg. claw weight/CL	Std. Dev	Avg. vas def. weight (g)	Std. Dev	Avg. VDf	Std. Dev
67.5	24	0	0.35	0	0.14	0	44	0
72.5	31	2.54951	0.43250	0.027726	0.16	0.027386	43.75	6.139015
77.5	43	3.21455	0.54667	0.041298	0.23583333	0.087126	52	12.79323
82.5	51.38462	5.955456	0.62769	0.069852	0.4125	0.136389	69.15385	29.49014
87.5	60.66667	17.48832	0.70048	0.202378	0.5195	0.189776	72.68571	30.94287
92.5	81.28571	11.53522	0.88857	0.126539	0.58857143	0.129882	77.14286	18.2712
97.5	99.38462	33.03969	1.02385	0.334607	0.71076923	0.221827	81.53846	20.42854
102.5	127.25000	20.33316	1.25250	0.195048	0.95	0.472043	91.375	42.38495
107.5	141.33333	31.82941	1.31778	0.284049	1.07444444	0.232336	87.22222	17.88095
112.5	163.12500	39.40316	1.45625	0.354116	1.34375	0.578358	93.625	39.54408
117.5	183.90000	70.14763	1.71000	0.299366	1.642	0.262747	104.7	17.65814
122.5	257.50000	50.11986	2.12250	0.419814	1.61125	1.046846	89	58.34809
127.5	139.16667	104.9181	1.10667	0.831959	2.42666667	0.547925	121	27.61038
132.5	355	0	2.71000	0	2.9	0	128	0
137.5	409	14	3.03000	0.1	2.6	0.1	106	4
147.5	475	0	3.28	0	3.7	0	122	0
152.5	623	0	4.1	0	5.9	0	168	0
157.5	469	0	3.03	0	3.6	0	97	0

Table A5iii.1 Linear regressions statistics for lobster CPL-CL relationships.

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff.	Std. Error	t-statistic	P
Bridlington	206	0.839	0.916	5.516	1,204	<0.001	a	-22.467	3.955	-5.68	<0.001
Males,1989							b	1.53	0.047	32.628	<0.001
Bridlington	241	0.843	0.918	3.938	1,239	<0.001	a	10.189	2.547	4	<0.001
Females, 1989							b	1.081	0.03	35.836	<0.001
Bridlington	44	0.965	0.982	6.325	1,42	<0.001	a	-33.487	4.514	-7.419	<0.001
Males,1990							b	1.665	0.049	34.129	<0.001
Bridlington	51	0.963	0.982	3.285	1,49	<0.001	a	11.498	2.602	4.418	<0.001
Females, 1990							b	1.08	0.03	35.899	<0.001
Dale	69	0.907	0.953	8.837	1,67	<0.001	a	-28.387	6.99	-4.061	<0.001
Males,1989							b	1.571	0.061	25.623	<0.001
Dale	92	0.916	0.957	5.131	1,90	<0.001	a	17.246	3.823	4.511	<0.001
Females, 1989							b	1.046	0.033	31.247	<0.001
Selsey	333	0.829	0.91	4.853	1,331	<0.001	a	-16.92	3.025	-5.592	<0.001
Males,1989							b	1.518	0.038	39.998	<0.001
Selsey	405	0.938	0.968	6.7	1,403	<0.001	a	3.315	1.311	2.529	0.012
Females, 1989							b	1.211	0.016	77.762	<0.001
Selsey	51	0.896	0.946	5.213	1,49	<0.001	a	-32.286	6.934	-4.656	<0.001
Males,1990							b	1.72	0.084	20.525	<0.001
Selsey	89	0.847	0.92	3.298	1,87	<0.001	a	13.073	4.392	2.977	0.004
Females, 1990							b	1.105	0.05	21.942	<0.001

Table A5iii.2 Natural logarithm regressions statistics for lobster CPL-CL relationships.

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff.	Std. Error	t-statistic	P
Bridlington	206	0.833	0.913	0.052	1,204	<0.001	a	-0.646	0.166	-3.883	<0.001
Males,1989							b	1.198	0.038	31.882	<0.001
Bridlington	241	0.843	0.918	0.039	1,239	<0.001	a	0.544	0.113	4.796	<0.001
Females, 1989							b	0.919	0.026	35.862	<0.001
Bridlington	44	0.965	0.983	0.045	1,42	<0.001	a	-0.752	0.161	-4.682	<0.001
Males,1990							b	1.223	0.036	34.193	<0.001
Bridlington	51	0.952	0.976	0.033	1,49	<0.001	a	0.638	0.128	4.999	<0.001
Females, 1990							b	0.9	0.029	31.277	<0.001
Dale	69	0.922	0.96	0.056	1,67	<0.001	a	-0.625	0.199	-3.136	0.003
Males,1989							b	1.19	0.042	28.165	<0.001
Dale	92	0.727	0.853	.0.077	1,90	<0.001	a	0.809	0.261	3.101	0.003
Females, 1989							b	0.866	0.055	15.666	<0.001
Selsey	333	0.776	0.881	0.104	1,331	<0.001	a	-1.02	0.165	-6.176	<0.001
Males,1989							b	1.293	0.038	34.25	<0.001
Selsey	405	0.924	0.961	0.074	1,403	<0.001	a	0.049	0.065	0.762	0.447
Females, 1989							b	1.04	0.015	70.631	<0.001
Selsey	51	0.44	0.664	0.121	1,49	<0.001	a	0.596	0.612	0.974	0.334
Males,1990							b	0.92	0.139	6.638	<0.001
Selsey	89	0.792	0.89	0.042	1,87	<0.001	a	0.772	0.213	3.625	<0.001
Females, 1990							b	0.877	0.048	18.39	<0.001

Table A5iii.3 Polynomial regressions statistics for lobster CPL-CL relationships.

Site	N	R-Square	r	Sy/x	F(df,df)	P(F)		Coeff	P
Bridlington	206	0.842	0.9176	5.482	2,204	<0.001	a	34.64	<0.001
Males, 1989							b	0.1758	
							c	0.008	
Bridlington	241	0.849	0.9214	3.873	2,239	<0.001	a	-27.11	<0.001
Females, 1989							b	1.934	
							c	-0.005	
Bridlington	44	0.969	0.9844	6.072	2,42	<0.001	a	19.88	<0.001
Males, 1990							b	0.6124	
							c	0.005	
Bridlington	51	0.963	0.9813	3.318	2,49	<0.001	a	10.37	<0.001
Females, 1990							b	1.103	
							c	-0.00011	
Dale	69	0.908	0.9529	8.869	2,67	<0.001	a	1.696	<0.001
Males, 1989							b	1.018	
							c	0.002	
Dale	92	0.916	0.9571	5.156	2,90	<0.001	a	8.057	<0.001
Females, 1989							b	1.212	
							c	-0.00073	
Selsey	333	0.867	0.9311	3.927	2,331	<0.001	a	4.587	<0.001
Males, 1989							b	0.8806	
							c	0.005	
Selsey	405	0.854	0.9241	3.678	2,403	<0.001	a	4.628	<0.001
Females, 1989							b	1.134	
							c	0.00075	
Selsey	51	0.902	0.9497	5.111	2,49	<0.001	a	19.52	<0.001
Males, 1990							b	0.05488	
							c	0.007	
Selsey	89	0.855	0.9247	3.847	2,87	<0.001	a	-41.39	<0.001
Females, 1990							b	2.321	
							c	-0.007	

Table A5iii.4 Linear regressions statistics for lobster AI-CL relationships.

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff.	Std. Error	t-statistic	P
Bridlington	206	0.73	0.854	28.289	1,204	<0.001	a	-324.884	20.285	-16.016	<0.001
Males,1989							b	5.65	0.241	23.486	<0.001
Bridlington	241	0.655	0.809	15.453	1,239	<0.001	a	-95.137	9.993	-9.52	<0.001
Females, 1989							b	2.552	0.118	21.306	<0.001
Bridlington	44	0.927	0.963	49.544	1,42	<0.001	a	-590.981	35.356	-16.715	<0.001
Males,1990							b	8.799	0.382	23.025	<0.001
Bridlington	51	0.915	0.957	12.535	1,49	<0.001	a	-107.084	9.931	-10.783	<0.001
Females, 1990							b	2.641	0.115	23.01	<0.001
Dale	69	0.749	0.865	85.094	1,67	<0.001	a	-606.719	67.308	-9.014	<0.001
Males,1989							b	8.339	0.59	14.125	<0.001
Dale	92	0.818	0.904	22.876	1,90	<0.001	a	-133.239	17.044	-7.817	<0.001
Females, 1989							b	3.002	0.149	20.119	<0.001
Selsey	333	0.074	0.272	129.479	1,331	<0.001	a	-261.675	80.722	-3.242	0.001
Males,1989							b	5.214	1.013	5.15	<0.001
Selsey	405	0.723	0.851	43.976	1,403	<0.001	a	-147.697	8.605	-17.165	<0.001
Females, 1989							b	3.32	0.102	32.468	<0.001
Selsey	51	0.803	0.896	35.316	1,49	<0.001	a	-488.404	46.975	-10.397	<0.001
Males,1990							b	8.03	0.568	14.146	<0.001
Selsey	89	0.666	0.816	3.008	1,87	<0.001	a	1.192	3.363	0.355	0.724
Females, 1990							b	0.508	0.039	13.166	<0.001
Staithes	268	0.82	0.906	70.766	1,266	<0.001	a	-318.269	0.82	14.931	<0.001
1980 to 1981							b	5.593	0.16	0.16	<0.001
St. Davids	204	0.873	0.934	57.332	1,202	<0.001	a	-543.032	21.755	-24.962	<0.001
1980 to 1981							b	7.882	0.211	37.311	<0.001

Table A5iii.5 Natural logarithm regressions statistics for lobster AI-CL relationships.

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff.	Std. Error	t-statistic	P
Bridlington	206	0.747	0.864	0.178	1,204	<0.001	a	-8.877	0.564	-15.751	<0.001
Males,1989							b	3.123	0.127	24.529	<0.001
Bridlington	241	0.679	0.824	0.129	1,239	<0.001	a	-3.789	0.38	-9.981	<0.001
Females, 1989							b	1.926	0.086	22.46	<0.001
Bridlington	44	0.934	0.967	0.157	1,42	<0.001	a	-8.632	0.562	-15.365	<0.001
Males,1990							b	3.061	0.125	24.455	<0.001
Bridlington	51	0.877	0.937	0.106	1,49	<0.001	a	-3.005	0.413	-7.278	<0.001
Females, 1990							b	1.744	0.093	18.275	<0.001
Dale	69	0.837	0.915	0.208	1,67	<0.001	a	-8.043	0.741	-10.857	<0.001
Males,1989							b	2.913	0.157	18.538	<0.001
Dale	92	0.792	0.89	0.127	1,90	<0.001	a	-2.761	0.43	-6.42	<0.001
Females, 1989							b	1.706	0.091	18.719	<0.001
Selsey	333	0.519	0.721	0.464	1,331	<0.001	a	-9.138	0.736	-12.424	<0.001
Males,1989							b	3.219	0.168	19.14	<0.001
Selsey	405	0.808	0.899	0.307	1,403	<0.001	a	-6.296	0.267	-23.6	<0.001
Females, 1989							b	2.521	0.061	41.592	<0.001
Selsey	51	0.427	0.653	0.341	1,49	<0.001	a	-6.136	1.724	-3.559	<0.001
Males,1990							b	2.525	0.391	6.46	<0.001
Selsey	89	0.537	0.733	0.137	1,87	<0.001	a	-2.114	0.692	-3.054	0.003
Females, 1990							b	1.577	0.155	10.165	<0.001
Staithes	268	0.947	0.973	0.219	1,266	<0.001	a	-8.439	0.196	-43.142	<0.001
1980 to 1981							b	3.008	0.044	68.929	<0.001
St. Davids	204	0.928	0.963	0.154	1,202	<0.001	a	-8.621	0.274	-31.415	<0.001
1980 to 1981							b	3.041	0.06	51.023	<0.001

Table A5iii.6 Polynomial regressions statistics for lobster AI-CL relationships.

Site	N	R-Square	r	Sy/x	F(df,df)	P(F)		Coeff	P
Bridlington	206	0.742	0.8614	27.709	2,204	<0.001	a	152.7	<0.001
Males, 1989							b	-5.679	
							c	0.067	
Bridlington	241	0.675	0.8216	15.033	2,239	<0.001	a	-277.8	<0.001
Females, 1989							b	6.697	
							c	-0.024	
Bridlington	44	0.951	0.9752	40.98	2,42	<0.001	a	168.5	<0.001
Males, 1990							b	-6.183	
							c	0.07	
Bridlington	51	0.931	0.9649	11.42	2,49	<0.001	a	8.702	<0.001
Females, 1990							b	0.2511	
							c	0.012	
Dale	69	0.777	0.8815	80.835	2,67	<0.001	a	475.7	<0.001
Males, 1989							b	-11.57	
							c	0.089	
Dale	92	0.818	0.9044	23.004	2,90	<0.001	a	-136.2	<0.001
Females, 1989							b	3.056	
							c	-0.00024	
Selsey	333	0.109	0.3163	124.917	2,331	<0.001	a	123.6	<0.001
Males, 1989							b	-6.305	
							c	0.083	
Selsey	405	0.648	0.805	16.866	2,403	<0.001	a	-97.98	<0.001
Females, 1989							b	2.18	
							c	0.006	
Selsey	51	0.88	0.9381	27.916	2,49	<0.001	a	415.5	<0.001
Males, 1990							b	-12.4	
							c	0.1135	
Selsey	89	0.668	0.8173	3.016	2,87	<0.001	a	-13.2	<0.001
Females, 1990							b	0.8289	
							c	-0.00178	
Staithes	268	0.928	0.9633	31.419	2,266	<0.001	a	339.6	<0.001
1980 to 1981							b	-10.02	
							c	0.089	
St. Davids	204	0.886	0.9413	54.457	2,202	<0.001	a	-63.34	<0.001
1980 to 1981							b	-1.297	
							c	0.042	

Table A5iii.7 Linear regressions statistics for lobster CPI-CL relationships.

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff.	Std. Error	t-statistic	P
Bridlington	206	0.283	0.532	3.664	1,204	<0.001	a	-2.919	2.627	-1.111	0.268
Males,1989							b	0.28	0.031	8.973	<0.001
Bridlington	241	0.004	0.065	2.059	1,239	0.315	a	17.748	1.332	13.328	<0.001
Females, 1989							b	-0.016	0.016	-1.007	0.315
Bridlington	44	0.688	0.83	3.449	1,42	<0.001	a	-1.699	2.461	-0.69	0.494
Males,1990							b	0.256	0.027	9.625	<0.001
Bridlington	51	0.146	0.382	1.612	1,49	0.006	a	19.654	1.277	15.39	<0.001
Females, 1990							b	-0.043	0.015	-2.896	0.006
Dale	69	0.38	0.616	4.935	1,67	<0.001	a	-0.231	3.904	-0.059	0.953
Males,1989							b	0.219	0.034	6.404	<0.001
Dale	92	0.133	0.365	1.874	1,90	<0.001	a	21.057	1.396	15.081	<0.001
Females, 1989							b	-0.045	0.012	-3.716	<0.001
Selsey	333	0.014	0.118	16.967	1,331	0.032	a	0.847	10.578	0.08	0.936
Males,1989							b	0.286	0.133	2.156	0.032
Selsey	405	0.018	0.134	4.06	1,403	0.007	a	16.167	0.794	20.352	<0.001
Females, 1989							b	0.026	0.009	2.71	0.007
Selsey	51	0.348	0.59	4.242	1,49	<0.001	a	-4.206	5.642	-0.745	0.46
Males,1990							b	0.349	0.068	5.114	<0.001
Selsey	89	0.283	0.532	2.738	1,87	<0.001	a	6.783	3.062	2.215	0.029
Females, 1990							b	0.206	0.035	5.863	<0.001

Table A5iii.8 Natural logarithm regressions statistics for lobster CPI-CL relationships.

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff.	Std. Error	t-statistic	P
Bridlington	206	0.276	0.525	0.178	1,204	<0.001	a	-1.969	0.564	-3.494	<0.001
Males,1989							b	1.123	0.127	8.821	<0.001
Bridlington	241	0.003	0.056	0.129	1,239	0.387	a	3.119	0.38	8.217	<0.001
Females, 1989							b	-0.074	0.086	-0.867	0.387
Bridlington	44	0.631	0.794	0.157	1,42	<0.001	a	-1.725	0.562	-3.07	0.004
Males,1990							b	1.061	0.125	8.474	<0.001
Bridlington	51	0.134	0.366	0.106	1,49	0.008	a	3.903	0.413	9.451	<0.001
Females, 1990							b	-0.256	0.093	-2.751	0.008
Dale	69	0.334	0.578	0.208	1,67	<0.001	a	-1.14	0.744	-1.533	0.13
Males,1989							b	0.913	0.158	5.791	<0.001
Dale	92	0.108	0.329	0.134	1,90	<0.001	a	4.277	0.459	9.324	<0.001
Females, 1989							b	-0.323	0.097	-3.327	<0.001
Selsey	333	0.134	0.366	0.464	1,331	<0.001	a	-2.23	0.736	-3.032	0.003
Males,1989							b	1.219	0.168	7.248	<0.001
Selsey	405	0.152	0.389	0.292	1,403	0.007	a	0.726	0.254	2.856	0.005
Females, 1989							b	0.495	0.058	8.572	<0.001
Selsey	51	0.031	0.177	0.341	1,49	0.185	a	0.772	1.724	0.448	0.656
Males,1990							b	0.525	0.391	1.343	0.185
Selsey	89	0.076	0.276	0.138	1,87	0.008	a	4.785	0.694	6.89	0.029
Females, 1990							b	-0.421	0.156	-2.705	0.008

Table A5iii.9 Polynomial regressions statistics for lobster CPI-CL relationships.

Site	N	R-Square	r	Sy/x	F(df,df)	P(F)		Coeff	P
Bridlington	206	0.284	0.5329	3.671	2,204	<0.001	a	6.181	<0.001
Males, 1989							b	0.064	
							c	0.00127	
Bridlington	241	0.081	0.2846	1.983	2,239	<0.001	a	-10.34	0.001
Females, 1989							b	0.6262	
							c	-0.004	
Bridlington	44	0.688	0.8295	3.49	2,42	<0.001	a	-3.502	<0.001
Males, 1990							b	0.2916	
							c	-0.00017	
Bridlington	51	0.146	0.3821	1.629	2,49	0.023	a	19.84	0.048
Females, 1990							b	-0.047	
							c	1.9E-05	
Dale	69	0.383	0.6189	4.958	2,67	<0.001	a	14.03	<0.001
Males, 1989							b	-0.043	
							c	0.00118	
Dale	92	0.147	0.3834	1.869	2,90	<0.001	a	10.09	0.007
Females, 1989							b	0.1525	
							c	-0.00088	
Selsey	333	0.036	0.1897	16.21	2,331	0.002	a	-0.954	0.014
Males, 1989							b	0.01144	
							c	0.002	
Selsey	405	0.028	0.1673	2.209	2,403	0.003	a	-12.92	0.017
Females, 1989							b	0.7385	
							c	-0.004	
Selsey	51	0.349	0.5908	4.281	2,49	<0.001	a	3.891	<0.001
Males, 1990							b	0.1657	
							c	0.00102	
Selsey	89	0.284	0.5329	2.753	2,87	<0.001	a	2.589	<0.001
Females, 1990							b	0.02994	
							c	-0.00052	

Table A5iii.10 Linear regressions statistics for lobster CPL-CL relationships (5mm CL groups).

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff.	Std. Error	t-statistic	P
Bridlington	10	0.982	0.991	2.949	1,8	<0.001	a	-11.303	5.783	-1.954	0.086
Males,1989							b	1.413	0.068	20.933	<0.001
Bridlington	12	0.985	0.993	2.679	1,10	<0.001	a	16.091	3.6	4.47	0.001
Females, 1989							b	0.993	0.038	26.004	<0.001
Bridlington	11	0.985	0.992	6.336	1,9	<0.001	a	-31.031	7.084	-4.381	0.002
Males,1990							b	1.648	0.068	24.222	<0.001
Bridlington	12	0.997	0.998	1.795	1,10	<0.001	a	10.636	1.888	5.633	<0.001
Females, 1990							b	1.086	0.019	56.825	<0.001
Dale	15	0.977	0.988	5.661	1,13	<0.001	a	-20.588	7.088	-2.905	0.012
Males,1989							b	1.505	0.064	23.47	<0.001
Dale	14	0.993	0.997	1.917	1,12	<0.001	a	13.853	2.969	4.667	<0.001
Females, 1989							b	1.07	0.025	42.074	<0.001
Selsey	9	0.991	0.996	1.896	1,7	<0.001	a	-8.715	4.088	-2.132	0.071
Males,1989							b	1.398	0.049	28.557	<0.001
Selsey	9	0.988	0.994	1.932	1,7	<0.001	a	4.247	4.165	1.02	0.342
Females, 1989							b	1.199	0.05	24.033	<0.001
Selsey	8	0.973	0.986	6.018	1,6	<0.001	a	-44.781	11.102	-4.033	0.007
Males,1990							b	1.849	0.126	14.707	<0.001
Selsey	11	0.958	0.979	3.913	1,9	<0.001	a	16.004	7.002	2.286	0.048
Females, 1990							b	1.063	0.075	14.242	<0.001

Table A5iii.11 Polynomial regressions statistics for lobster CPL-CL relationships (5mm CL groups).

Site	N	R-Square	r	Sy/x	F(df,df)	P(F)		Coeff	P
Bridlington	10	0.989	0.99448	2.416	2,8	<0.001	a	58.69	<0.001
Males, 1989							b	-0.2851	
							c	0.01	
Bridlington	12	0.987	0.99347	2.667	2,10	<0.001	a	-2.113	<0.001
Females, 1989							b	1.394	
							c	-0.002	
Bridlington	11	0.989	0.9945	5.845	2,9	<0.001	a	19.26	<0.001
Males, 1990							b	0.6459	
							c	0.005	
Bridlington	12	0.997	0.9985	1.893	2,10	<0.001	a	10.64	<0.001
Females, 1990							b	1.086	
							c	3.5E-07	
Dale	15	0.982	0.99096	5.147	2,13	<0.001	a	3.611	<0.001
Males, 1989							b	0.4302	
							c	0.005	
Dale	14	0.994	0.997	1.909	2,12	<0.001	a	32.95	<0.001
Females, 1989							b	0.7271	
							c	0.00149	
Selsey	9	0.996	0.998	1.402	2,7	<0.001	a	-64.07	<0.001
Males, 1989							b	2.774	
							c	-0.008	
Selsey	9	0.991	0.9955	1.76	2,7	<0.001	a	45.791	<0.001
Females, 1989							b	0.1662	
							c	0.006	
Selsey	8	0.982	0.99096	5.447	2,6	<0.001	a	23.76	<0.001
Males, 1990							b	0.3175	
							c	0.008	
Selsey	11	0.969	0.98438	3.571	2,9	<0.001	a	-51.82	<0.001
Females, 1990							b	2.573	
							c	-0.008	

Table A5iii.12 Linear regressions statistics for lobster AI-CL relationships (5mm CL groups).

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff.	Std. Error	t-statistic	P
Bridlington	10	0.958	0.979	16.764	1,8	<0.001	a	-278.42	32.88	-8.468	<0.001
Males,1989							b	5.196	0.384	13.537	<0.001
Bridlington	12	0.876	0.936	17.995	1,10	<0.001	a	-70.755	24.182	-2.926	0.015
Females, 1989							b	2.154	0.256	8.397	<0.001
Bridlington	11	0.962	0.981	53.881	1,9	<0.001	a	-576.88	60.237	-9.577	<0.001
Males,1990							b	8.786	0.579	15.181	<0.001
Bridlington	12	0.952	0.976	18.362	1,10	<0.001	a	-117.58	19.31	-6.089	<0.001
Females, 1990							b	2.743	0.195	14.036	<0.001
Dale	15	0.865	0.93	80.817	1,13	<0.001	a	-589.02	101.197	-5.821	<0.001
Males,1989							b	8.355	0.915	9.126	<0.001
Dale	14	0.966	0.983	13.03	1,12	<0.001	a	-153.34	20.172	-7.602	<0.001
Females, 1989							b	3.189	0.173	18.456	<0.001
Selsey	9	0.977	0.988	11.09	1,7	<0.001	a	-244.56	23.911	-10.228	<0.001
Males, 1989							b	4.917	0.286	17.171	<0.001
Selsey	9	0.988	0.994	5.315	1,7	<0.001	a	-142.52	11.458	-12.438	<0.001
Females, 1989							b	3.244	0.137	26.639	<0.001
Selsey	8	0.914	0.956	54.966	1,6	<0.001	a	-577.98	101.407	-5.7	0.001
Males,1990							b	9.165	1.148	7.983	<0.001
Selsey	11	0.978	0.989	1.368	1,9	<0.001	a	-0.397	2.448	-0.162	0.875
Females, 1990							b	0.521	0.026	19.992	<0.001
Staithes	16	0.927	0.963	42.39	1,14	<0.001	a	-359.64	44.947	-8.001	<0.001
1980 to 1981							b	6.142	0.46	13.358	<0.001
St. Davids	19	0.935	0.967	63.74	1,17	<0.001	a	-576.13	61.824	-9.319	<0.001
1980 to 1981							b	8.377	0.534	15.689	<0.001

Table A5iii.13 Polynomial regressions statistics for lobster AI-CL relationships (5mm CL groups).

Site	N	R-Square	r	Sy/x	F(df,df)	P(F)		Coeff	P
Bridlington	10	0.984	0.99197	11.065	2,8	<0.001	a	208.9	<0.001
Males, 1989							b	-6.629	
							c	0.07	
Bridlington	12	0.878	0.93702	18.837	2,10	<0.001	a	-114.4	<0.001
Females, 1989							b	3.117	
							c	-0.005	
Bridlington	11	0.99	0.99499	28.874	2,9	<0.001	a	171	<0.001
Males, 1990							b	-6.124	
							c	0.069	
Bridlington	12	0.973	0.98641	14.547	2,10	<0.001	a	29.26	<0.001
Females, 1990							b	-0.334	
							c	0.015	
Dale	15	0.959	0.97929	46.566	2,13	<0.001	a	796.6	<0.001
Males, 1989							b	-17.91	
							c	0.1191	
Dale	14	0.97	0.98489	12.864	2,12	<0.001	a	-13.35	<0.001
Females, 1989							b	0.6771	
							c	0.011	
Selsey	9	0.978	0.98894	11.718	2,7	<0.001	a	-152.3	<0.001
Males, 1989							b	2.625	
							c	0.014	
Selsey	9	0.991	0.99549	4.852	2,7	<0.001	a	-28.8	<0.001
Females, 1989							b	0.4177	
							c	0.017	
Selsey	8	0.985	0.99247	25.433	2,6	<0.001	a	429.2	<0.001
Males, 1990							b	-13.34	
							c	0.1309	
Selsey	11	0.978	0.98894	1.443	2,6	<0.001	a	4.437	<0.001
Females, 1990							b	0.4138	
							c	0.00058	
Staithes	16	0.949	0.97417	36.842	2,14	<0.001	a	29.97	<0.001
1980 to 1981							b	-2.573	
							c	0.046	
St. Davids	19	0.953	0.97622	56.099	2,17	<0.001	a	-16.79	<0.001
1980 to 1981							b	-2.193	
							c	0.047	

Table A5iii.14 Linear regressions statistics for lobster CPI-CL relationships (5mm CL groups).

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff.	Std. Error	t-statistic	P
Bridlington	10	0.862	0.929	1.297	1,8	<0.001	a	3.19	2.544	1.254	0.245
Males,1989							b	0.21	0.03	7.083	<0.001
Bridlington	12	0.26	0.51	1.807	1,10	0.09	a	19.423	2.428	8	<0.001
Females, 1989							b	-0.048	0.026	-1.876	0.09
Bridlington	11	0.947	0.973	1.775	1,9	<0.001	a	-0.066	1.985	-0.033	0.974
Males,1990							b	0.243	0.019	12.723	<0.001
Bridlington	12	0.285	0.534	1.475	1,10	0.074	a	18.103	1.551	11.669	<0.001
Females, 1990							b	-0.031	0.016	-1.998	0.074
Dale	15	0.763	0.874	3.035	1,13	<0.001	a	-0.275	3.8	-0.072	0.943
Males,1989							b	0.223	0.034	6.476	<0.001
Dale	14	0.151	0.388	2.295	1,12	0.17	a	21.362	3.552	6.013	<0.001
Females, 1989							b	-0.044	0.03	-1.459	0.17
Selsey	9	0.725	0.852	1.761	1,7	0.004	a	6.539	3.797	1.722	0.129
Males,1989							b	0.195	0.045	4.297	0.004
Selsey	9	0.511	0.715	1.042	1,7	0.03	a	11.881	2.248	5.286	0.001
Females, 1989							b	0.073	0.027	2.703	0.03
Selsey	8	0.917	0.958	2.499	1,6	<0.001	a	-11.621	4.611	-2.52	0.045
Males,1990							b	0.426	0.052	8.158	<0.001
Selsey	11	0.614	0.783	2.605	1,9	0.004	a	8.794	4.661	1.887	0.092
Females, 1990							b	0.188	0.05	3.782	0.004

Table A5iii.15 Polynomial regressions statistics for lobster CPI-CL relationships (5mm CL groups).

Site	N	R-Square	r	Sy/x	F(df,df)	P(F)		Coeff	P
Bridlington	10	0.878	0.93702	1.308	2,8	<0.001	a	19.09	0.002
Males, 1989							b	-0.1755	
							c	0.002	
Bridlington	12	0.458	0.67676	1.631	2,10	0.064	a	0.137	0.083
Females, 1989							b	0.3769	
							c	-0.002	
Bridlington	11	0.947	0.97314	1.882	2,9	<0.001	a	0.693	<0.001
Males, 1990							b	0.2275	
							c	7E-05	
Bridlington	12	0.304	0.55136	1.535	2,10	0.196	a	20.97	0.195
Females, 1990							b	-0.091	
							c	0.00029	
Dale	15	0.83	0.91104	2.674	2,13	<0.001	a	32.98	<0.001
Males, 1989							b	-0.4077	
							c	0.003	
Dale	14	0.178	0.4219	2.357	2,12	0.339	a	7.704	0.298
Females, 1989							b	0.2007	
							c	-0.00107	
Selsey	9	0.821	0.90609	1.536	2,7	0.006	a	-35.05	0.01
Males, 1989							b	1.229	
							c	-0.006	
Selsey	9	0.601	0.77524	1.017	2,7	0.064	a	-6.028	0.078
Females, 1989							b	0.5178	
							c	-0.003	
Selsey	8	0.919	0.95864	2.705	2,6	0.002	a	-19.43	0.003
Males, 1990							b	0.6004	
							c	-0.00094	
Selsey	11	0.62	0.7874	2.74	2,9	0.021	a	20.04	0.034
Females, 1990							b	-0.063	
							c	0.00135	

Table A5iii.16 ANCOVA results for CPL with CL at Bridlington, between years

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	114966.68	1	114966.68	1000	0
Effects	3998.6488	2	1999.3244	65.685	0
Sex	3817.8866	1	3817.8866	125.43	0
Year	186.6174	1	186.6174	6.131	0.0136
Sex and year interactions	40.154397	1	40.154397	1.319	0.2512
Residual	16345.349	537	30.438266		
Total	135350.84	541			

Table A5iii.17 ANCOVA results for AI with CL at Bridlington, between years

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	1655027	1	1655027	1000	0
Effects	195931.35	2	97965.68	70.103	0
Sex	191457.06	1	191457.06	137.004	0
Year	4681.3	1	4681.3	3.35	0.0678
Sex and year interactions	14353.704	1	14353.704	10.271	0.0014
Residual	750431.35	537	1397.4513		
Total	2615743.4	541			

Table A5iii.18 ANCOVA results for CPI with CL at Bridlington, between years

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	1067.7867	1	1067.7867	101.111	0
Effects	2436.8663	2	1218.4332	115.376	0
Sex	2431.4201	1	2431.4201	230.236	0
Year	4.671	1	4.671	0.442	0.5134
Sex and year interactions	8.0835535	1	8.0835352	0.765	0.3914
Residual	5671.0234	537	10.560565		
Total	9183.76	541			

Table A5iii.19 ANCOVA results for CPL with CL at Selsey, between years

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	78728.054	1	78728.054	1000	0
Effects	3717.4385	2	1858.7193	68.769	0
Sex	3606.5354	1	3606.5354	133.434	0
Year	102.284	1	102.384	3.784	0.521
Sex and year interactions	47.998545	1	47.998545	1.776	0.183
Residual	23839.151	882	27.028552		
Total	106332.64	886			

Table A5iii.20 ANCOVA results for AI with CL at Selsey, between years

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	766223.36	1	766223.36	119.952	0
Effects	330223.15	2	165111.58	25.848	0
Sex	324958.24	1	324958.24	50.872	0
Year	4705.59	1	4705.59	0.737	0.4001
Sex and year interactions	177.69134	1	177.69134	0.028	0.8694
Residual	5633976	882	6387.7279		
Total	6730600.2	886			

Table A5iii.21 ANCOVA results for CPI with CL at Selsey, between years

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	442.65223	1	442.65223	4.169	0.0415
Effects	6707.453	2	3353.7265	31.584	0
Sex	6608.8607	1	6608.8607	62.239	0
Year	87.6901	1	87.6901	0.826	0.3734
Sex and year interactions	5.8909442	1	5.8909442	0.055	0.8164
Residual	93655.422	882	106.18529		
Total	100811.42	886			

Table A5iii.22 ANCOVA results for CPL with CL between Bridlington, Dale and Selsey males

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	289866.77	1	289866.77	1000	0
Effects	2933.8579	3	977.9526	23.586	0
Site	2909.9464	2	1454.9732	35.091	0
Year	89.3874	1	89.3874	2.156	0.1425
Site and year interactions	254.5552	1	254.5552	6.139	0.0135
Residual	29148.131	703	41.46249		
Total	322203.31	708			

Table A5iii.23 ANCOVA results for AI with CL between Bridlington, Dale and Selsey males

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	5693486.4	1	5693486.4	642.42	0
Effects	214013.2	3	71337.73	8.049	0
Site	214013.19	2	107006.59	12.074	0
Year	2649.54	1	2649.54	0.299	0.5906
Site and year interactions	10327.12	1	10327.12	1.165	0.2807
Residual	6230383	703	8862.5647		
Total	12148210	708			

Table A5iii.24 ANCOVA results for CPI with CL between Bridlington, Dale and Selsey males

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	3587.1181	1	3587.1181	26.55	0
Effects	3621.9478	3	1207.3159	8.971	0
Site	137.3808	2	1798.956	13.367	0
Year	7.0202906	1	137.3808	1.021	0.3127
Site and year interactions	7.0202906	1	7.0202906	0.052	0.8218
Residual	94608.48	703	134.57821		
Total	101824.57	708			

Table A5iii.25 ANCOVA results for AI with CL between sites at Bridlington, Dale, Selsey, Staithes and St. Davids males

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	14221312	1	14221212	100	0
Site effect	415663.44	4	103915.86	16.365	0
Residual	7461135.4	1175	6349.9025		
Total	22098110	1180			

Table A5iii.26 ANCOVA results for AI with CL at Selsey, between years at Bridlington, Dale, Selsey, Staithes and St. Davids males

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	14221312	1	14221312	1000	0
Year effect	162487.69	2	81243.847	12.396	0
Residual	7714311.2	1177	6554.2151		
Total	22098110	1180			

Table A5iii.27 ANCOVA results for CPL with CL between Bridlington, Dale and Selsey females

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	188892.57	1	188892.57	1000	0
Effects	2670.223	3	890.0743	53.695	0
Site	2560.4685	2	1280.2343	77.232	0
Year	86.704	1	86.704	5.231	0.0224
Site and year interactions	5.990635	1	5.9906935	0.361	0.5543
Residual	14471.209	873	16.576414		
Total	206040	878			

Table A5iii.28 ANCOVA results for AI with CL between Bridlington, Dale and Selsey females

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	1222518.4	1	1222518.4	100	0
Effects	35299.935	3	11766.645	39.486	0
Site	35264.369	2	17632.185	59.17	0
Year	0.855	1	0.855	0.003	0.9579
Site and year interactions	344.4957	1	344.4957	1.156	0.2826
Residual	260149.1	873	297.99438		
Total	1518311.9	878			

Table A5iii.29 ANCOVA results for CPI with CL between Bridlington, Dale and Selsey females

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	262.6607	1	262.66701	56.519	0
Effects	688.01619	3	229.33873	49.348	0
Siite	681.62862	2	340.81431	73.334	0
Year	0.72516	1	0.72516	0.156	0.6972
Site and year interactions	14.303513	1	14.303513	3.078	0.0797
Residual	4057.1835	873	4.6474037		
Total	5022.1702	878			

Table A5iii.30 ANCOVA results for CPL with CL at Bridlington 1989, between sexes

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	50644.778	1	50644.778	1000	0
Sex effect	2856.9858	1	2856.9858	110.735	0
Residual	11455.257	444	25.800128		
Total	64957.02	446			

Table A5iii.31 ANCOVA results for AI with CL at Bridlington 1989, between sexes

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	472712.49	1	472712.49	711.397	0
Sex effect	120182.97	1	120182.97	180.866	0
Residual	295031.11	444	664.48447		
Total	887926.56	446			

Table A5iii.32 ANCOVA results for CPI with CL at Bridlington 1989, between sexes

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	409.66116	1	409.66116	41.172	0
Sex effect	1902.7387	1	1902.7387	191.23	0
Residual	4417.8078	444	9.9500176		
Total	6730.2077	446			

Table A5iii.33 ANCOVA results for CPL with CL at Bridlington 1990, between sexes

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	61642.117	1	61642.117	1000	0
Sex effect	870.00021	1	870.00021	17.405	0.001
Residual	4598.7884	92	49.986831		
Total	67110.905	94			

Table A5iii.34 ANCOVA results for AI with CL at Bridlington 1990, between sexes

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	1231044.4	1	1231044.4	301.8	0
Sex effect	67150.152	1	67150.152	16.462	0.001
Residual	375269.18	92	4079.0128		
Total	1673463.7	94			

Table A5iii.35 ANCOVA results for CPI with CL at Bridlington 1990, between sexes

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	680.45438	1	680.45438	50.097	0
Sex effect	519.8002	1	519.8002	38.27	0
Residual	1249.5995	92	13.582603		
Total	2449.8541	94			

Table A5iii.36 ANCOVA results for CPL with CL at Dale 1989, between sexes

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	70511.894	1	70511.894	1000	0
Sex effect	7412.9088	1	7412.9088	109.825	0
Residual	10597.098	157	67.497437		
Total	88521.9	159			

Table A5iii.37 ANCOVA results for AI with CL at Dale 1989, between sexes

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	1292621.9	1	1292621.9	239.842	0
Sex effect	652402.15	1	652402.15	121.051	0
Residual	846147.58	157	5389.475		
Total	2791171.6	157			

Table A5iii.38 ANCOVA results for CPI with CL at Dale 1989, between sexes

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	250.53273	1	250.53273	14.527	0.0002
Sex effect	2920.1068	1	2920.1068	169.32	0
Residual	2707.635	157	17.246083		
Total	5878.2745	159			

Table A5iii.39 ANCOVA results for CPL with CL at Selsey 1989, between sexes

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	60472.559	1	60472.559	1000	0
Sex effect	3568.7705	1	3568.7705	227.088	0
Residual	11535.091	734	15.715382		
Total	75576.421	736			

Table A5iii.40 ANCOVA results for AI with CL at Selsey 1989, between sexes

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	605215.34	1	605215.34	82.551	0
Sex effect	274018.01	1	274018.01	37376	0
Residual	5381232.2	734	7331.3791		
Total	6260465.6	736			

Table A5iii.41 ANCOVA results for CPI with CL at Selsey 1989, between sexes

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	785.4348	1	785.4348	6.376	0.0118
Sex effect	5909.5963	1	5909.5963	47.974	0
Residual	90416.16	734	123.18278		
Total	97111.191	736			

Table A5iii.42 ANCOVA results for CPL with CL at Selsey 1990, between sexes

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	15089.026	1	15089.026	189.804	0
Sex effect	166.82583	1	166.82583	2.098	0.1496
Residual	11606.725	146	79.498118		
Total	26862.577	148			

Table A5iii.43 ANCOVA results for AI with CL at Selsey 1990, between sexes

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	147562.22	1	147562.22	87.404	0
Sex effect	50587.377	1	50587.377	29.964	0
Residual	246488.96	146	1688.2805		
Total	444638.55	148			

Table A5iii.44 ANCOVA results for CPI with CL at Selsey 1990, between sexes

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	5.9897793	1	5.9897793	0.299	0.5913
Sex effect	732.08016	1	732.08016	36.529	0
Residual	2925.98	146	20.041014		
Total	3664.058	148			

Table A5iii.45 Male and female CPL-CL linear regression intersections

Site	CL (mm)	CPL (mm
Bridlington, 1989	72.7305	88.81
Bridlington, 1990	76.897	94.547
Dale, 1989	86.92	108.164
Selsey, 1989	65.912	83.1345
Selsey, 1990	73.7545	94.57

Table A5iii.46 Male and female AI-CL linear regression intersections

Site	CL (mm)	AI
Bridlington, 1989	74.159	94.1187
Bridlington, 1990	78.682	101.346
Dale, 1989	88.717	133.0921
Selsey, 1989	60.178	52.09
Selsey, 1990	65.088	34.256

Table A5iii.47 Male and female CPI-CL linear regression intersections

Site	CL (mm)	CPI
Bridlington, 1989	69.821	16.63
Bridlington, 1990	71.415	16.58
Dale, 1989	80.636	17.428
Selsey, 1989	58.93	17.7023
Selsey, 1990	76.846	22.613

Table A5iii.48 Male and female CPL-CL Natural logarithm regression intersections

Site	CL (mm)	CPL (mm
Bridlington, 1989	71.179	86.808
Bridlington, 1990	73.95	91.019
Dale, 1989	83.59	103.736
Selsey, 1989	68.395	85.056
Selsey, 1990	59.921	78.381

Table A5iii.49 Male and female AI-CL Natural logarithm regression intersections

Site	CL (mm)	AI
Bridlington, 1989	70.149	81.264
Bridlington, 1990	71.707	85.3189
Dale, 1989	79.53	110.464
Selsey, 1989	58.653	52.91
Selsey, 1990	69.59	97.185

Table A5iii.50 Male and female CPL-CL Natural logarithm regression intersections

Site	CL (mm)	CPI
Bridlington, 1989	70.149	16.518
Bridlington, 1990	71.762	16.594
Dale, 1989	80.053	17.486
Selsey, 1989	59.316	15.596
Selsey, 1990	69.552	20.067

Table A5iii.51 Male and female CPL-CL polynomial regression intersections

Site	CL (mm)	CPL (mm
Bridlington, 1989	-	-
Bridlington, 1990	69.059	86.017
Dale, 1989	95.45	117.086
Selsey, 1989	59.776	75.094
Selsey, 1990	-	-

Table A5iii.52 Male and female AI-CL polynomial regression intersections

Site	CL (mm)	AI
Bridlington, 1989	-	-
Bridlington, 1990	73.393	91.7684
Dale, 1989	-	-
Selsey, 1989	67.669	77.012
Selsey, 1990	-	-

Table A5iii.53 Male and female CPI-CL polynomial regression intersections

Site	CL (mm)	CPI
Bridlington, 1989	-	-
Bridlington, 1990	-	-
Dale, 1989	-	-
Selsey, 1989	-	-
Selsey, 1990	-	-

Table A5iii.54 Potential inflexion points, AI plots

Site	CL (mm)
Bridlington, 1989	77.5
Bridlington, 1990	90
Dale, 1989	102.5
Selsey, 1989	77.5
Selsey, 1990	-
Staithes, 1980 to 1981	83.5
St. Davids, 1980 to 1981	86.5

Table A5iii.55 RHW-CL linear regression statistics

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Dale, 1989	6	0.221	0.47	0.583	1,4	0.347	a	2.523	1.458	1.73	0.159
							b	0.015	0.014	1.064	0.347
Bridlington,	11	0.000626	0.025	0.674	1,9	0.942	a	4.191	2.992	1.401	0.195
1989 to 1990							b	0.003	0.034	0.075	0.942
Selsey,	23	0.038	0.195	0.853	1,21	0.373	a	2.463	2.307	1.068	0.298
1989 to 1991							b	0.024	0.027	0.91	0.373

Table A5iii.56 RHW-CL polynomial regression statistics

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	P
Dale, 1989	6	0.934	0.9664	0.196	2,4	0.017	a	21.88	0.019
							b	-0.3489	
							c	0.001661	
Bridlington,	11	0.229	0.4785	0.628	2,9	0.353	a	-51.61	0.307
1989 to 1990							b	1.29	
							c	-0.007	
Selsey,	23	0.101	0.3178	0.845	2,21	0.345	a	-0.1402	0.302
1989 to 1991							b	0.4525	
							c	-0.003	

Table A5iii.57 RHW-CL natural logarithm linear regression statistics

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Dale, 1989	6	0.128	0.357	0.147	1,4	0.487	a	0.056	1.747	0.032	0.976
							b	0.289	0.378	0.765	0.487
Bridlington,	11	0.001119	0.033	0.164	1,9	0.922	a	1.15	3.231	0.356	0.73
1989 to 1990							b	0.073	0.724	0.1	0.922
Selsey,	23	0.046	0.214	0.85	1,21	0.327	a	-4.582	9.104	-0.503	0.62
1989 to 1991							b	2.051	2.042	1.004	0.327

Table A5iii.58 VDW-CL linear regression statistics

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Dale, 1989	6	0.969	0.985	0.152	1,4	<0.001	a	-3.28	0.381	-8.616	<0.001
							b	0.041	0.004	11.241	<0.001
Bridlington,	11	0.5	0.707	0.157	1,9	0.015	a	-1.532	0.697	-2.199	0.055
1989 to 1990							b	0.024	0.008	3.003	0.15
Selsey,	23	0.377	0.614	0.194	1,21	0.002	a	-1.265	0.524	-2.415	0.025
1989 to 1991							b	0.022	0.006	3.564	0.002

Table A5iii.59 VDW-CL polynomial regression statistics

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	P
Dale, 1989	6	0.991	0.995	0.097	2,4	<0.001	a	1.119	0.001
							b	-0.042	
							c	0.000377	
Bridlington,	11	0.772	0.8786	0.112	2,9	0.003	a	-21.57	0.006
1989 to 1990							b	0.4865	
							c	-0.003	
Selsey,	23	0.388	0.6229	0.197	2,21	0.007	a	0.71	0.02
1989 to 1991							b	-0.03	
							c	0.000327	

Table A5iii.60 VDW-CL natural logarithm linear regression statistics

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Dale, 1989	6	0.968	0.984	0.16	1,4	<0.001	a	-21.115	1.903	-11.095	<0.001
							b	4.502	0.412	10.932	<0.001
Bridlington,	11	0.547	0.74	0.441	1,9	0.009	a	-29.38	8.69	-3.381	0.008
1989 to 1990							b	6.423	1.947	3.3	0.009
Selsey,	23	0.657	0.811	0.331	1,21	<0.001	a	23.111	3.545	-6.52	<0.001
1989 to 1991							b	5.045	0.795	6.345	<0.001

Table A5iii.61 RVDW-CL linear regression statistics

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Dale, 1989	6	0.567	0.753	0.00029	1,4	0.084	a	-0.000394	0.0007252	-0.544	0.615
							b	1.595E-05	6.968E-06	2.289	0.084
Bridlington,	11	0.171	0.414	0.000354	1,9	0.205	a	-0.001037	0.001571	-0.661	0.525
1989 to 1990							b	2.458E-05	1.801E-05	1.365	0.205
Selsey,	23	0.011	0.107	0.001892	1,21	0.629	a	0.0007416	0.005	-0.145	0.886
1989 to 1991							b	2.895E-05	5.897E-05	0.491	0.629

Table A5iii.62 RVDW-CL polynomial regression statistics

Site	N	R-Square	r	Sy/x	F(df, df)	P(F)		Coeff	P
Dale, 1989	6	1	1	2.19E+228	2,4		a	-8.75E-05	<0.001
							b	1.02E-05	
							c	2.64E-08	
Bridlington,	11	1	1	2.19E+228	2,9		a	-0.047	<0.001
1989 to 1990							b	0.001096	
							c	-6.15E-06	
Selsey,	23	0.027	0.164	0.001847	2,21	0.763	a	-0.02	0.607
1989 to 1991							b	0.0005417	
							c	-3.27E-06	

Table A5iii.63 RVDW-CL natural logarithm linear regression statistics

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Dale, 1989	6	0.541	0.736	0.255	1,4	0.096	a	-13.331	3.038	-4.388	0.012
							b	1.428	0.657	2.172	0.096
Bridlington,	11	0.31	0.557	0.416	1,9	0.075	a	-23.361	8.192	-2.852	0.019
1989 to 1990							b	3.69	1.835	2.011	0.075
Selsey,	23	0.125	0.353	0.549	1,21	0.098	a	-16.744	5.887	-2.844	0.01
1989 to 1991							b	2.285	1.321	1.73	0.098

Table A5iii.64 Vdf-CL linear regression statistics

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Dale, 1989	6	0.794	0.891	9.979	1,4	0.017	a	-24.63	24.943	-0.987	0.379
							b	0.942	0.24	3.929	0.017
Bridlington,	11	0.114	0.338	27.821	1,9	0.309	a	-51.103	123.484	-0.414	0.689
1989 to 1990							b	1.526	1.416	1.078	0.309
Selsey,	23	0.056	0.237	31.049	1,21	0.276	a	-14.422	83.965	-0.172	0.865
1989 to 1991							b	1.083	0.968	1.12	0.276

Table A5iii.65 Vdf-CL polynomial regression statistics

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	P
Dale, 1989	6	0.882	0.9391	8.713	2,4	0.04	a	-251.2	0.044
							b	5.199	
							c	-0.019	
Bridlington,	11	0.696	0.8343	17.301	2,9	0.009	a	-395.2	0.016
1989 to 1990							b	91.54	
							c	-0.5169	
Selsey,	23	0.067	0.2588	31.627	2,21	0.497	a	-269.1	0.405
1989 to 1991							b	7.7	
							c	-0.042	

Table A5iii.66 Vdf-CL natural logarithm linear regression statistics

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Dale, 1989	6	0.769	0.877	0.16	1,4	0.022	a	-2.694	1.903	-1.416	0.23
							b	1.502	0.412	3.647	0.022
Bridlington,	11	0.255	0.505	0.441	1,9	0.113	a	-10.949	8.694	-1.259	0.24
1989 to 1990							b	3.421	1.947	1.757	0.113
Selsey,	23	0.114	0.338	0.421	1,21	0.115	a	-3.126	4.512	-0.693	0.496
1989 to 1991							b	1.664	1.012	1.644	0.115

Table A5iii.67 Vdf-RHW linear regression statistics

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Dale, 1989	6	0.052	0.228	21.422	1,4	0.665	a	41.352	66.286	0.624	0.567
							b	7.578	16.211	0.467	0.665
Bridlington,	11	0.164	0.405	27.029	1,9	0.217	a	3.276	59.565	0.055	0.957
1989 to 1990							b	17.761	13.636	1.329	0.217
Selsey,	23	0.367	0.605	25.438	1,21	0.002	a	-22.089	29.563	-0.747	0.463
1989 to 1991							b	22.248	6.382	3.486	0.002

Table A5iii.68 Vdf-RHW polynomial regression statistics

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	P
Dale, 1989	6	0.434	0.6588	19.104	2,4	0.425	a	792.6	0.362
							b	-351.5	
							c	42.12	
Bridlington,	11	0.655	0.8093	18.407	2,9	0.014	a	905.6	0.025
1989 to 1990							b	-424.8	
							c	52.94	
Selsey,	23	0.369	0.6075	26.01	2,21	0.01	a	-76.79	0.025
1989 to 1991							b	47.42	
							c	-2.796	

Table A5iii.69 Vdf-RHW natural logarithm linear regression statistics

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Dale, 1989	6	0.932	0.965	0.176	1,4	0.002	a	-12.333	2.101	-5.869	0.004
							b	3.363	0.455	7.396	0.002
Bridlington,	11	0.569	0.754	0.185	1,9	0.007	a	-9.49	3.638	-2.609	0.028
1989 to 1990							b	2.81	0.815	3.448	0.007
Selsey,	23	0.739	0.86	0.185	1,21	<0.001	a	-12.375	1.983	-6.24	<0.001
1989 to 1991							b	3.434	0.445	7.718	<0.001

Table A5iii.70 HWT-CL linea regression statistics (5 mm CL groups)

Site	N	R-square	r	S/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Dale, 1989	4	0.959	0.979	6.32	1,2	0.021	a	-72.542	15.545	-4.666	0.043
							b	0.995	0.145	6.853	0.021
Bridlington,	5	0.72	0.849	3.48	1,3	0.069	a	-34.583	20.254	-1.707	0.186
1989 to 1990							b	0.641	0.231	2.778	0.069
Selsey,	6	0.874	0.935	2.77	1,4	0.006	a	-24.801	8.108	-3.059	0.038
1989 to 1991							b	0.509	0.096	5.278	0.006

Table A5iii.71 HWT-CL polynomial regression statistics (5 mm CL groups)

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	P
Dale, 1989	4	0.995	0.995	2.974	2,2	0.07	a	78.14	0.063
							b	-1.825	
							c	0.013	
Bridlington,	5	0.978	0.989	1.252	2,3	0.022	a	-527.8	0.022
1989 to 1990							b	11.99	
							c	-0.065	
Selsey,	6	0.956	0.978	1.821	2,4	0.009	a	-110.6	0.011
1989 to 1991							b	2.711	
							c	-0.014	

Table A5iii.72 RHW-CL linear regression statistics (5 mm CL groups)

Site	N	R-square	r	Sy/	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Dale, 1989	4	0.328	0.573	0.68	1,2	0.427	a	0.2591	1.682	1.54	0.263
							b	0.016	0.016	0.988	0.427
Bridlington,	5	0.035	0.187	0.43	1,3	0.763	a	3.617	2.363	1.53	0.223
1989 to 1990							b	0.009	0.027	0.33	0.763
Selsey,	6	0.255	0.505	0.74	1,4	0.307	a	1.862	2.245	0.829	0.453
1989 to 1991							b	0.031	0.027	1.17	0.307

Table A5iii.73 RHW-CL polynomial regression statistics (5 mm CL groups)

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	P
Dale, 1989	4	0.991	0.995	3.796	2,2	0.093	a	-265.1	0.083
							b	5.397	
							c	-0.02	
Bridlington,	5	0.823	0.907	0.223	2,3	0.177	a	-50.56	0.164
1989 to 1990							b	1.255	
							c	-0.007	
Selsey,	6	0.592	0.769	24.679	2,4	0.261	a	-844.1	0.237
1989 to 1991							b	22.45	
							c	-0.1341	

Table A5iii.74 VDWT-CL linear regression statistics (5 mm CL groups)

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Dale, 1989	4	0.857	0.926	0.00021	1,2	0.074	a	-0.000606	0.0005445	-1.112	0.382
							b	1.763E-05	5.087E-06	3.466	0.074
Bridlington,	5	0.41	0.64	0.00037	1,3	0.245	a	-0.001907	0.002	-0.939	0.417
1989 to 1990							b	3.36E-05	2.313E-05	1.443	0.245
Selsey,	6	0.065	0.255	0.003	1,4	0.626	a	-0.003	0.01	-0.282	0.792
1989 to 1991							b	6.522E-05	0.0001237	0.527	0.626

Table A5iii.75 VDWT-CL polynomial regression statistics (5 mm CL groups)

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	P
Dale, 1989	4	1	1	2E+228	2,2	<0.001	a	-0.002	<0.001
							b	4.4E-05	
							c	-1.19E-07	
Bridlington,	5	1	1	2E+228	2,3	<.001	a	-0.051	<0.001
1989 to 1990							b	0.001168	
							c	6.48E-06	
Selsey,	6	0.142	0.3768	0.004	2,4	0.795	a	-0.052	0.653
1989 to 1991							b	0.001313	
							c	-7.82E-06	

Table A5iii.76 RVDW-CL linear regression statistics (5 mm CL groups)

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Dale, 1989	4	0.988	0.994	0.129	1,2	0.006	a	-3.155	0.333	-9.481	0.011
							b	0.04	0.003	12.838	0.006
Bridlington,	5	0.665	0.816	0.171	1,3	0.092	a	-1.792	0.951	-1.885	0.156
1989 to 1990							b	0.026	0.011	2.443	0.092
Selsey,	6	0.778	0.882	0.134	1,4	0.02	a	-0.998	0.405	-2.464	0.069
1989 to 1991							b	0.018	0.005	3.749	0.02

Table A5iii.77 RVDW-CL polynomial regression statistics (5 mm CL groups)

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	P
Dale, 1989	4	1	1	0.00168	2,2	<0.001	a	0.286	<.001
							b	-0.024	
							c	0.00039	
Bridlington,	5	0.993	0.9965	0.031	2,3	0.007	a	-25.64	0.007
1989 to 1990							b	0.5752	
							c	-0.003	
Selsey,	6	0.826	0.9088	0.137	2,4	0.072	a	-3.462	0.076
1989 to 1991							b	0.081	
							c	-0.000397	

Table A5iii.78 Vdf-CL linear regression statistics (5 mm CL groups)

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Dale, 1989	4	0.896	0.947	0.934	1,2	0.053	a	-26.695	24.069	-1.109	0.383
							b	0.935	0.225	4.158	0.053
Bridlington, 1989 to 1990	5	0.307	0.554	31.055	1,3	0.333	a	-123.209	172.419	-0.715	0.526
							b	2.264	1.964	1.153	0.333
Selsey, 1989 to 1991	6	0.197	0.444	29.964	1,4	0.377	a	-10.66	90.766	-0.117	0.912
							b	1.07	1.079	0.992	0.377

Table A5iii.79 CPW-CL linear regression statistics

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Staithes	129	0.859	0.927	33.298	1,127	<0.001	a	-320.706	15.607	-20.55	<0.001
1980 to 1981							b	4.654	0.167	27.862	<0.001
St. Davids,	121	0.841	0.917	41.674	1,119	<0.001	a	-389.336	20.959	-18.576	<0.001
1980 to 1981							b	5.236	0.208	25.116	<0.001

Table A5iii.80 CPW-CL polynomial regression statistics

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	P
Staithes,	129	0.945	0.9721	20.928	2,127	<0.001	a	376.7	<.001
							b	-10.58	
1980 to 1981							c	0.08	
St. Davids,	121	0.911	0.9545	31.273	2,119	<.001	a	330.3	<0.001
							b	-8.936	
1980 to 1981							c	0.067	

Table A5iii.81 CPW-CL natural logarithm linear regression statistics

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Staithes	129	0.969	0.984	0.141	1,127	<0.001	a	-14.013	0.293	-47.89	<0.001
1980 to 1981							b	4.081	0.065	62.836	<0.001
St. Davids,	121	0.877	0.937	0.325	1,119	<0.001	a	-12.92	0.422	-30.611	<0.001
1980 to 1981							b	3.862	0.092	41.529	<0.001

Table A5iii.82 RCPW-CL linear regression statistics

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Staithes	139	0.375	0.613	0.468	1,137	<0.001	a	-4.108	0.931	-4.411	<0.001
1980 to 1981							b	1.877	0.207	9.07	<0.001
St. Davids,	122	0.837	0.915	0.284	1,120	<0.001	a	-2.286	0.142	-16.08	<0.001
1980 to 1981							b	0.035	0.001412	24.816	<0.001

Table A5iii.83 RCPW-CL polynomial regression statistics

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	P
Staithes,	129	0.925	0.9618	0.184	2,127	<0.001	a	1.725	<.001
							b	-0.05	
1980 to 1981							c	0.000452	
St. Davids,	121	0.862	0.9284	0.262	2,119	<.001	a	0.629	<0.001
							b	-0.022	
1980 to 1981							c	0.000274	

Table A5iii.84 RCPW-CL natural logarithm linear regression statistics

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Staithes	129	0.947	0.973	0.14	1,127	<0.001	a	-14.073	0.292	-48.256	<0.001
1980 to 1981							b	3.094	0.065	47.799	<0.001
St. Davids,	122	0.886	0.941	0.182	1,120	<0.001	a	-12.871	0.423	-30.399	<0.001
1980 to 1981							b	2.815	0.092	30.471	<0.001

Table A5iii.85 VDWT-CL linear regression statistics

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Staithes	139	0.704	0.839	0.487	1,137	<0.001	a	-3.002	0.219	-13.7	<0.001
1980 to 1981							b	0.043	0.002	18.065	<0.001
St. Davids,	120	0.82	0.905	0.396	1,118	<0.001	a	-3.465	0.198	-17.492	<0.001
1980 to 1981							b	0.046	0.001965	23.16	<0.001

Table A5iii.86 VDWT-CL polynomial regression statistics

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	P
Staithes,	129	0.807	0.8983	0.395	2,127	<0.001	a	4.514	<.001
							b	-0.1226	
1980 to 1981							c	0.000875	
St. Davids,	121	0.876	0.9359	0.33	2,119	<.001	a	2.277	<0.001
							b	-0.067	
1980 to 1981							c	0.000537	

Table A5iii.87 VDWT-CL natural logarithm linear regression statistics

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Staithes	139	0.84	0.917	0.397	1,137	<0.001	a	-21.791	0.791	-27.566	<0.001
1980 to 1981							b	4.717	0.176	26.856	<0.001
St. Davids,	120	0.816	0.903	0.39	1,118	<0.001	a	-21.057	0.907	-23.214	<0.001
1980 to 1981							b	4.528	0.198	22.88	<0.001

Table A5iii.88 Vdf-CL linear regression statistics

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Staithes	139	0.284	0.533	42.527	1,137	<0.001	a	-50.308	19.136	-2.629	0.01
1980 to 1981							b	1.516	0.206	7.373	<0.001
St. Davids,	120	0.433	0.658	23.506	1,118	<0.001	a	-23.573	11.766	-2.003	0.047
1980 to 1981							b	1.108	0.117	9.49	<0.001

Table A5iii.89 Vdf-CL polynomial regression statistics

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	P
Staithes,	129	0.287	0.5357	42.586	2,127	<0.001	a	23.72	<.001
							b	-0.1108	
1980 to 1981							c	0.009	
St. Davids,	121	0.451	0.6716	23.232	2,119	<.001	a	-132.2	<0.001
							b	3.244	
1980 to 1981							c	-0.01	

Table A5iii.90 Vdf-CL natural logarithm linear regression statistics

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Staithes	139	0.375	0.613	0.468	1,137	<0.001	a	-4.108	0.931	-4.411	<0.001
1980 to 1981							b	1.877	0.207	9.07	<0.001
St. Davids,	120	0.461	0.679	0.28	1,118	<0.001	a	-2.144	0.651	-3.292	0.001
1980 to 1981							b	1.426	0.142	10.039	<0.001

Table A5iii.91 Vdf-CPWT linear regression statistics

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Staithes	128	0.31	0.556	42.443	1,126	<0.001	a	56.139	5.902	9.511	<0.001
1980 to 1981							b	0.32	0.043	7.517	<0.001
St. Davids,	115	0.396	0.63	24.256	1,113	<0.001	a	62.014	3.585	17.3	<0.001
1980 to 1981							b	0.19	0.022	8.616	<0.001

Table A5iii.92 Vdf-CPWT polynomial regression statistics

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	P
Staithes,	129	0.31	0.5568	42.609	2,127	<0.001	a	55.22	<.001
							b	0.3379	
1980 to 1981							c	-5.22E-05	
St. Davids,	121	0.471	0.6863	22.806	2,119	<0.001	a	47.09	<0.001
							b	0.404	
1980 to 1981							c	-0.000454	

Table A5iii.93 VDWT-CPWT linear regression statistics

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Staithes	128	0.849	0.922	0.355	1,126	<0.001	a	-0.098	0.049	-1.993	0.048
1980 to 1981							b	0.009	0.0003557	26.66	<0.001
St. Davids,	115	0.877	0.937	0.325	1,113	<0.001	a	-0.036	0.048	-0.756	0.451
1980 to 1981							b	0.008	0.0002965	28.439	<0.001

Table A5iii.94 VDWT-CPWT polynomial regression statistics

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	P
Staithes,	129	0.857	0.9257	0.347	2,127	<0.001	a	0.041	<.001
							b	0.007	
1980 to 1981							c	7.92E-06	
St. Davids,	121	0.877	0.9365	0.327	2,119	<0.001	a	-0.049	<0.001
							b	0.009	
1980 to 1981							c	3.78E-07	

Table A5iii.95 CPWT-CL linear regression statistics (5 mm CL groups)

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Staithes	15	0.89	0.943	42.476	1,13	<0.001	a	-366.717	50.7	-7.233	<0.001
1980 to 1981							b	5.203	0.508	10.248	<0.001
St. Davids,	18	0.854	0.924	71.619	1,16	<0.001	a	-457.568	70.869	-6.457	<0.001
1980 to 1981							b	6	0.621	9.662	<0.001

Table A5iii.96 CPWT-CL polynomial regression statistics (5 mm CL groups)

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	P
Staithes,	15	0.977	0.9884	20.278	2,13	<0.001	a	399.4	<0.001
							b	-11.32	
1980 to 1981							c	0.085	
St. Davids,	18	0.918	0.9581	55.315	2,16	<0.001	a	319.2	<0.001
							b	-8.695	
1980 to 1981							c	0.065	

Table A5iii.97 RCPWT-CL linear regression statistics (5 mm CL groups)

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Staithes	15	0.909	0.953	0.281	1,13	<0.001	a	-2.457	0.335	-7.33	<0.001
1980 to 1981							b	0.038	0.003	11.395	<0.001
St. Davids,	18	0.866	0.93	0.427	1,16	<0.001	a	-2.519	0.423	-5.962	<0.001
1980 to 1981							b	0.038	0.004	10.157	<0.001

Table A5iii.98 RCPWT-CL polynomial regression statistics (5 mm CL groups)

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	P
Staithes,	15	0.97	0.9849	0.169	2,13	<0.001	a	2.194	<0.001
							b	-0.062	
1980 to 1981							c	0.000514	
St. Davids,	18	0.891	0.9438	0.396	2,16	<0.001	a	0.536	<0.001
							b	-0.02	
1980 to 1981							c	0.000257	

Table A5iii.99 VDWT-CL linear regression statistics (5 mm CL groups)

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Staithes	15	0.891	0.944	14.064	1,13	<0.001	a	-68.581	16.787	-4.085	0.001
1980 to 1981							b	1.732	0.168	10.304	<0.001
St. Davids,	18	0.76	0.872	15.832	1,16	<0.001	a	-16.625	15.666	-1.061	0.304
1980 to 1981							b	0.976	0.137	7.111	<0.001

Table A5iii.100 VDWT-CL polynomial regression statistics (5 mm CL groups)

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	P
Staithes,	15	0.911	0.9545	13.233	2,13	<0.001	a	53.5	<0.001
							b	-0.9015	
1980 to 1981							c	0.014	
St. Davids,	18	0.782	0.8843	15.579	2,16	<0.001	a	-95.18	<0.001
							b	2.462	
1980 to 1981							c	-0.007	

Table A5iii.101 Vdf-CL linear regression statistics (5 mm CL groups)

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	Std. Error	t-statistic	P
Staithes	15	0.87	0.933	0.453	1,13	<0.001	a	-3.62	0.54	-6.7	<0.001
1980 to 1981							b	0.05	0.005	9.311	<0.001
St. Davids,	18	0.837	0.915	0.648	1,16	<0.001	a	-3.959	0.641	-6.171	<0.001
1980 to 1981							b	0.051	0.006	9.075	<0.001

Table A5iii.102 Vdf-CL polynomial regression statistics (5 mm CL groups)

Site	N	R-square	r	Sy/x	F(df,df)	P(F)		Coeff	P
Staithes,	15	0.98	0.9899	0.182	2,13	<0.001	a	4.853	<0.001
							b	-0.1324	
1980 to 1981							c	0.000937	
St. Davids,	18	0.894	0.9455	0.541	2,16	<0.001	a	2.289	<0.001
							b	-0.067	
1980 to 1981							c	0.000526	

Table A5iii.103 ANCOVA results for VDWT with CL between Bridlington, Dale and Selsey males

Source of variation	SSQ	df.	MSQ	Fs	Signif.
CL	3.897631	1	3.897631	101.433	0
Site	0.118498	2	0.059245	1.542	0.2278
Residual	1.383319	36	0.038426		
Total	5.39944	39			

Table A5iii.104 ANCOVA results for Vdf with CL between Bridlington, Dale and Selsey males

Source of variation	SSQ	df.	MSQ	Fs	Signif.
CL	1627.452	1	1627.452	2.114	0.1546
Site	2279.058	2	1139.529	1.48	0.2412
Residual	27717.61	36	769.9335		
Total	31624.12	39			

Table A5iii.105 ANCOVA results for HWT with CL between Bridlington, Dale and Selsey males

Source of variation	SSQ	df.	MSQ	Fs	Signif.
CL	2493.541	1	2493.541	136.637	0
Site	104.7626	2	52.38132	2.87	0.0697
Residual	656.9792	36	18.24942		
Total	3255.283	39			

Table A5iii.106 ANCOVA results for RHW with CL between Bridlington, Dale and Selsey males

Source of variation	SSQ	df.	MSQ	Fs	Signif.
CL	0.043285	1	0.043285	0.075	0.7891
Site	2.027113	2	1.013557	1.748	0.1886
Residual	20.87501	36	0.579861		
Total	22.9454	39			

Table A5iii.107 ANCOVA results for RVDWT with CL between Bridlington, Dale and Selsey males

Source of variation	SSQ	df.	MSQ	Fs	Signif.
CL	4.84E-06	1	4.84E-06	0.019	0.8932
Site	0.000199	2	9.94E-05	0.386	0.6828
Residual	0.009285	36	0.000258		
Total	0.009488	39			

Table A5iii.108 ANCOVA results for HWT with CL between Bridlington, Dale and Selsey males (5 mm CL groups)

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	2658.836	1	2658.836	1000	0
Site effect	1.364E-12	2	6.82E-13	1000	0
Residual	8.504E-28	11	7.73E-29		
Total	2658.836	14			

Table A5iii.109 ANCOVA results for RHW with CL between Bridlington, Dale and Selsey males (5 mm CL groups)

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	0.4039754	1	0.4039754	1.181	0.3004
Site effect	0.7754271	2	0.3877136	1.133	0.3568
Residual	3.7626546	11	0.3420595		
Total	4.9420571	14			

Table A5iii.110 ANCOVA results for VDWT with CL between Bridlington, Dale and Selsey males (5 mm CL groups)

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	3.6479423	1	3.6479423	87.632	0
Site effect	0.0638057	2	0.0319029	0.766	0.488
Residual	0.457908	11	0.041628		
Total	4.1696561	14			

Table A5iii.111 ANCOVA results for RVDWT with CL between Bridlington, Dale and Selsey males (5 mm CL groups)

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	3.77E-07	1	3.77E-07	0.085	0.7793
Site effect	9.538E-06	2	4.77E-06	1.073	0.3751
Residual	4.887E-05	11	4.43E-06		
Total	5.879E-05	14			

Table A5iii.112 ANCOVA results for Vdf with CL between Bridlington, Dale and Selsey males (5 mm CL groups)

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	1783.6787	1	1783.6787	2.784	0.1234
Site effect	1627.0231	2	813.51153	1.27	0.3191
Residual	7048.3275	11	640.75704		
Total	10459.029	14			

Table A5iii.113 ANCOVA results for VDWT with CL between Bridlington, Dale, Selsey Staithes and St. Davids males (5 mm CL groups)

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	62.789679	1	62.789679	247.537	0
Site effect	1.394685	4	0.3486712	1.375	0.2591
Residual	10.653621	42	0.2536576		
Total	74.837985	47			

Table A5iii.114 ANCOVA results for Vdf with CL between Bridlington, Dale, Selsey Staithes and St. Davids males (5 mm CL groups)

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	31867.887	1	31867.887	82.116	0
Site effect	7329.6741	4	1832.4185	4.722	0.0031
Residual	16299.441	42	388.08192		
Total	55497.001	47			

Table A5iii.115 ANCOVA results for CPWT with CL between Staithes and St. Davids males

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	1874437.6	1	1874437.6	1000	0
Site effect	11023.925	1	11023.925	7.897	0.0054
Residual	335015.76	240	1395.899		
Total	2220477.3	242			

Table A5iii.116 ANCOVA results for RCPWT with CL between Staithes and St. Davids males

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	94.378801	1	94.378801	1000	0
Site effect	0.7846119	1	0.7846119	12.413	0.0005
Residual	15.170517	240	0.0632105		
Total	110.33393	242			

Table A5iii.117 ANCOVA results for VDWT with CL between Staithes and St. Davids males

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	153.2803	1	762.563	762.563	0
Site effect	2.0702656	1	2.0702656	10.299	0.0015
Residual	48.241605	240	0.2010067		
Total	203.59217	242			

Table A5iii.118 ANCOVA results for Vdf with CL between Staithes and St. Davids males

Source of variation	SSQ	df	MSQ	Fs	Signif
Covariate (CL)	125563.52	1	125563.52	98.997	0
Site effect	10126.946	1	10126.946	7.984	0.0051
Residual	304405.16	240	1268.3548		
Total	440095.62	242			

Table A5iii.119 CPWT, RCPWT and VDWT plot intersections, Staithes and St. Davids

Site	Index	CL (mm)
Staithes, 1980 to 1981	CPW (g)	90
	RCPW	90
	VDW (g)	90
St. Davids, 1980 to 1981	CPW (g)	86.5
	RCPW	84.5
	VDW (g)	85.5

Table A5iv.1 ANOVA between external indicator methods

Source of variation	DF	SSQ	MSQ	F	P
Between sites	8	1152.8663	144.1083	1.598	0.164
Residual	32	2885.3402	90.1669		
Total	40	4038.2065			

Table A5iv.2 ANOVA of SOM results, between sites

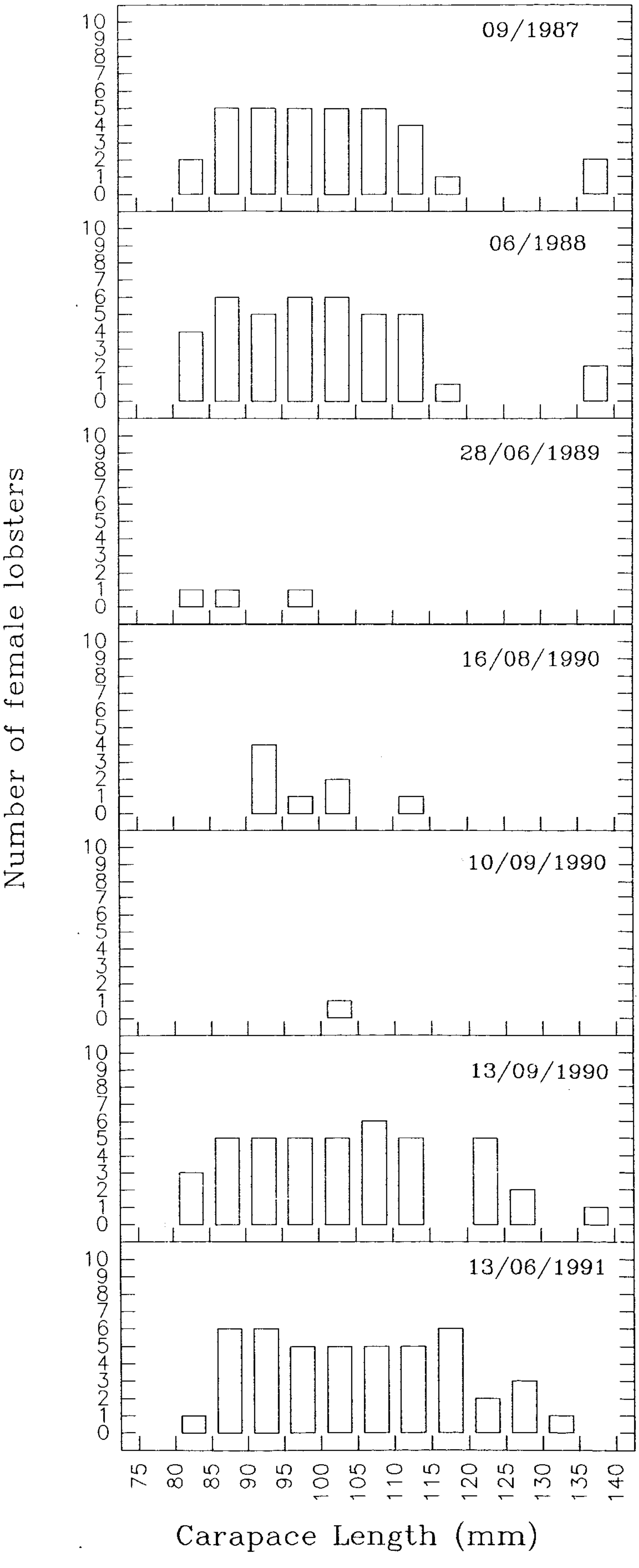
Source of variation	DF	SSQ	MSQ	F	P
Between sites	6	2698.5004	449.7501	11.414	<0.001
Residual	34	1339.7061	39.4031		
Total	40	4038.2065			

Table A5iv.3 Student-Newmann-Keuls pairwise comparisons test to investigate differences in SOM estimates between sites

Site and year	Bridlington 1990	Dale 1989	Selsey 1989	Selsey 1990	Staithes 1980 to 1981	St. Davids 1980 to 1981
Bridlington, 1989	n.s.	<0.005	<0.005	n.s.	n.s.	n.s.
Bridlington, 1990		<0.005	<0.005	n.s.	n.s.	n.s.
Dale, 1989			<0.005	<0.005	n.s.	n.s.
Selsey, 1989				n.s.	<0.005	<0.005
Selsey, 1990					n.s.	n.s.
Staithes, 1980 to 1981						n.s.

Size frequencies of females used in fecundity work

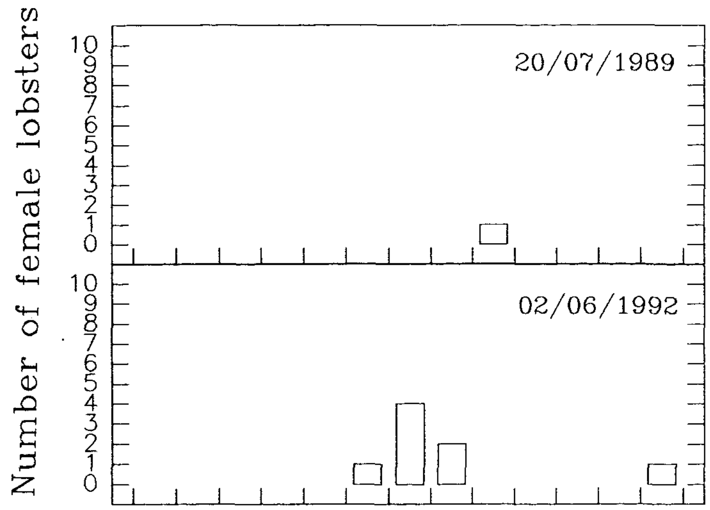
Bridlington 1987 to 1991



Appendix A6i.Fig. 1

Size frequencies of females used in fecundity work

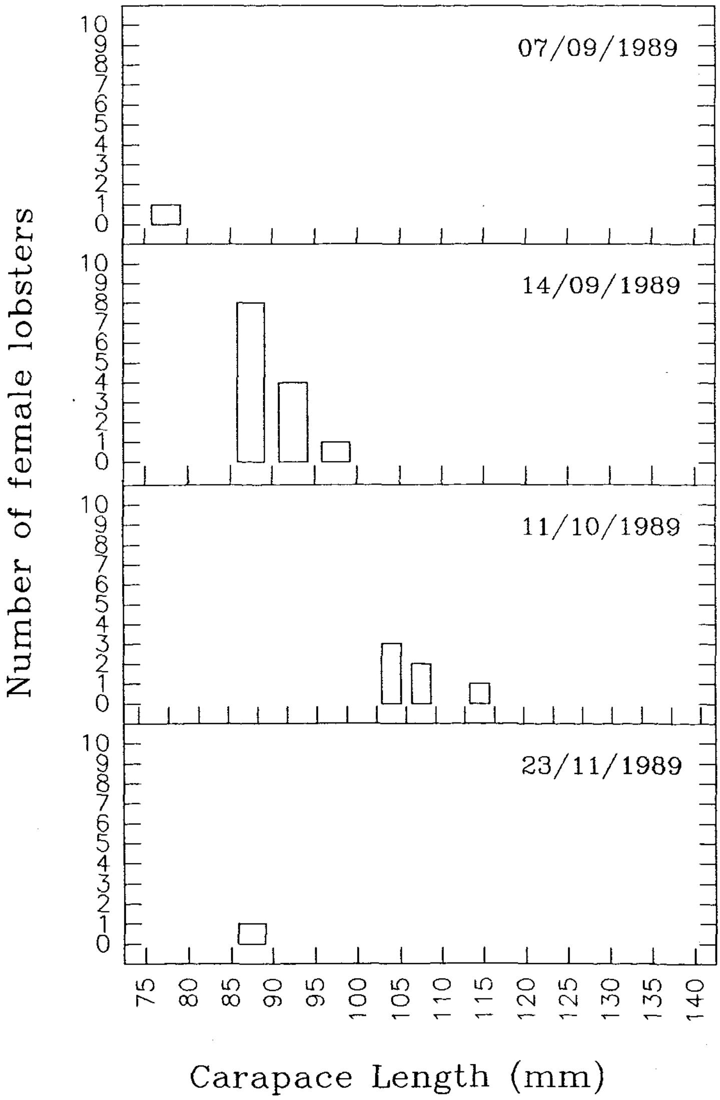
Dale 1989 and 1992



Appendix A6i.Fig. 2

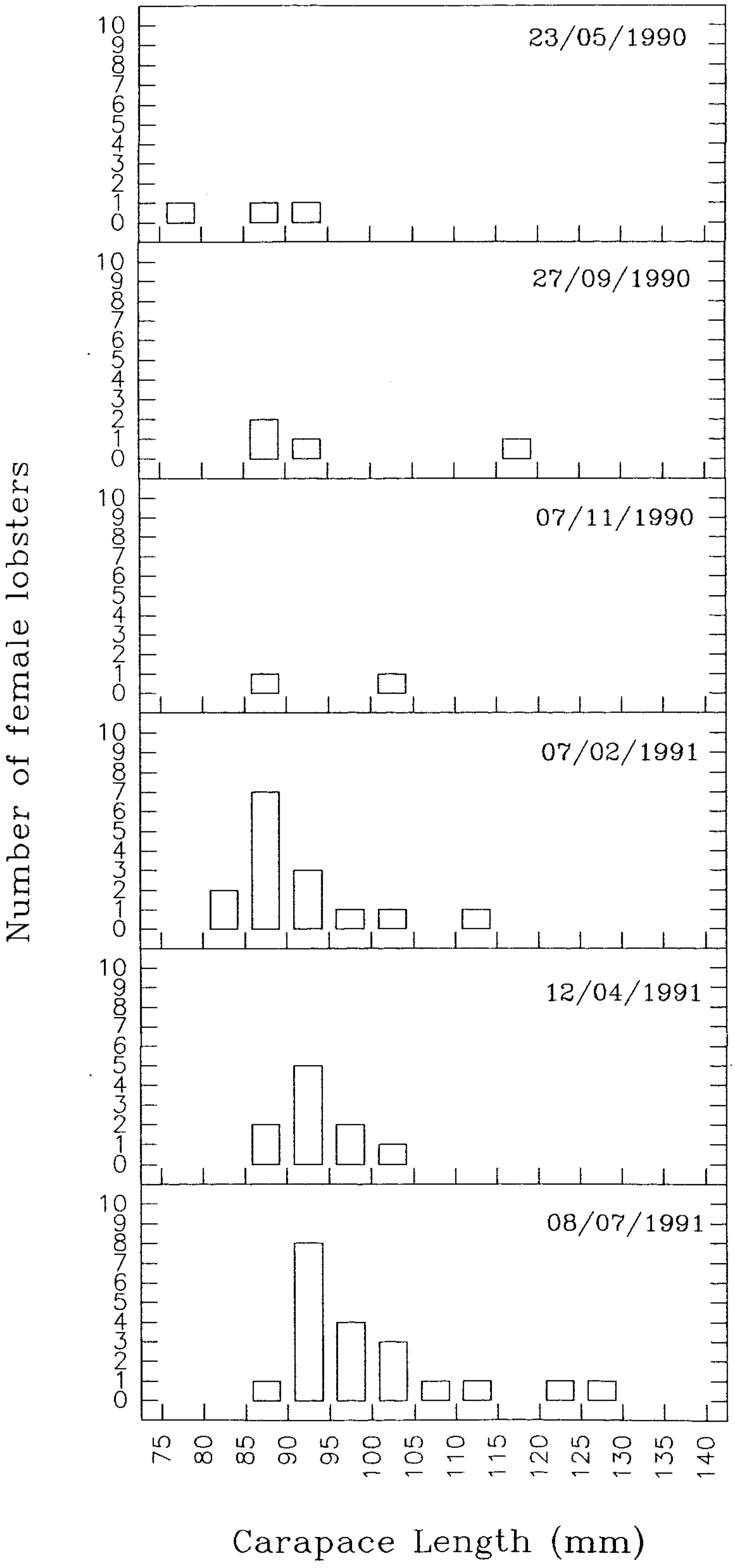
Size frequencies of females used in fecundity work

Selsey 1989



Appendix A6i.Fig. 3

Size frequencies of females used in fecundity work
Selsey 1990 and 1991



Appendix A6i.Fig. 4

Appendix Table A6i.1 Summary statistics of female sizes used for fecundity studies

Site	Sample size	Average CL (mm)	Median CL (mm)	Minimum CL (mm)	Maximum CL (mm)	Std. Dev. CL (mm)
Bridlington						
09/1987	34	101.382	100	83	136	12.5626
06/1988	40	99.95	98	81	139	13.1382
28/06/1989	3	89.667	89	84	96	6.0277
16/08/1990	8	97.25	94.5	91	111	7.0051
10/09/1990	1	103	103	103	103	0
13/09/1990	45	105.444	102	81	155	15.9567
13/06/1991	45	105.111	103	84	131	13.0405
Dale						
20/07/1989	1	115	115	115	115	0
02/06/1992	8	111.375	108	101	139	11.7466
Selsey						
07/09/1989	4	87.25	89.5	76	94	7.80491
14/09/1989	13	88.6923	89	85	98	3.75021
11/10/1989	6	90.5	89	86	101	5.46809
23/11/1989	1	89	89	89	89	0
23/05/1990	3	85.6667	88	79	90	5.85947
27/09/1990	4	95.75	89.5	87	117	14.2215
07/11/1990	2	93	93	85	101	11.3137
07/02/1991	15	90.667	88	84	110	7.04746
12/04/1991	10	92.6	91.5	85	101	4.7888
08/07/1991	20	98.85	96.5	86	126	10.8544

Appendix Table A6ii.1 Repeat counts of clutch sizes used for comparisons of methodology

Egg no. by hand count	Egg no. by subsample count		Egg no. by hand count	Egg. no. by machine count
11252	11356		11808	11798
7393	7302		17818	17425
9370	9478		9942	8693
12166	11901		12066	11962
10344	10568		9059	9510
8089	8220		6588	6357
8757	8898		11494	11009
10041	9778		10589	10489
10822	10443		9558	8923
10742	10718		19088	18178

Appendix Table A6ii.2 Results of t-Test comparing hand counted and subsample-counted clutch size estimates

	N	Mean	Std. Dev.	SEM	t	df	P
Hand count	10	9897.6	1486.636	470.1157	0.048	18	0.962
Subsample count	10	9866.2	1425.626	450.8225			
Difference		31.4		651.3445			

Appendix Table A6ii.3 Results of t-Test comparing hand counted and automatic machine-counted clutch size estimates

	N	Mean	Std. Dev.	SEM	t	df	P
Hand count	10	11800	3860.325	1220.742	0.216	18	0.832
Machine count	10	11430	3743.95	1183.9409			
Difference		370		1700.5667			

Appendix Table A6ii.4 Bridlington 1987 fecundity estimates

Date	CL (mm)	AW (mm)	Number of eggs	Counting Method	Number of eggs^2	Counting Method^2	Egg Diameter	Std. Dev. Egg Diam	P.E.I.
22/09/1987	93	55	9942	1	8693	3	1.94125	0.155826	0
22/09/1987	104	63	11576	1			1.8212	0.12303	0
22/09/1987	97	61	13704	2			1.92775	0.105658	150
22/09/1987	98	63	9476	3			1.7074	0.138018	0
22/09/1987	93	58	10083	1			1.74375	0.098393	0
22/09/1987	112	73	21075	1			2.05225	0.124233	0
22/09/1987	88	58	12066	1	11962	3	1.7875	0.088828	0
22/09/1987	107	69	16923	1			2.0465	0.125151	0
23/09/1987	88	53	7396	3			1.812	0.113153	0
23/09/1987	98	59	8103	3			1.89825	0.121289	147.75
23/09/1987	93	56	9059	1	9510	3	1.94225	0.12677	202.75
24/09/1987	83	51	7010	3			1.844	0.122646	156.15
24/09/1987	102	63	14845	2			1.95525	0.108649	0
24/09/1987	93	57	11341	1			1.85425	0.086331	0
24/09/1987	88	54	11900	1			1.8088	0.16086	0
24/09/1987	136	92	18739	3			2.04025	0.099355	160
24/09/1987	115	72	14799	3			1.95875	0.095184	0
24/09/1987	98	58	10515	1			1.74275	0.176152	0
24/09/1987	97	63	10623	3			1.9605	0.119839	0
24/09/1987	106	64	18262	1			1.91075	0.12422	0
24/09/1987	88	56	6743	3			1.5924	0.093813	0
25/09/1987	107	65	9252	3			1.937	0.123811	0
25/09/1987	103	65	17818	1	17425	3	1.924	0.170285	0
25/09/1987	103	64	7879	3			1.8055	0.136723	0
25/09/1987	92	55	11808	1	11798	3	1.92325	0.132605	0
25/09/1987	113	73	9477	2			1.7862	0.069045	0
28/09/1987	113	76	14838	3			1.8716	0.142748	0
28/09/1987	135	86	30838	1			2.0036	0.098852	0
29/09/1987	107	71	9170	3			1.9085	0.109711	160
29/09/1987	108	71	11900	3			1.9604	0.172518	0
30/09/1987	84	50	5464	3			1.77275	0.116139	141.5
30/09/1987	103	67	14740	3			1.999	0.109581	0
30/09/1987	114	77	20266	1			1.927	0.166586	0
30/09/1987	88	52	6781	3			1.7404	0.122841	0

Method 1, total hand count

Method 2, subsample count

Method 3, automatic-machine count

Appendix Table A6ii.5 Bridlington 1988 fecundity estimates

Date	CL (mm)	AW (mm)	Number of eggs	Counting Method	Number of eggs^2	Counting Method^2	Egg Diameter	Std. Dev. Egg Diam	P.E.I.
07/06/1988	93	58	8887	2			1.98658	0.114586	393.6
07/06/1988	92	56	5690	3			1.975862	0.147854	463.9
07/06/1988	92	60	9087	3			1.814658	0.139868	439.2
07/06/1988	102	64	8016	3			2.02583	0.122431	287.8
07/06/1988	103	64	11494	1	11009	3	1.798854	0.109863	465.25
07/06/1988	93	57	9558	1	8923	3	2.08569	0.132986	524.2
07/06/1988	87	53	7340	3			1.76689	0.139657	119.25
07/06/1988	136	93	25176	3			2.09864	0.18569	597.2
07/06/1988	98	61	5504	3			2.06895	0.138741	653.2
07/06/1988	87	54	3568	3			1.98611	0.149652	663.2
07/06/1988	115	75	16660	3			1.88765	0.120589	541.6
07/06/1988	112	72	15586	3			2.03723	0.129287	431.75
07/06/1988	92	56	9781	3			2.06954	0.098756	512.6
12/06/1988	87	55	7022	3			1.9258	0.15869	537.8
12/06/1988	97	58	10589	1	10489	3	1.8088	0.160859	555.2
12/06/1988	98	60	6474	3			2.02925	0.139514	546.75
12/06/1988	97	60	4418	3			2.178	0.159519	665
14/06/1988	84	51	7739	3			1.916	0.102197	497
14/06/1988	88	52	5943	3			1.89775	0.129239	582.5
14/06/1988	114	77	14478	3			1.89547	0.14578	0
15/06/1988	139	99	25244	3			2.11369	0.154789	658.8
15/06/1988	97	57	9391	3			2.07512	0.162347	643.8
15/06/1988	98	61	7029	3			1.7775	0.2102	329
16/06/1988	82	49	6588	1	6357	3	1.76775	0.091185	483
16/06/1988	102	60	5108	3			1.96475	0.157953	596.75
16/06/1988	88	53	3870	2			1.93025	0.12333	601.25
16/06/1988	82	47	5260	3			1.83475	0.135128	452.5
16/06/1988	106	68	15446	3			1.948	0.125231	446.25
16/06/1988	109	70	14694	3			2.0755	0.143484	439
19/06/1988	85	49	3435	3			2.2755	0.145875	640.75
21/06/1988	81	47	4339	3			1.912	0.12812	552.25
21/06/1988	101	63	13566	3			1.9995	0.126975	384.5
21/06/1988	112	73	17818	1			2.003	0.07904	196
21/06/1988	108	76	19088	2	18178	3	2.127	0.135414	612.25
21/06/1988	102	65	10374	3			1.9485	0.148975	482.8
23/06/1988	102	65	12357	3			1.863	0.13589	0
23/06/1988	112	69	15724	1			2.115	0.124907	558.25
23/06/1988	113	71	19274	1			2.08475	0.156069	534.25
23/06/1988	106	66	17787	3			2.044	0.139044	465.25
24/06/1988	106	66	13486	3			1.93975	0.148756	0

Method 1, total hand count

Method 2, subsample count

Method 3, automatic-machine count

Appendix Table A6ii.6 Bridlington 1989 and 1990 fecundity estimates

Date	CL (mm)	AW (mm)	Number of eggs	Counting Method	Number of eggs^2	Counting Method^2	Egg Diameter	Std. Dev. Egg Diam	P.E.I.
28/06/1989	89	53	5553	1			1.926	0.15675	385.5
28/06/1989	96	58	29562	1			1.92475	0.18112	423.75
28/06/1989	84	53	11025	1			1.8255	0.117359	421
16/08/1990	111	72	20061	2			1.929	0.120665	0
16/08/1990	100	62	21835	2			1.842	0.101823	0
16/08/1990	92	57	13124	2			2.0265	0.082822	0
16/08/1990	96	60	14578	2			1.795	0.142333	0
16/08/1990	103	65	15748	2			2.0605	0.152718	0
16/08/1990	91	60	7629	2			1.9635	0.13429	0
16/08/1990	93	52	10023	2			1.8515	0.129896	0
16/08/1990	92	60	12231	2			1.89683	0.09568	0
10/09/1990	103	65	24281	2			1.9055	0.156366	309.25
13/09/1990	90	60	10742	1	10718	2	1.852	0.122616	0
13/09/1990	97	62	13489	2			1.787	0.107234	0
13/09/1990	114	72	22005	2			1.8735	0.091252	91.5
13/09/1990	111	75	16057	2			1.872	0.090545	0
13/09/1990	123	83	13808	2			1.9925	0.081083	0
13/09/1990	98	60	12201	2			1.851	0.103027	0
13/09/1990	108	71	16277	2			1.9135	0.100365	0
13/09/1990	94	59	8682	2			1.858	0.095649	0
13/09/1990	101	64	11571	2			1.9035	0.121003	0
13/09/1990	97	59	9953	2			2.11	0.137308	0
13/09/1990	102	68	18265	2			1.9665	0.130914	0
13/09/1990	92	55	9603	2			1.991	0.104881	0
13/09/1990	92	57	9543	2			2.031	0.090851	0
13/09/1990	114	75	19236	2			1.972	0.100404	147.5
13/09/1990	88	55	9300	2			1.9085	0.150567	0
13/09/1990	88	56	8960	2			1.7855	0.118512	0
13/09/1990	93	55	8820	2			1.866	0.078981	136
13/09/1990	97	56	12078	2			1.797	0.115738	0
13/09/1990	97	60	9858	2			1.8165	0.086584	0
13/09/1990	102	63	12621	2			1.834	0.101633	0
13/09/1990	106	65	12540	2			1.823	0.081561	0
13/09/1990	102	61	8265	2			1.772	0.061628	0
13/09/1990	129	84	24897	2			1.9225	0.101032	0
13/09/1990	102	63	12477	2			1.912	0.124426	0
13/09/1990	87	51	7494	2			1.79	0.125357	0
13/09/1990	113	73	21375	2			1.8665	0.088942	0
13/09/1990	107	69	15818	2			1.81	0.095689	0
13/09/1990	86	52	7752	2			1.736	0.101358	0
13/09/1990	83	52	7984	2			1.768	0.095258	0
13/09/1990	87	53	8623	2			1.795	0.097457	0
13/09/1990	81	47	6733	2			1.836	0.093608	134
13/09/1990	113	73	14810	2			2.115	0.094006	0
13/09/1990	137	97	29213	2			1.8615	0.109821	0
13/09/1990	121	79	24949	2			2.092	0.081321	0
13/09/1990	124	87	24273	2			1.942	0.086671	0
13/09/1990	128	86	17909	2			2.007	0.099578	0
13/09/1990	118	74	20869	2			2.038	0.117578	0
13/09/1990	108	70	14590	2			2.0055	0.105363	0
13/09/1990	109	69	15573	2			2.007	0.104571	0
13/09/1990	155	99	36483	2			2.0495	0.102014	0
13/09/1990	105	66	9903	2			1.9255	0.1275	0
13/09/1990	123	86	22331	2			1.8995	0.09832	113.5
13/09/1990	123	72	20616	2			2.0365	0.077427	0
13/09/1990	83	52	8101	2			1.813	0.115426	0
13/09/1990	117	78	16234	2			1.9475	0.13109	133.5

Method 1, total hand count

Method 2, subsample count

Method 3, automatic-machine count

Appendix Table A6ii.7 Bridlington 1991 fecundity estimates

Date	CL (mm)	AW (mm)	Number of eggs	Counting Method	Number of eggs^2	Counting Method^2	Egg Diameter	Std. Dev. Egg Diam	P.E.I.
13/06/1991	98	62	9777	2			2.268947	0.168217	670
13/06/1991	84	55	8518	2			1.985789	0.091357	676.8
13/06/1991	92	56	9578	2			2.124736	0.116083	494.7
13/06/1991	97	60	9977	2			2.138421	0.104335	390
13/06/1991	112	75	16161	2			2.305789	0.096474	510
13/06/1991	93	52	10530	2			2.124736	0.096243	382.105
13/06/1991	85	50	5635	2			2.328421	0.090862	612.1
13/06/1991	89	55	8628	2			2.30947	0.084713	448.4
13/06/1991	103	64	12916	2			2.47	1.57737	453.7
13/06/1991	88	52	8929	2			2.0855	0.092035	390.5
13/06/1991	96	64	12016	2			2.172	0.101781	401
13/06/1991	98	63	10438	2			2.057	0.055292	372.5
13/06/1991	103	65	13885	2			1.9335	0.051526	401.5
13/06/1991	107	68	11687	2			2.0745	0.07464	433
13/06/1991	131	87	26046	2			2.169	0.087286	266.5
13/06/1991	98	65	6536	2			2.161	0.120401	464
13/06/1991	107	71	12056	2			2.1155	0.077029	399
13/06/1991	113	74	11663	2			2.121	0.086452	437
13/06/1991	116	75	19521	2			1.9415	0.101763	230
13/06/1991	113	72	12747	2			2.074	0.082754	464
13/06/1991	93	56	10479	2			2.047	0.099534	519
13/06/1991	89	56	9090	2			1.962	0.088644	404.5
13/06/1991	124	83	25175	2			2.079	0.089595	313
13/06/1991	107	66	7683	2			2.085	0.072705	572
13/06/1991	118	79	20081	2			1.9725	0.10111	277
13/06/1991	93	59	9801	2			2.1615	0.095765	456.5
13/06/1991	117	75	20742	2			2.374	0.103145	500.5
13/06/1991	118	80	9523	2			2.1265	0.089913	455
13/06/1991	128	89	8619	2			2.343	0.101884	397
13/06/1991	87	54	6764	2			1.8785	0.061852	425
13/06/1991	92	58	10428	2			1.908	0.058756	422
13/06/1991	113	76	16003	2			2.253	0.061296	465.5
13/06/1991	103	69	11866	2			2.0935	0.0796	489
13/06/1991	102	62	16370	2			2.051	0.051009	446
13/06/1991	94	60	9618	2			2.1055	0.052349	445
13/06/1991	102	62	16370	2			2.051	0.051009	446
13/06/1991	94	60	9618	2			2.1055	0.052349	445
13/06/1991	88	53	8651	2			1.949	0.078629	437.5
13/06/1991	107	66	11366	2			2.1135	0.086746	436.5
13/06/1991	103	61	9052	2			2.2275	0.068296	447
13/06/1991	109	71	23514	2			2.435714	0.105487	475.5
13/06/1991	118	76	22332	2			2.16874	0.106674	563.2
13/06/1991	117	78	17433	2			2.1585	0.089047	548
13/06/1991	113	73	20537	2			2.138461	0.104975	448.4
13/06/1991	120	82	11965	2			2.188461	0.083802	369.2
13/06/1991	125	86	23270	2			2.251945	0.056964	380.7
13/06/1991	129	81	19622	2			2.45	0.083684	461

Method 1, total hand count

Method 2, subsample count

Method 3, automatic-machine count

Appendix Table A6ii.8 Dale 1989 and 1992 fecundity estimates

Date	CL (mm)	AW (mm)	Number of eggs	Counting Method	Number of eggs^2	Counting Method^2	Egg Diameter	Std. Dev. Egg Diam	P.E.I.
20/07/1989	115	71	14327	1			2.00225	0.13459	405.5
02/06/1992	139	85	21335	2			2.2456	0.18108	692
02/06/1992	101	64	5979	2			2.5313	0.10445	691
02/06/1992	112	70	16026	2			2.0488	0.1799	423
02/06/1992	112	73	15254	2			1.9543	0.08629	439
02/06/1992	106	68	12050	2			2.0451	0.12237	504
02/06/1992	107	64	9869	2			2.5319	0.13541	317
02/06/1992	109	73	16899	2			1.9255	0.1449	308
02/06/1992	105	69	13095	2			2.1535	0.14108	440

Appendix Table A6ii.9 Selsey 1989 fecundity estimates

Date	CL (mm)	AW (mm)	Number of eggs	Counting Method	Number of eggs^2	Counting Method^2	Egg Diameter	Std. Dev. Egg Diam	P.E.I.
7/9/1989	89	54	7459	2			1.96175	0.086637	0
7/9/1989	94	58	8312	2			1.95375	0.127189	0
7/9/1989	90	54	5643	2			1.999	0.0929	0
7/9/1989	76	42	8757	1	8898	2	2.02725	0.132098	0
14/09/1989	98	58	12166	1	11901	2	1.86475	0.076881	0
14/09/1989	90	55	7362	1			1.8695	0.129954	0
14/09/1989	87	51	8076	1			1.94975	0.106649	0
14/09/1989	93	56	13107	1			1.84275	0.117116	0
14/09/1989	86	54	7676	1			1.80375	0.108723	0
14/09/1989	85	50	9289	1			1.87375	0.118783	0
14/09/1989	89	54	8381	1			2.04975	0.128463	0
14/09/1989	85	47	7393	1	7302		1.92275	0.133217	0
14/09/1989	90	58	10344	1	10568	2	1.9245	0.120866	0
14/09/1989	90	57	11252	1	11356	2	1.93584	0.115487	0
14/09/1989	86	53	7523	1			1.972	0.090191	0
14/09/1989	85	47	9634	1			1.9605	0.067378	0
14/09/1989	89	51	9370	1	9478	2	2.07855	0.164585	0
11/10/1989	90	53	8363	1			1.98875	0.110626	0
11/10/1989	101	64	14004	1			1.99225	0.116955	0
11/10/1989	87	53	10041	1	9778	2	2.02896	0.145858	0
11/10/1989	91	58	9188	2			2.07325	0.164585	0
11/10/1989	86	52	6812	2			1.90148	0.122238	0
11/10/1989	88	56	10822	1	10443	2	1.886	0.073427	0
23/11/1989	89	52	8543	1			1.92575	0.1617	0

Method 1, total hand count

Method 2, subsample count

Method 3, automatic-machine count

Appendix Table A6ii.10 Selsey 1990 and 1991 fecundity estimates

Date	CL (mm)	AW (mm)	Number of eggs	Counting Method	Number of eggs^2	Counting Method^2	Egg Diameter	Std. Dev. Egg Diam	P.E.I.
23/05/1990	88	52	4071	1			2.0368	0.115891	435
23/05/1990	79	44	3656	1			1.9755	0.121387	426
23/05/1990	90	53	7287	2			2.1415	0.128336	449.5
27/09/1990	90	60	11013	2			1.808	0.095202	0
27/09/1990	117	77	25891	1			1.9865	0.136304	0
27/09/1990	87	55	3792	2			1.888	0.155441	0
27/09/1990	89	53	9941	2			1.924	0.103475	0
07/11/1990	85	54	6675	2			2.2885	0.107649	0
07/11/1990	101	62	14146	2			2.0215	0.118402	0
07/02/1991	84	50	6849	1			1.858	0.10553	94.5
07/02/1991	86	52	7312	1			2.104	0.108547	148
07/02/1991	92	59	12303	1			1.9735	0.105228	240.5
07/02/1991	87	53	8070	1			2.032	0.101012	426
07/02/1991	84	49	8089	1	8220	2	1.9258	0.111543	325.5
07/02/1991	86	52	8102	1			1.891	0.074281	180
07/02/1991	91	57	10780	1			2.158	0.085017	446
07/02/1991	88	54	8595	1			2.1145	0.071486	328
07/02/1991	97	61	3379	2			2.124	0.120797	411.5
07/02/1991	87	53	7329	1			1.9775	0.078432	357
07/02/1991	88	51	7947	2			2.59	0.102335	550
07/02/1991	87	52	9272	1			1.9325	0.107864	124
07/02/1991	93	59	11644	1			2.2335	0.125737	374
07/02/1991	100	69	13534	1			2.1925	0.110993	402.5
07/02/1991	110	75	5819	1			2.1465	0.099872	237.5
12/04/1991	91	52	8580	2			2.16855	0.091104	309.5
12/04/1991	92	56	9778	2			2.257	0.110215	402
12/04/1991	85	52	6533	2			2.395	0.124017	494
12/04/1991	98	63	13050	2			2.541	0.163642	248
12/04/1991	101	61	7546	2			2.89	0.102335	551
12/04/1991	92	60	5235	2			2.344	0.085239	460.5
12/04/1991	97	63	10492	2			2.32	0.114013	591
12/04/1991	91	52	8713	2			1.8655	0.101311	254
12/04/1991	88	51	5861	2			2.216	0.093479	317
12/04/1991	91	56	12110	2			2.2155	0.103536	404.5
08/07/1991	99	65	9774	2			2.2221	0.11398	565
08/07/1991	90	53	5353	2			2.044	0.122949	0
08/07/1991	91	53	4329	2			1.8965	0.07605	498
08/07/1991	90	52	7066	2			2.0894	0.11584	598
08/07/1991	99	65	9977	2			2.25176	0.098475	586
08/07/1991	96	64	9749	2			2.2542	0.134128	666.8
08/07/1991	97	58	5519	2			2.281052	0.21699	669
08/07/1991	121	82	18505	2			2.31631	0.138019	655
08/07/1991	111	74	15647	2			2.351	0.17965	620.5
08/07/1991	104	66	10457	2			2.3926	0.1281	660
08/07/1991	90	53	7786	2			2.1432	0.12035	503
08/07/1991	90	52	7296	2			2.083157	0.12314	619
08/07/1991	108	71	13931	2			2.00894	0.1405	0
08/07/1991	104	65	20940	2			2.36578	0.1331	511
08/07/1991	86	50	13609	2			2.08368	0.112672	473
08/07/1991	101	61	9349	2			2.1784	0.1459	578
08/07/1991	91	52	6713	2			2.0595	0.15129	442
08/07/1991	92	55	8327	2			2.2947	0.146955	633

Method 1, total hand count

Method 2, subsample count

Method 3, automatic-machine count

Appendix Table A6ii.11 Linear regression statistics for clutch size-CL relationships

Site	N	R-square	r	Sx/y	F(df,df)	P		Coefficient	Std. Error	t	P
Bridlington	27	0.585	0.765	3478.53	1,25	<0.001	a	-23899.5	6265.55	-3.814	<0.001
1987							b	363.204	61.18646	5.936	<0.001
Bridlington	34	0.804	0.897	2699.54	1,32	<0.001	a	-28606	3445.31	-8.313	<0.001
1988							b	394.666	34.39356	11.48	<0.001
Bridlington	47	0.79	0.889	2925.25	1,45	<0.001	a	-23831.3	2978.07	-8.002	<0.001
1990							b	369.3551	28.38046	13.01	<0.001
Bridlington	42	0.459	0.678	3761.94	1,40	<0.001	a	-15675.3	4895.65	-3.202	0.003
1991							b	272.61036	46.77356	5.828	<0.001
Dale	8	0.67	0.819	2906.26	1,6	0.013	a	-22548	10465.6	-2.154	0.075
1992							b	326.4769	93.51357	3.491	0.013
Selsey	24	0.288	0.537	1741.51	1,22	0.007	a	-10972.3	6749.38	-1.626	0.118
1989							b	226.28418	75.80146	2.985	0.007
Selsey	6	0.93	0.964	2291.76	1,4	0.002	a	-45969.5	8018.19	-5.733	0.005
1990							b	610.32535	83.97281	7.268	0.002
Selsey	29	0.232	0.482	3463.52	1,27	0.008	a	-11951.9	7375.33	-1.621	0.117
1991							b	225.74402	79.00256	2.857	0.008

Appendix Table A6ii.12 Polynomial regression statistics for clutch size-CL relationships

Site	N	R-square	r	Sx/y	F(df,df)	P		Coefficient	P
Bridlington	27	0.648	0.805	3270.91	2,24	<0.001	a	56530	<0.001
1987							b	-1170	
							c	7.213	
Bridlington	34	0.805	0.897	2736.75	2,31	<0.001	a	-21330	<0.001
1988							b	255.6	
							c	0.6503	
Bridlington	47	0.798	0.893	2898.54	2,44	<0.001	a	-2304	<0.001
1990							b	-23.85	
							c	1.753	
Bridlington	42	0.461	0.679	3803.81	2,39	<0.001	a	-30700	<0.001
1991							b	561.3	
							c	-1.368	
Dale	8	0.857	0.926	2099.36	2,5	0.008	a	-284000	0.012
1992							b	4698	
							c	-18	
Selsey	24	0.439	0.663	1581.98	2,21	0.002	a	128100	0.009
1989							b	-2901	
							c	17.53	
Selsey	6	0.931	0.965	2621.49	2,3	0.018	a	-16910	0.021
1990							b	26.37	
							c	2.887	
Selsey	29	0.258	0.508	3468.52	2,26	0.02	a	51270	0.043
1991							b	-1055	
							c	6.414	

Appendix Table A6ii.13 Linear regression statistics for clutch size-AW relationships

Site	N	R-square	r	Sx/y	F(df,df)	P		Coefficient	Std. Error	t	P
Bridlington	27	0.562	0.75	3572.41	1,25	<0.001	a	-16997.2	5352.02	-3.176	0.004
1987							b	469.41473	82.83656	5.667	<0.001
Bridlington	34	0.823	0.907	2570.59	1,32	<0.001	a	-18667.4	2439.38	-7.653	<0.001
1988							b	470.68374	38.62369	12.19	<0.001
Bridlington	47	0.699	0.836	3501.22	1,45	<0.001	a	-12441.4	2685.29	-4.633	<0.001
1990							b	414.48581	40.51841	10.23	<0.001
Bridlington	42	0.406	0.637	3941.1	1,40	<0.001	a	-8096.38	4013.55	-2.014	0.05
1991							b	312.06069	59.65696	5.231	<0.001
Dale	8	0.836	0.914	2047.98	1,6	0.001	a	-31332.2	8189.47	-3.826	0.009
1992							b	638.10063	115.2989	5.534	0.001
Selsey	24	0.235	0.485	1805.03	1,22	0.016	a	-2527.03	4500.84	-0.561	0.58
1989							b	217.71919	83.6501	2.603	0.016
Selsey	6	0.894	0.946	2806.18	1,4	0.004	a	-37069.9	8489.85	-4.366	0.012
1990							b	814.06454	139.8149	5.822	0.004
Selsey	29	0.225	0.475	3479.1	1,27	0.009	a	-4409.57	4844.26	-0.91	0.371
1991							b	234.29705	83.62078	2.802	0.009

Appendix Table A6ii.14 Polynomial regression statistics for clutch size-AW relationships

Site	N	R-square	r	Sx/y	F(df,df)	P		Coefficient	P
Bridlington	27	0.633	0.796	3339.69	2,24	<0.001	a	54410	<0.001
1987							b	-1710	
							c	16.35	
Bridlington	34	0.825	0.908	2596.97	2,31	<0.001	a	-24950	<0.001
1988							b	657.1	
							c	-1.33	
Bridlington	47	0.752	0.867	3215.57	2,44	<0.001	a	16490	<0.001
1990							b	-455.2	
							c	6.296	
Bridlington	42	0.423	0.65	3936.74	2,39	<0.001	a	-35720	<0.001
1991							b	1142	
							c	-6.084	
Dale	8	0.916	0.954	1605.72	2,5	0.002	a	18000	0.003
1992							b	4674	
							c	-27.14	
Selsey	24	0.429	0.655	1596.05	2,21	0.003	a	7154	0.01
1989							b	-2606	
							c	26.71	
Selsey	6	0.9	0.949	3157.8	2,3	0.032	a	2342	0.035
1990							b	-422.2	
							c	9.484	
Selsey	29	0.235	0.485	3522.53	2,26	0.031	a	15270	0.056
1991							b	-402.6	
							c	5.031	

Appendix Table A6ii.15 Linear regression statistics for egg diameter-CL relationships

Site	N	R-square	r	Sx/y	F(df,df)	P		Coefficient	Std. Error	t	P
Bridlington	27	0.002	0.048	0.34722	1,25	0.81	a	1.95849	0.62541	3.132	0.004
1987							b	-0.00148	0.00611	-0.242	0.81
Bridlington	34	0.128	0.358	0.11571	1,32	0.038	a	1.66964	0.14768	11.31	<0.001
1988							b	0.0032	0.00147	2.169	0.038
Bridlington	47	0.221	0.471	0.09167	1,45	<0.001	a	1.57859	0.09333	16.91	<0.001
1990							b	0.00318	0.00089	3.577	<0.001
Bridlington	42	0.193	0.439	0.12966	1,40	0.004	a	1.63458	0.16873	9.688	<0.001
1991							b	0.00498	0.00161	3.091	0.004
Dale	8	0.011	0.106	0.25782	1,6	0.802	a	2.42127	0.92842	2.608	0.04
1992							b	-0.00217	0.0083	-2.62	0.802
Selsey	24	0.007	0.085	0.07398	1,22	0.693	a	2.06389	0.28671	7.199	<0.001
1989							b	-0.00129	0.00322	-0.401	0.693
Selsey	6	0.006	0.074	0.18516	1,4	0.888	a	2.0822	0.64781	3.214	0.032
1990							b	-0.00101	0.00678	-0.149	0.888
Selsey	32	0.324	0.569	0.12755	1,27	<0.001	a	1.20654	0.2514	4.799	<0.001
1991							b	0.0101	0.00267	3.79	<0.001

Appendix Table A6ii.16 Polynomial regression statistics for egg diameter-CL relationships

Site	N	R-square	r	Sx/y	F(df,df)	P		Coefficient	P
Bridlington	27	0.002	0.447	0.35437	2,24	0.972	a	2.068	0.867
1987							b	-0.004	
							c	9.87E-06	
Bridlington	34	0.129	0.359	0.1175	2,31	0.117	a	1.514	0.14
1988							b	0.006	
							c	-1.39E-05	
Bridlington	47	0.244	0.494	0.09136	2,44	0.002	a	1.006	0.011
1990							b	0.014	
							c	-4.67E-05	
Bridlington	42	0.16	0.4	0.13392	2,39	0.033	a	2.122	0.061
1991							b	-0.005	
							c	7.35E-05	
Dale	8	0.491	0.701	0.20267	2,5	0.185	a	23.91	0.181
1992							b	-0.3614	
							c	1479	
Selsey	24	0.021	0.145	0.07518	2,21	0.798	a	3.587	0.638
1989							b	-0.036	
							c	0.000192	
Selsey	6	0.127	0.356	0.20037	2,3	0.816	a	8.077	0.673
1990							b	-0.1215	
							c	0.000596	
Selsey	32	0.389	0.624	0.12331	2,26	<0.001	a	-2.732	0.005
1991							b	0.09	
							c	-0.000401	

Appendix Table A6ii.17 Linear regression statistics for egg diameter-AW relationships

Site	N	R-square	r	Sx/y	F(df,df)	P		Coefficient	Std. Error	t	P
Bridlington	27	6.25E-05	0.008	0.34761	1,25	0.969	a	1.8282	0.52078	3.511	0.002
1987							b	-0.00032	0.00806	-0.04	0.969
Bridlington	34	0.115	0.34	0.11656	1,32	0.049	a	1.76478	0.11061	15.96	<0.001
1988							b	0.00358	0.00175	2.043	0.049
Bridlington	47	0.181	0.426	0.094	1,45	0.003	a	1.68556	0.0721	23.38	<0.001
1990							b	0.00343	0.00109	3.156	0.003
Bridlington	42	0.157	0.397	0.13247	1,40	0.009	a	1.78801	0.13487	13.26	<0.001
1991							b	0.00548	0.002	2.733	0.009
Dale	8	0.151	0.388	0.23898	1,6	0.342	a	3.16092	0.95563	3.308	0.016
1992							b	-0.01387	0.01345	-1.031	0.342
Selsey	24	0.014	0.117	0.07374	1,22	0.585	a	2.05266	0.18386	11.15	<0.001
1989							b	-0.00189	0.00342	-0.554	0.585
Selsey	6	0.012	0.109	0.18457	1,4	0.837	a	2.1073	0.5584	3.774	0.02
1990							b	-0.00201	0.0092	-0.219	0.837
Selsey	32	0.313	0.56	0.12856	1,27	<0.001	a	1.5482	0.16582	9.337	<0.001
1991							b	0.0104	0.00281	3.698	<0.001

Appendix Table A6ii.18 Polynomial regression statistics for egg diameter-AW relationships

Site	N	R-square	r	Sx/y	F(df,df)	P		Coefficient	P
Bridlington	27	0.005	0.071	0.35396	2,24	0.945	a	3.009	0.814
1987							b	-0.036	
							c	0.2703	
Bridlington	34	0.115	0.339	0.11842	2,31	0.15	a	1.755	0.165
1988							b	0.004	
							c	-2.03E-06	
Bridlington	47	0.196	0.443	0.13103	2,44	0.014	a	2.236	0.035
1990							b	-0.007	
							c	5.48E-05	
Bridlington	42	0.196	0.443	0.13103	2,39	0.014	a	2.236	0.035
1991							b	-0.007	
							c	5.48E-05	
Dale	8	0.954	0.977	0.06117	2,5	<0.001	a	27.31	<0.001
1992							b	-0.6696	
							c	0.004	
Selsey	24	0.06	0.245	0.07369	2,21	0.523	a	3.349	0.423
1989							b	-0.051	
							c	0.000468	
Selsey	6	0.093	0.305	0.20417	2,3	0.864	a	5.421	0.721
1990							b	-0.106	
							c	0.000797	
Selsey	32	0.398	0.631	0.1224	2,26	<0.001	a	-0.712	0.004
1991							b	0.084	
							c	-0.000581	

Appendix Table A6ii.19 Linear regression statistics for clutch size-CL relationships (5 mm CL groups)

Site	PEI	N	R-square	r	Sx/y	F(df,df)	P		Coefficient	Std. Error	t	P
Bridlington	0	7	0.948	0.974	1847	1,5	<0.001	a	-30957.85	4851.145	-6.382	0.001
1987								b	435.835	45.566	9.565	<0.001
Bridlington	>300	8	0.922	0.96	2132	1,6	<0.001	a	-28185.46	4828.91	-5.837	0.001
1988								b	390.914	46.534	46.534	<0.001
Bridlington	0	12	0.977	0.988	1403	1,10	<0.001	a	-26687	2203.753	-12.11	<0.001
1990								b	394.691	19.327	20.422	<0.001
Bridlington	>300	10	0.957	0.978	1011	1,8	<0.001	a	-17694.09	2358.419	-7.503	<0.001
1991								b	297.382	22.254	13.363	<0.001
Dale	>300	4	0.818	0.905	3329	1,2	0.095	a	-28664.55	14314.91	-2.002	0.183
1992								b	370.848	123.633	3	0.095
Selsey	0	5	0.723	0.85	1478	1,3	0.068	a	-9122.21	7062.49	-1.292	0.287
1989								b	214.807	76.84684	2.795	0.068
Selsey	>300	6	0.991	0.996	506.5	1,4	<0.001	a	-25948.07	1792.617	-14.475	<0.001
1991								b	365.747	17.372	21.054	<0.001

Appendix Table A6ii.20 Polynomial regression statistics for clutch size-CL relationships (5 mm CL groups)

Site	PEI	N	R-square	r	Sx/y	F(df,df)	P		Coefficien	P
Bridlington	0	7	0.995	0.9975	645.49	2,5	<0.001	a	43810	<0.001
1987								b	-918	
								c	5.988	
Bridlington	>300	8	0.922	0.96	233.06	2,6	0.002	a	-24540	0.003
1988								b	322.8	
								c	0.3097	
Bridlington	0	12	0.985	0.9925	1201.2	2,10	<0.001	a	-6597	<0.001
1990								b	42.25	
								c	1.493	
Bridlington	>300	10	0.983	0.9915	684.08	2,8	<0.001	a	23980	<0.001
1991								b	-511.5	
								c	3.852	
Dale	>300	4	0.986	0.993	1320.5	2,2	0.12	a	-352500	0.107
1992								b	5796	
								c	-22.38	
Selsey	0	5	0.973	0.9864	567.32	2,3	0.027	a	119100	0.027
1989								b	-2668	
								c	16.05	
Selsey	>300	6	0.992	0.996	554.53	2,4	<0.001	a	-37850	<0.001
								b	595.2	
1991								c	-1.091	

Appendix Table A6ii.21 ANCOVA results for clutch size/CL relationships between Bridlington September 1987 (PEI=0) and June 1988 (PEI>300)

Source of variation	SSQ	df	MSQ	F-ratio	Sig. Level
Covariate (CL)	7.479E+08	1	7.479E+08	88.587	0
Main effect (egg loss)	656004.33	1	656004.33	0.078	0.7881
Residual	1.013E+08	12	8442048.9		
Total (Corr.)	8.498E+08	14			

Appendix Table A6ii.22 ANCOVA results for clutch size/CL relationships between Bridlington September 1990 (PEI=0) and June 1991 (PEI>300)

Source of variation	SSQ	df	MSQ	F-ratio	Sig. Level
Covariate (CL)	1.067E+09	1	1.067E+09	483.843	0
Main effect (egg loss)	10578000	1	10578000	4.796	0.0412
Residual	41905000	19	2205500		
Total (Corr.)	1.12E+09	21			

Appendix Table A6ii.23 ANCOVA results for clutch size/CL relationships between Selsey September 1989 (PEI=0) and June 1991 (PEI>300)

Source of variation	SSQ	df	MSQ	F-ratio	Sig. Level
Covariate (CL)	1.203E+08	1	1.202E+08	20.809	0.0038
Main effect (egg loss)	16979000	1	16979000	2.937	0.1374
Residual	34686000	6	5781000		
Total (Corr.)	1.72E+08	8			