UNIVERSITY OF SOUTHAMPTON

INTERACTIVE PROCESSES IN A *LANICE CONCHILEGA* (ANNELIDA: POLYCHAETA) DOMINATED INTERTIDAL COMMUNITY

by

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ABSTRACT

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INTERACTIVE PROCESSES IN A *LANICE CONCHILEGA* (ANNELIDA: POLYCHAETA) DOMINATED INTERTIDAL COMMUNITY

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An investigation was conducted into the factors influencing a soft-sediment intertidal benthic community dominated by the large tube building polychaete *Lanice conchilega* (Pallas, 1766). The environmental and biological characteristics of a mid-shore sampling site on a relatively sheltered sandflat were monitored over a two year period. A total of 115 taxa were recorded. Temporal variability in the community is discussed in relation to the sporadic occurrence of macroalgae, harsh winter conditions and physical disturbance to the sedimentary environment. *Lanice conchilega* had a significantly contagious distribution on the shore. The population was analysed using width measurements of both worms and tubes. Recruiting *Lanice conchilega* juveniles observed during the first year of the study were initially randomly distributed, but as these individuals developed the overall distribution of the population returned to being contagious. The presence of excess tubes towards the end of the sampling period indicated that individual *Lanice conchilega* were dying, being removed by predation or emigrating.

Further sampling was designed to investigate the macrofauna and meiofauna in areas of sediment containing different densities of *Lanice conchilega* tubes. A consistently significant positive correlation existed between tube density and macrofaunal abundance, which was attributed to sediment-mediated interactions. At higher tube densities, an increase in the depth of sediment above the underlying clay equated to an increase in the volume of available infaunal space. In addition, *Lanice conchilega*-derived mucus and its associated microbes potentially enhanced levels of food resources available to deposit feeders. Species living at or near the sediment-water interface would also have been positively influenced by any sediment stabilisation in high tube density areas. Possible causes of a positive correlation observed between tube density and *Exogone hebes* abundance are discussed.

No significant relationship existed between tube density and the abundance of macrofaunal juveniles, indicating that any inhibitory or facilitatory *Lanice conchilega*-juvenile interactions were either insignificant or acting in opposition to to produce an overall neutral effect. Details of the developmental morphology of several polychaete species are described.

Meiofaunal abundance (in particular nematode and harpacticoid abundance) was consistently greater in samples taken from areas of high tube density. Potential mechanisms responsible for this relationship include the provision of habitat heterogeneity and areas of refuge by tubes, and the enhancement of sediment stability and food resources by mucus. Particle accumulation in high tube density areas also potentially influenced meiofaunal settlement and resettlement patterns.

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CHAPTER 1

Introduction

1.1 Background

Animals inhabiting intertidal sediments are subject to numerous influences and disturbances from oceanic, terrestrial, natural and anthropogenic sources. In some coastal regions natural background physical disturbances (e.g. wave action, emersion time, salinity fluctuations) are extreme, and such perturbations are clearly reflected in the faunal assemblages inhabiting the substratum. Conversely, shores of less extreme physical variation may contain assemblages similar to those existing subtidally in the same region, even though the intertidal animals are regularly emersed during each tidal cycle. In particular, sheltered estuarine mud or sand flats can provide relatively stable environments for infaunal animals, and are often inhabited by large numbers of sedentary or discretely mobile species.

In estuarine areas the temperature and salinity of seawater may vary both seasonally and diurnally. In addition, benthic organisms inhabiting the intertidal zone are potentially exposed to more extreme temperature fluctuations during periods of emersion. Consequently, these intertidal animals often show marked seasonal changes in abundance, and are particularly susceptible to climatic variations which may greatly alter community structure (Beukema, 1979; Newell, 1964; Buhr, 1981). Furthermore, human activity is commonly more intense in estuaries and may cause local environmental changes that radically affect benthic communities.

Sporadic physical disturbances such as storm events have the potential to significantly influence the fauna of soft sediments (e.g. Eagle, 1975; Rees *et al.* 1977). The effects of such disturbances can be addressed at three different faunal levels (Hall, 1994). Firstly, at the level of the individual, disturbance may increase the likelihood of death or injury, influence the availability of food and space, increase exposure to predation or displacement, create a need for re-establishment and influence reproductive output. Secondly, at the population level, disturbance may result in changes in density, dispersion and recruitment. Thirdly, at the community level it may influence species diversity, overall abundance and productivity, and may have an impact on energy flow or nutrient recycling. To survive in a particular environment, individual species must be able to resist or recover from disturbances, however infrequently they occur. Recovery of a population can occur through direct recolonisation by adults or through the settlement and development of juveniles (e.g. McCall, 1977; Dauer and Simon, 1976; Woodin, 1981; Zajac and Whitlatch, 1982a, 1982b).

The prevailing hydrodynamic conditions in a region play an important role in determining macrofaunal distributions. Planktonic larvae of benthic invertebrates are subject to transport and deposition like all other suspended particles (Eckman, *et al.*, 1983). Large scale water movements transport these larvae between areas, and near-bed flow conditions determine levels of larval supply to the benthos on a local scale. Following passive deposition on the sediment surface, larvae may be able to accept or reject an area on the basis of positive or negative cues (Woodin, 1991). The flow regime may therefore influence the expression of habitat selection mechanisms. In addition, increased near-bed flow may passively re-suspend newly recruited juvenile macrofauna. This process is a potentially significant dispersal mechanism for both recently settled juveniles and the early developmental stages of species with entirely benthic lifecycles (Sigurdsson *et al.*, 1976).

The sedimentary regime in a particular location is largely determined by local near-bed flow conditions. In any benthic habitat, the physico-chemical characteristics of the sediment are fundamentally important when investigating the mechanisms controlling benthic populations and community structure. The size distribution of sediment particles in an area reflects the hydrodynamic characteristics (i.e. tidal regime, currents, wave action) and the geological history of that area. This particle size distribution covaries with many other physico-chemical parameters (e.g. organic content, porosity, shear stress, oxygenation), all of which influence infaunal species.

Differences in sediment properties will affect infaunal populations on every spatial scale. The organic components of a sediment are particularly important to deposit feeding species as they are used to satisfy the nutritional requirements of these species. The pool of organic detritus present in a sediment includes plant material (seagrasses and seaweeds), faecal pellets, microalgae, bacteria, fungi and protozoa. Seasonal changes in the organic content of sediments often occur in near-shore regions where inputs from macro- and microalgae are high. In addition, the physiology, growth and production of the microbes associated with dead organic matter and the rate of decay of the organic matter itself are affected by sedimentation rates, environmental (e.g. temperature) factors and food chain (e.g. grazing) factors. These factors therefore influence the availability of food to detritivores (Tenore, 1989). However, sedimentary organic material is very heterogeneous and the characterisation of the specific food resources used by different deposit feeders is far from complete (Lopez and Levington, 1987; Lopez *et al.*, 1989).

The biological characteristics of an infaunal community are clearly influenced by the supply and nutritional composition of the food resources available to its component species. Intraspecific and interspecific competition for food or space may therefore act as possible limiting factors affecting species distributions and abundance. However, the ways in which competitive interactions influence infaunal patterns are poorly understood. In benthic communities dominated by deposit feeders in relatively low numbers, competition is more likely to occur through the indirect mechanism of exploitation of food resources. Comparisons between natural food levels and artificially enhanced food levels suggest that benthos is food-limited under natural conditions (e.g. Grémare *et al.*, 1989; Levington and Bianchi, 1981). Although food supply appears not to directly affect the survival of adult benthic invertebrates, there is a strong indication that both individual growth and reproductive output are sensitive to food levels (Olafsson *et al.*, 1994). In addition, a number of studies have indicated that food shortage is responsible for mortality in the juveniles of benthic species (reviewed in Olafsson *et al.*, 1994).

The three dimensional nature of soft sediments reduces the frequency of direct competitive encounters between infaunal animals. Direct interactions are most often found between closely related species that usually live at similar depths in the sediment (Croker and Hatfield, 1980; Grant, 1981; Wilson, 1991b). Interference interactions between infaunal animals may occur in extremely dense assemblages when feeding areas overlap and appendages of adjacent animals are likely to come into contact with each other, as described by Levin (1982).

The different roles played by other biological interactions in the organisation of intertidal soft-sediment communities are also not clearly established (Peterson, 1979; Wilson, 1991b). The significance of predation by epibenthic animals such as birds, fish, gastropods, crabs and other crustaceans has frequently been investigated. The experimental exclusion of epibenthic predators often results in increases in faunal abundance and biomass, but there is a considerable degree of variation between results, both within and between different habitat types (see Olafsson *et al.*, 1994; Wilson, 1991b for reviews). Nevertheless, the potential impact of large numbers of epibenthic predators cannot be ignored, particularly on estuarine flats where wading birds and demersal fish periodically occur in great numbers. The effects of infaunal predation have been investigated relatively infrequently, but there is evidence to suggest that infaunal predators can greatly influence community structure (Wilson, 1991b).

Sediment-mediated biological interactions also potentially influence infaunal distributions and abundance. Bioturbation and tube building activity can both significantly alter the sedimentary environment (Wilson, 1991b), and sedimentary changes caused by the activity of one species or functional group may influence another. Firstly, disturbance caused by large bioturbators can have a deleterious effect on suspension feeders and tube builders (Peterson, 1977; Posey, 1986; Reise, 1983; Wilson, 1981). Secondly, high densities of tube building species may be associated with diminished numbers of burrowing animals, although they have not been observed to totally exclude burrowers (Wilson, 1991b; Woodin, 1974).

Biogenic structures, such as tubes that extend above the sediment surface, also influence local near-bed hydrodynamics and consequently affect the stability of the substratum. Extremely dense aggregations of tubes may stabilise sediments by collectively producing a "skimming flow" effect, but this effect has yet to be demonstrated using real tube beds (Hall, 1994). It appears that hydrodynamic stabilisation is only likely to occur in exceptional circumstances and correlations between animal tubes and stabilised sediments are more often a result of sediment binding by mucus (Eckman *et al.*, 1981).

Woodin (1976) suggested that tube builders occupying a large proportion of the available space should effectively inhibit larvae through their feeding and defecation on the sediment surface. In addition, local hydrodynamics are expected to influence larval settlement on at least some spatial scale (Snelgrove and Butman, 1994). Therefore, as animal tubes exert important effects on flow above the sediment surface, they are likely to influence larval settlement and consequently adult abundances. Furthermore, some studies have indicated that local changes in sediment chemistry caused by the activities of adult invertebrates may alter the behaviour of settling larvae (e.g. Woodin, 1991).

The relative importance of the numerous physical and biological parameters influencing soft sediment benthic communities can vary both temporally and spatially. An appreciation of natural variability in infaunal communities can only be gained by using long term monitoring programmes. It may also be possible to interpret temporal and spatial changes in faunal characteristics by examining concomitant variations in environmental parameters. The absence of background data on natural variability potentially confounds the interpretation of environmental impact assessments. Similarly, experiments designed to investigate biological interactions in a community would clearly benefit from detailed information on natural background variability being available.

Benthic populations existing at a particular site at any one time will have been affected by different physical, chemical and biological parameters at various previous points in time. In addition, controlling parameters are often closely interrelated. Tenore (1989) pointed out that studies of marine deposit feeders usually search for a single limiting factor rather than an "interactive hierarchy" of different regulatory mechanisms. A combination of time series data produced by a regular monitoring programme and additional data from specifically designed experimental sampling should be used for any investigation exploring the processes controlling faunal patterns and the interactions between them.

The present study was undertaken to investigate the parameters influencing infaunal populations in an intertidal soft sediment community. The main study site was the mid-shore area at Solent Breezes near Southampton. The following section presents background information on the study site. The fauna at Solent Breezes was dominated by the large tube building polychaete worm *Lanice conchilega*. This key species is described subsequently in Section 1.3. Biogenic tubes and the activities of the animals living within them potentially influence co-occurring species through direct or indirect interactions. Consequently, much of the research programme was designed to investigate the role of *Lanice conchilega* in structuring infaunal distributions on the shore. Section 1.4 outlines the specific research objectives that shaped the overall direction of this study.

1.2 The Study Site

Solent Breezes (Latitude: 50°50'N, Longitude 01°17'W) is situated towards the mouth of Southampton Water on the eastern shore about 2km below the mouth of the river Hamble (Figure 1.1). The shore is relatively sheltered with limited wave action, being protected from the south by the Isle of Wight. There is a tidal range of 4.8m but the double high tide leads to the site being covered for longer than would be expected if there was the usual single high tide per cycle. Tidal water movements are characterised by relatively rapid lamellate encroachment and retreat across the sediment flat and there is no significant channelisation.

The main sampling site selected for this study was mid-shore on the extensive sediment flat at a tidal height of approximately 1.3m. Maximum emersion times at the mid-shore site were approximately 2.5 hours per cycle during spring tides. The surface sediment was a well mixed muddy-sand with a clay/silt fraction (<63µm) generally between 2% and 5%. Below the muddy-sand layer there was a distinctive underlying base of London clay, which was intermittently mixed with large shell fragments and stones. In addition, stones and shells on the surface provided some attachment sites for ephemeral macroalgae during the summer.

The relatively remote location of Solent Breezes restricted the level of human activity at the site. A small amount of bait digging was observed on the shore, but this was concentrated in an area close to the low water mark to the south of the main sampling site. Large numbers of wading birds were never observed at Solent Breezes, although the feeding activities of waterfowl potentially represented a significant source of disturbance to infaunal populations.

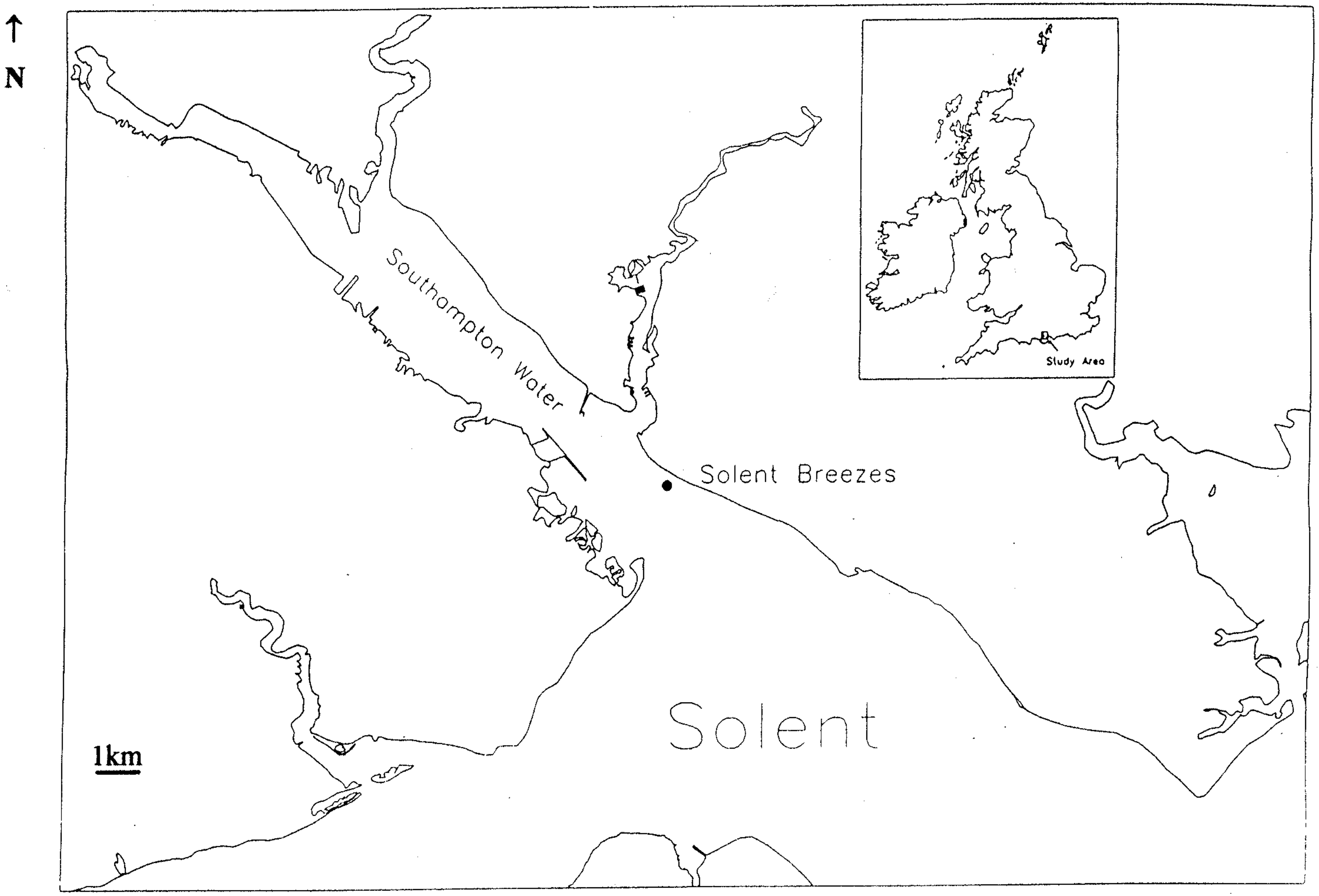


Figure 1.1 The geographical position of the sampling site.

Solent Breezes was chosen for this study primarily because of its location: the relatively sheltered nature of the site and its remote position away from significant anthropogenic disturbance potentially provided a suitable environment in which to investigate biological interactions. In addition, the presence of a well-established population of *Lanice conchilega* allowed an investigation to be conducted into the potential influences of this species on the other fauna. The following section briefly describes previously published literature on *Lanice conchilega* as an introduction to the general ecology of this important species.

1.3 *Lanice conchilega* (Pallas, 1766)

The sand mason worm *Lanice conchilega* is a common and often extremely abundant terebellid polychaete. Populations form an integral part of many littoral and sub-littoral sediments throughout N.W. Europe and its distribution extends to the Eastern North Atlantic, the Mediterranean, the Persian Gulf, the Pacific and Australia (Holthe, 1986). *Lanice conchilega* commonly lives in depths of up to 50m but has been recorded in depths exceeding 1700m (Holthe, 1986). In addition, populations extend into estuaries where they often encounter high turbidity and pollutants (Buhr and Winter, 1977).

Aspects of the biology, physiology, and morphology of *Lanice conchilega* that have previously been investigated include larval ecology (Bhaud, 1988; Bhaud and Cazaux, 1990), gamete production and spawning (Smith, 1989a; Smith, 1989b), feeding behaviour (Buhr, 1976; Buhr and Winter, 1977), tentacle morphology (Schulte and Riehl, 1976), secondary metabolites (Goerke and Weber 1990, Goerke and Weber, 1991) and the palaeoecology of its tubes (Carey, 1987).

Reproduction in *Lanice conchilega* involves the release of both eggs and sperm into the water column, and presumably depends on synchrony of spawning to effect fertilisation (Smith, 1989a). Unlike all other terebellid species (apart from *Loimia* spp.), *Lanice conchilega* has two planktonic larval stages separated by a benthic stage. The first pelagic phase (the trochophore) is short-lived, whereas the second (the aulophore) remains in the water column for close to eight weeks. The aulophore larva is at an advanced stage of development, possessing characteristics similar to the juvenile worm and carrying a transparent tube which acts as a floatation device. Larvae move vertically upwards by the secretion of mucus, and capture microparticles using tentacles that reach out of their tubes (Bhaud, 1988; Bhaud and Cazaux, 1990). On settling, sand tubes are first constructed by the attachment of grains to the mucoid tube.

Individuals construct characteristic tubes from sand grains and shell fragments. The tubes have a crown of fine projections extending above the sediment surface. Recent work has suggested that bromophenolic secondary metabolites produced by *Lanice conchilega* may inhibit the aerobic degradation of the tubes, as well as being important for wound healing (Goerke and Weber, 1991). *Lanice conchilega* may occur in densities of up to 20 000m^{-2} (Buhr, 1979), and such dense aggregations of tubes have been observed to resist erosion and accumulate sediment in association with macroalgae (Carey, 1987).

Terebellid polychaetes feed on detritus, benthic diatoms, other unicellular algae and small invertebrates including larvae (Fauchald and Jumars, 1979; Wilson, 1980). *Lanice conchilega* has been described as both a selective deposit feeder and a suspension feeder, using its tentacles to gather food from the surrounding sediment and holding its tentacles in a shallow U over the bottom to catch suspended material. Mucus producing cells and ciliated median cells collect and transport smaller particles along the tentacular groove to the lower parts of the tentacles from where the particles are transferred to the mouth by muscular lips. Large particles are also moved by the highly extensible tentacles which contract to pull them towards the mouth (Dales, 1955; Fauchald and Jumars, 1979). The fan-shaped crowns of *Lanice conchilega* tubes passively contribute to the collection of food particles, acting as snares for food and supporting filter-feeding tentacles. During bedload transport, the crown is orientated at right angles to the current, functioning as a baffle behind which transported material collects (Ziegelmeier, 1969).

The relative importance of the different modes of feeding may depend on the geographical position and the density of a *Lanice conchilega* population. Buhr (1976) describes *Lanice conchilega* as an example of a species "utilising alternatively different sources of food", and suggests that suspension-feeding may play a dominant role in dense populations. Considerable amounts of suspended material containing high primary productivity and abundant zooplankton supplied by strong currents may explain the high levels of density observed in some *Lanice conchilega* populations (Buhr and Winter, 1977).

1.4 Aims

The overall aim of this study was to investigate the interactive processes occurring in an intertidal soft-sediment community, with particular reference to the influence of *Lanice conchilega* on the other fauna. The following specific objectives were formulated to structure the overall direction of the research programme:

(i) To describe in detail the background environmental and biological characteristics of the shore at Solent Breezes.

(ii) To investigate temporal and spatial changes in the benthic community at the main mid-shore sampling site, and relate these changes to environmental parameters at the site (climate, sediment characteristics, disturbance).

(iii) To describe the population dynamics and general ecology of the dominant species *Lanice conchilega* at Solent Breezes.

(iv) To highlight any effects dense aggregations of *Lanice conchilega* had on the surrounding benthic environment.

(v) To investigate the potential direct and indirect influences of *Lanice conchilega* and its tubes on both macrofaunal and meiofaunal animals.

(vi) To assess the relative importance of *Lanice conchilega* among the interactive processes controlling spatial and temporal patterns in the fauna at Solent Breezes.

The structure of this thesis follows the sequence of objectives outlined above. A number of environmental variables were measured throughout the study in association with faunal samples. These are described in Chapter 2. The faunal patterns described in subsequent chapters could then be examined with particular reference to temporal and spatial fluctuations in environmental parameters.

A sampling transect taken between the mean high water mark and the mean low water mark was used to investigate the environmental and faunal changes that occurred down the shore at Solent Breezes (see Chapter 3). This enabled the main mid-shore site that was used for the majority of the macrofaunal and meiofaunal sampling to be put into context on the shore. The macrobenthic community at this mid-shore site was surveyed over a two year period. Chapter 4 examines the temporal changes that occurred in the mid-shore infaunal community in relation to the environmental parameters previously described in Chapter 2.

During the early stages of the study it became evident that *Lanice conchilega* was the most consistently dominant macrobenthic species at Solent Breezes in terms of abundance and biomass. This large sedentary polychaete was a potential structuring species and consequently an investigation into its population dynamics (recruitment, variability etc.) was considered to be an important part of this study. The *Lanice conchilega* population present at the mid-shore sampling site during the macrofaunal sampling period was therefore studied in some detail (Chapter 5).

Throughout the study, large numbers of *Lanice conchilega* tubes were visible on the sediment surface at Solent Breezes. The distribution of these tubes varied both spatially and temporally. Dense aggregations were often interspersed with areas of few or no tubes. Therefore, in addition to the routine monthly sampling programme, faunal samples were collected to specifically compare areas of differing *Lanice conchilega* tube densities. Chapter 6 describes an investigation designed to test the hypothesis that the presence of *Lanice conchilega* individuals and their tubes exerted a significant influence on the other macrofaunal species present either individually or collectively.

Finally, a sampling programme was designed to examine temporal changes in the meiofauna over one annual cycle, and to compare the meiofauna present within patches of *Lanice conchilega* tubes with the meiofauna occurring between patches throughout this period (Chapter 7). The study investigated both the permanent members of the meiofauna (i.e. those animals that remain within the meiofaunal size range) and the temporary members of the meiofauna - in particular the juveniles of macrofaunal polychaete species.

CHAPTER 2

The Physico-Chemical Environment at Solent Breezes

2.1 Introduction

The physico-chemical environment on the shore at Solent Breezes was monitored during the study by measuring a number of basic parameters. Firstly, temperature and salinity measurements made at Solent Breezes were used in conjunction with data obtained from the Meteorological Office to establish background seasonal fluctuations in meteorological and hydrological parameters (Section 2.2). Secondly, temporal and spatial changes in the sedimentary environment were monitored by routinely collecting and analysing samples of surface sediment throughout the study (Section 2.3).

2.2 Meteorological and Hydrological Data

2.2.1 Meteorological data

Comprehensive daily meteorological records were provided by the national Meteorological Office. Data were obtained from the Solent MRSC meteorological station (Latitude 50°48'N, Longitude 01°13'W) as this station was situated on the coast approximately 6.5km from the sampling site at Solent Breezes. Monthly data sheets of daily records were re-analysed to provide "between-sampling" means for each of the available meteorological parameters. This allowed conditions before each sampling date to be quantified. Temperature data were categorised into daily minimum and maximum values. In addition, minimum grass temperature data were available, which could be used to indicate periods of extremely low ground temperatures. Wind speed data were provided as daily means, but unfortunately no indication of wind direction was available. However, it was possible that the wind speed data could be used as an indicator of stormy conditions.

The "between-sampling" means calculated for the temperature and wind data are presented in Figures 2.1 and 2.2 (N.B. The mean value (± S.D.) shown for each sampling date is the mean value of data leading up to that sampling date).

Figure 2.1 shows data for the two year macrofaunal sampling period (i.e. between 30 November 1990 and 23 October 1992). Figure 2.2 shows data for the meiofaunal sampling period (i.e. between 5 February 1993 and 25 March 1994).

The temperature profiles show typical seasonal cycles, with annual winter minima occurring before the February 1991, February 1992, March 1993 and December 1993 sampling dates. Minimum temperatures were comparatively low in 1991: the average minimum temperature between the January 1991 and the February 1991 sampling dates was 0.0°C, and in subsequent years the lowest average minimum temperatures ranged between 2.0 and 3.2°C. The harsh winter conditions of 1991 are highlighted by the grass minimum profile which indicates that particularly low grass minimum temperatures occurred before the February 1991 sampling date (mean value -2.4°C), and the average minimum grass temperatures during 1992-1994 were all above +0.4°C. Highest average minimum temperatures occurred consistently before the August sampling date each year. Annual average maximum temperatures peaked at 22.6, 20.9 and 19.8°C before the sampling dates in September 1991, July 1992 and July 1993 respectively.

Wave action on the shore at Solent Breezes is relatively low compared to many other areas on the south coast because of the protective influence of the Isle of Wight. It was not possible to quantify wave action directly during the present study. However, wind speed measurements were used to estimate potential levels of wave action (see Section 2.2.1). Average wind speeds ranged between 7.1 and 17.1 knots. There was no obvious seasonal pattern in either the monthly average wind speed data or the maximum average daily wind speed data. However, particularly strong winds occurred before the January 1991, September 1992 and March 1994 sampling dates (average daily wind speed >30knots).

2.2.2 Seawater temperature and salinity measurements

Measurements were made of both the temperature and salinity of adjacent seawater during each visit to Solent Breezes. Temperature readings were taken to the nearest 0.1°C using a standard mercury-filled thermometer, and salinity readings were taken to the nearest 0.5ppt using a salinity refractometer.

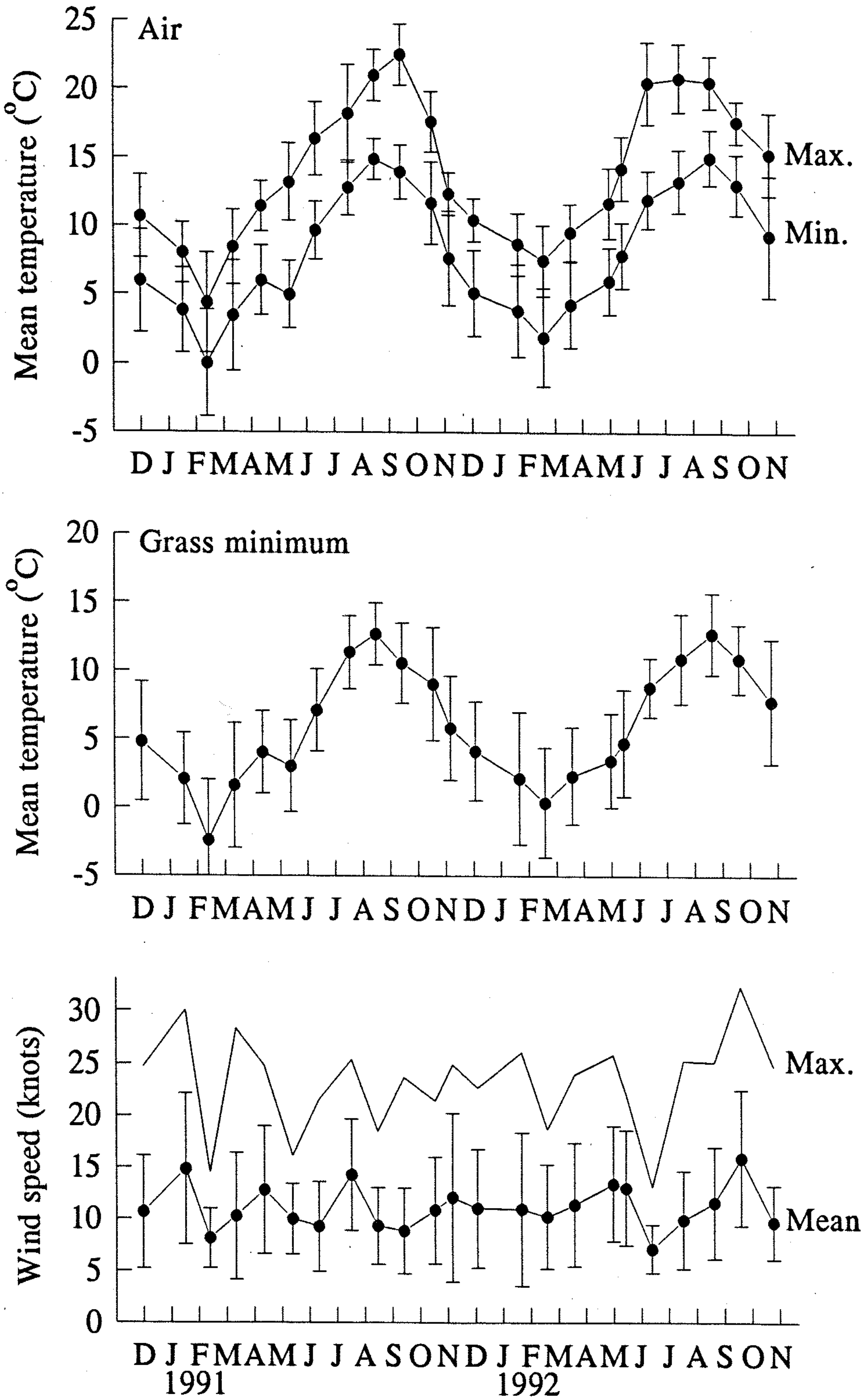


Figure 2.1 The Physico-Chemical Environment at Solent Breezes. Meteorological data from the nearby Solent MRSC station (November 1990 - October 1992). Values shown for each sampling date refer to mean values calculated for the "between-sampling period" leading up to that date.

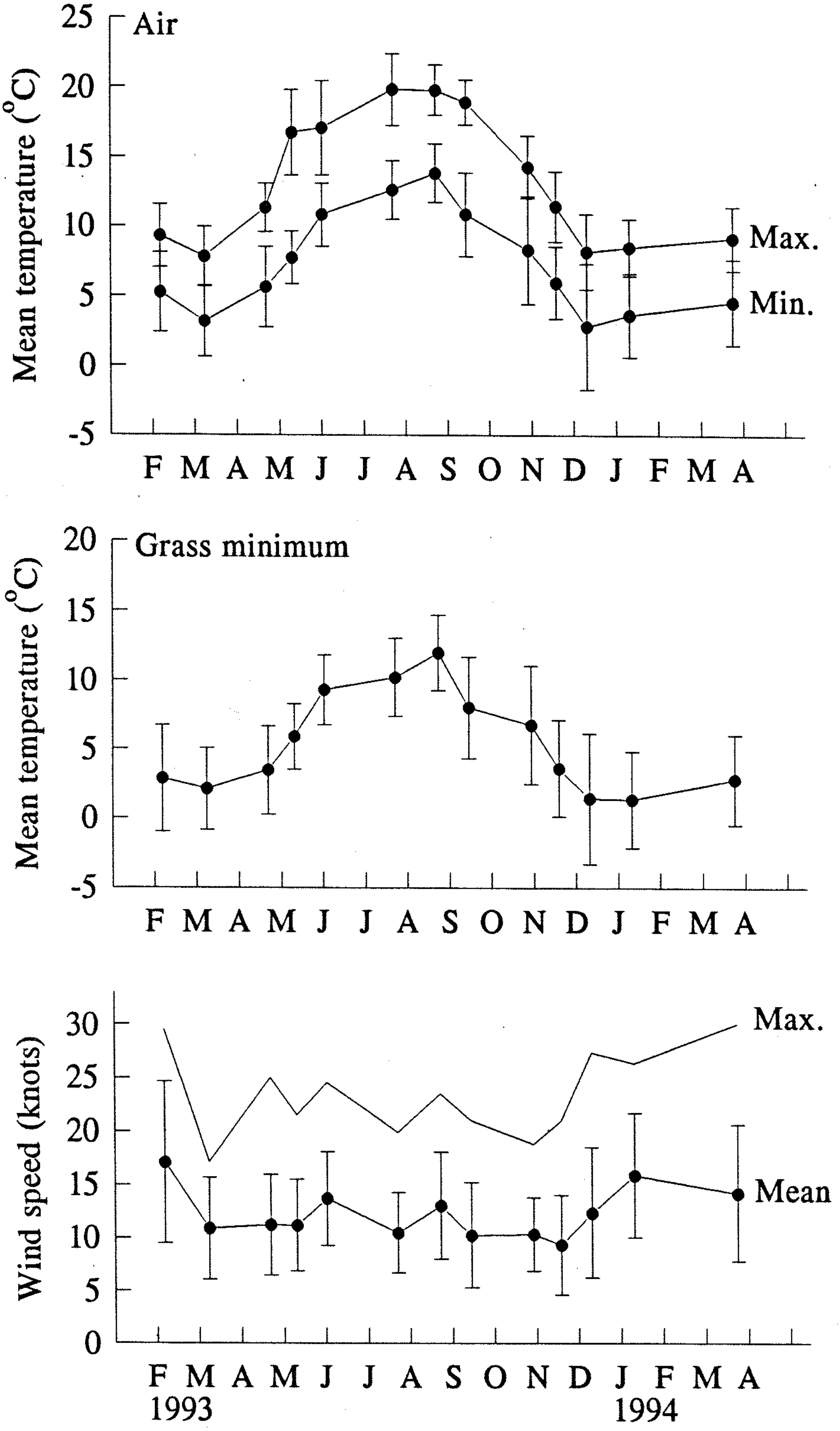


Figure 2.2 The Physico-Chemical Environment at Solent Breezes. Meteorological data from the nearby Solent MRSC station (February 1993 - March 1994). Values shown for each sampling date refer to mean values calculated for the "between-sampling period" leading up to that date.

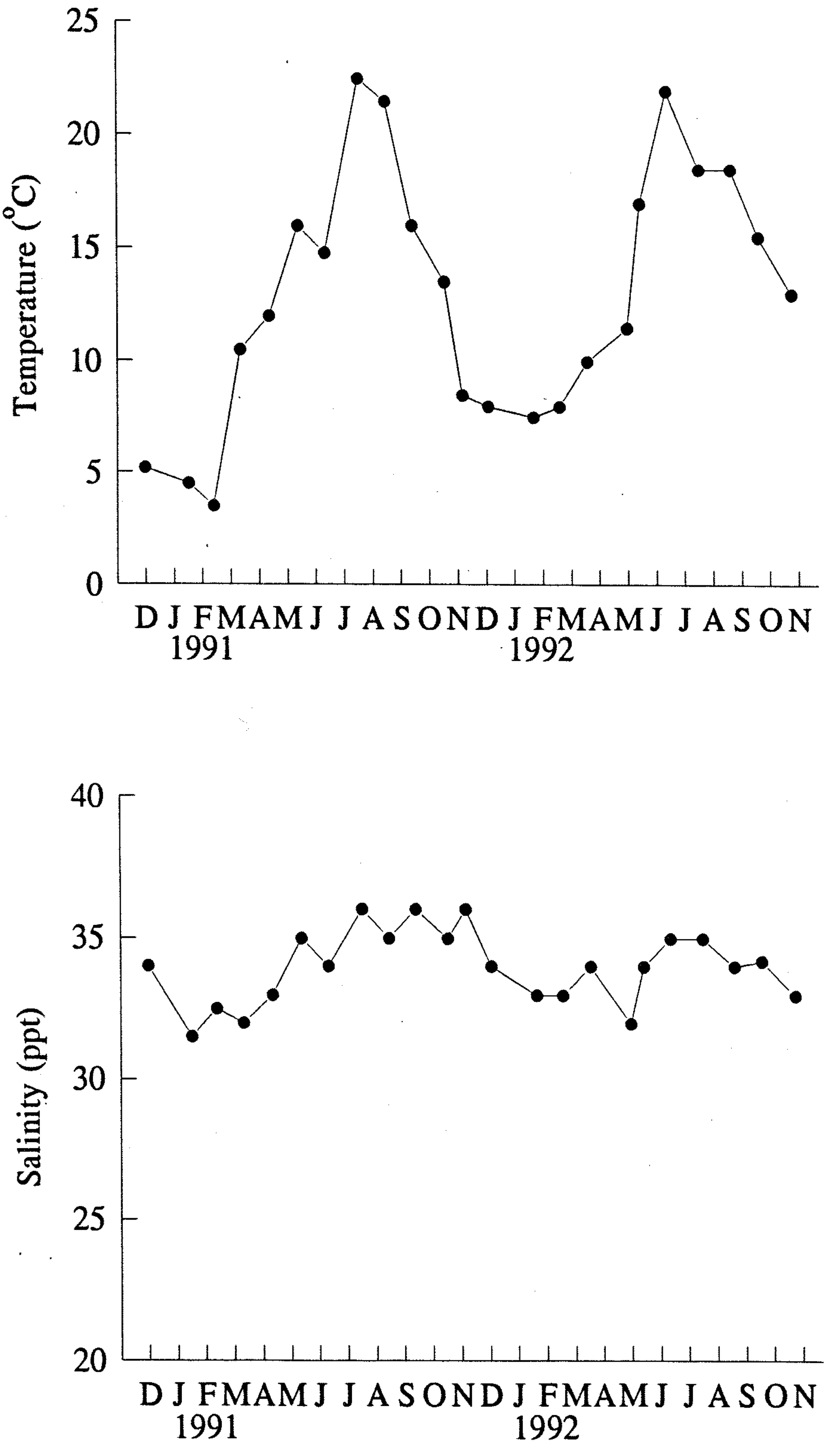
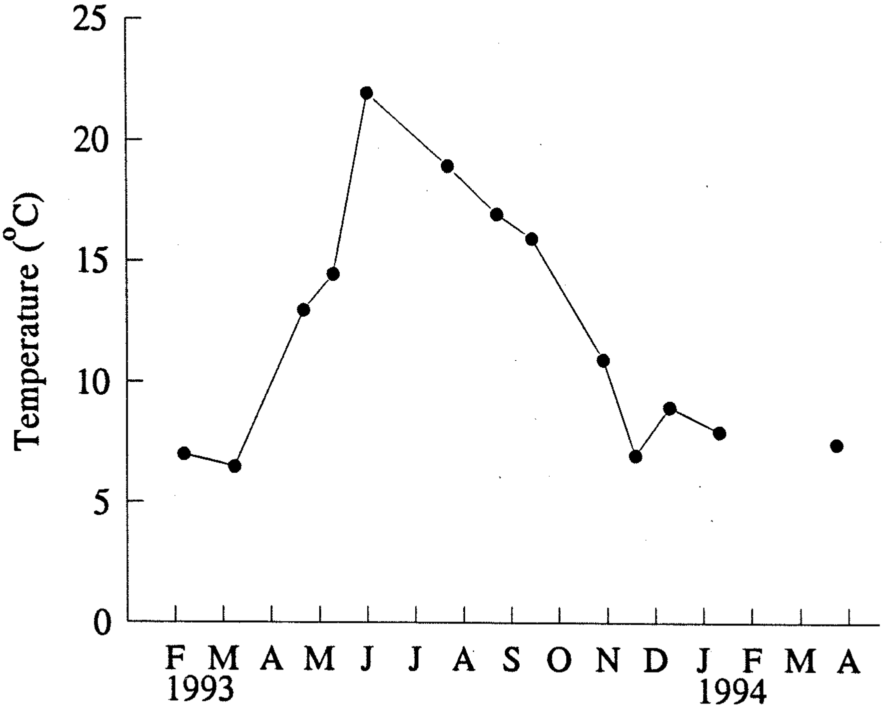


Figure 2.3 The Physico-Chemical Environment at Solent Breezes. The temperature and salinity of the seawater adjacent to the sampling site at Solent Breezes - measurements made during each of the monthly macrofaunal sampling visits (November 1990 - October 1992).



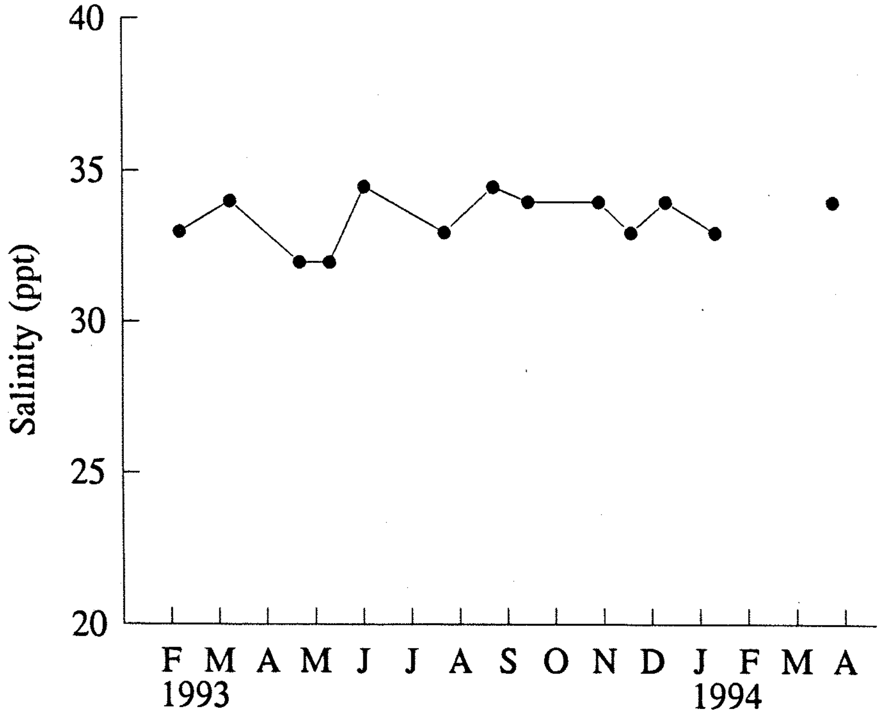


Figure 2.4 The Physico-Chemical Environment at Solent Breezes. The temperature and salinity of the seawater adjacent to the sampling site at Solent Breezes - measurements made during each of the monthly meiofaunal sampling visits (February 1993 - March 1994).

The temperature and salinity profiles from the single monthly measurements are given in Figures 2.3 and 2.4. The lowest ambient seawater temperatures were recorded in January and February 1991 when temperatures dropped to below 5°C. The subsequent three years all had minima that were no less than 7°C on their respective winter sampling dates. Peak temperatures (above 20°C) were recorded in July/August 1991, June 1992 and June 1993.

The salinity of the seawater adjacent to Solent Breezes remained relatively constant. The salinity was consistently above 31ppt, remaining close to full strength seawater throughout most of the sampling period. This was not unexpected as Solent Breezes is situated in the outer reaches of Southampton Water. Freshwater inputs to the estuary - primarily from the Test, Itchen and Hamble rivers - were clearly well mixed with seawater in the area surrounding Solent Breezes.

2.3 Sediment Analysis

Samples of surface sediment were collected in association with faunal samples on each visit to Solent Breezes. Throughout the regular macrofaunal sampling programme (November 1990 - October 1992) monthly sediment samples were taken from the mid-shore sampling site. Each month, areas of sediment that contained no visible *Lanice conchilega* tubes were sampled. Similarly, sediment samples collected from the five transect sites in June 1992 were from areas that contained no visible tubes on the sediment surface. On two occasions (June 1992 and September 1993) sediment samples were taken specifically from areas containing different densities of *Lanice conchilega* tubes. Finally, throughout the meiofaunal sampling programme (February 1993 - March 1994), four sediment samples were taken each month, i.e. two from areas of relatively high *Lanice conchilega* tube density (>560m^{-2}) and two from areas of zero tube density.

All sediment samples were taken to a depth of approximately 3cm and were returned to the laboratory within 2 hours of sampling. In the laboratory, samples were frozen, stored at -20°C, and subsequently analysed in suitably large batches to maximise comparability. The total organic content of each sample was determined by measuring the loss of weight on ignition at 550°C (see below). Particle size analysis was performed using the standard method described in Section 2.3.1 (Buchanan, 1984).

2.3.1 Methods

(i) Total organic content

Routine determination of organic matter was conducted using five replicate subsamples from each sediment sample. Carbonates were first removed from sediment samples by acid treatment. Each subsample was placed in a pre-weighed crucible, dried at 70°C, allowed to cool in a desiccator, and reweighed. Batches of subsamples were placed in a furnace at 550°C for 12 hours, removed and allowed to cool in a desiccator. Each sample was reweighed and the percentage weight lost by ignition at 550°C (i.e. the total organic matter) was calculated.

(ii) Particle size analysis

Frozen sediment samples were defrosted at room temperature and immediately mixed with a solution of 6% v/v hydrogen peroxide. This solution was used to degrade any organic material that could have caused particles to bind together. Each sediment sample was left in the hydrogen peroxide solution until there was no further reaction (usually 12-24 hours). Individual samples were then filtered and rinsed with distilled water to remove the hydrogen peroxide. A solution of sodium hexametaphosphate was used to reduce the electrical charges that may have caused fine particles to aggregate, thereby affecting the particle size distribution. 20ml of sodium hexametaphosphate ($6.2gl^{-1}$) was added to each sample of sediment and, after agitation, the samples were left to stand for 12 hours.

Each sample was then transferred to a 63µm mesh sieve placed in a white tray. The sample was washed through the sieve with distilled water and the material passing through the sieve was retained. Most of the particles smaller than 63µm were therefore removed during the wet sieving process. The sieve and its contents were oven dried at 70°C before the subsequent dry sieving process.

A stack of sieves with mesh sizes between 2mm and 63μm were arranged in sequence on a mechanical sieve shaker. The sieve mesh sizes were set at 0.5ϕ intervals on the Wentworth scale (i.e. between -1.0 and +4.0) and a suitable pan was placed below the finest mesh (63μm) to collect any remaining fine material. Each sediment sample was shaken through the sieve stack for 15 minutes. The fraction retained on each sieve was weighed and the fine material in the bottom pan was added to the wet sieved fraction.

The fine material (i.e. <63μm) was washed into a 1litre measuring cylinder and the volume was made up to exactly 1litre with distilled water. The cylinder was inverted and agitated to resuspend and mix the fine material. A 20ml sample was immediately pipetted from the cylinder and placed in a pre-weighed Petri dish. This sample was dried in an oven at 70°C, allowed to cool in a dessicator, and reweighed. The weight of the sediment in the Petri dish was multiplied by 50 to calculate the total weight of fine sediment in the cylinder (i.e. total weight of the <63μm fraction).

Particle size distributions were calculated for each sediment sample by converting raw weight data into percentage data. In addition, cumulative frequency curves were constructed from which a number of statistical measures could be derived. The measures outlined below were calculated to allow the characteristics of each sediment sample to be described.

1. The **Quartile Deviation** measures the number of phi units that lie between the first and third quartiles on the cumulative curve.

$$QD\phi = (Q_3\phi - Q_1\phi)/2$$

2. The **Phi Quartile Skewness** gives an indication of the skewness of a particle size distribution i.e. to which side of the median the data tends to be spread.

$$Sk_q\phi = (Q_1\phi + Q_3\phi)/2 - Md\phi$$

3. The **Inclusive Graphic Standard Deviation** measures the spread of the particle size data and indicates the level of sorting.

$$\sigma_1 = \frac{\phi 84 - \phi 16}{4} + \frac{\phi 95 - \phi 5}{6.6}$$

Values within particular ranges are given the following verbal classifications:

<0.35	very well sorted
0.35 - 0.50	well sorted
0.50 - 0.71	moderately well sorted
0.71 - 1.00	moderately sorted
1.00 - 2.00	poorly sorted
2.00 - 4.00	very poorly sorted

4. The **Inclusive Graphic Skewness** again indicates the level of skewness but makes use of the extremes (i.e. the "tails") of the cumulative curve.

$$Sk_1 = \frac{\phi 16 + \phi 84 - 2\phi 50}{2(\phi 84 - \phi 16)} + \frac{\phi 5 + \phi 95 - 2\phi 50}{2(\phi 95 - \phi 5)}$$

Values within particular ranges are given the following verbal classifications:

+1.0 to +0.3	strongly fine skewed
+0.3 to +0.1	fine skewed
+0.1 to -0.1	symmetrical
-0.1 to -0.3	coarse skewed
-0.3 to -1.0	strongly coarse skewed

5. The **Graphic Kurtosis** compares the particle size distribution to a normal distribution and measures its departure from that normal distribution.

$$K_G = \frac{\phi 95 - \phi 5}{2 \cdot 44(\phi 75 - \phi 25)}$$

Values of K_G within particular ranges are given the following verbal classifications:

<0.67	very platykurtic
0.67 - 0.90	platykurtic (flat peaked)
0.90 - 1.11	mesokurtic (nearly normal)
1.11 - 1.50	leptokurtic (excessively peaked)
1.50 - 3.00	very leptokurtic

6. The **Percentage Silt/Clay Fraction** is simply the fraction of total sediment that passed through the 63μm sieve (i.e. $>4.0\phi$).

(iii) Changes in sediment characteristics with depth

A number of additional sets of sediment samples were collected to investigate how the organic matter fraction changed with depth below the sediment surface. Samples were taken using a small hand corer (internal diameter 6cm). Each core was taken to a depth of 15cm and divided into 1cm sections. The total organic content of each section was determined by measuring its loss of weight on ignition at 550°C. The bioavailable protein in a similar set of samples was measured using a technique developed by Mayer *et al.* (1986) (Mattin, 1992).

(iv) The depth of sediment above the underlying clay layer

At the start of the sampling programme it was observed that an underlying base of London clay existed below the surface sediment at Solent Breezes. It was also noted that the depth at which this clay layer occurred below the surface varied markedly between samples. As a result, numerous sets of measurements were made of the depth of sediment above the clay layer during the project. In particular, areas of sediment containing different densities of *Lanice conchilega* tubes were examined. For each measurement the number of tubes within a randomly positioned 0.071m^2 circular quadrat was counted and a small transparent corer was used to extract a column of sediment to a depth of 30cm. The outside of the tube was then rinsed clean and the depth of the clay layer was measured.

2.3.2 Results

(i) Total organic content

Figure 2.5 shows the total organic content of sediment samples collected during regular monthly visits. Samples collected in February 1993 and March 1993 were unfortunately lost during storage before the analyses were completed. Mean organic content values ranged between 0.81% and 1.96%. Differences in the mean values were analysed using a standard one way analysis of variance (ANOVA) followed by the Student-Newman-Keuls Test for pairwise multiple comparisons. Sediment collected in February and March 1991 contained significantly higher amounts of organic matter than all other monthly samples ($p = 0.008$). There was no clear seasonal pattern during the macrofaunal sampling period (Figure 2.5; upper graph). A noticeable decline in organic content did occur between September and November in 1991, and between July and September in 1992. The latter decline was followed by a significant increase in October 1992.

Throughout the meiofaunal sampling period there was no **consistently** significant difference between the samples taken from areas containing no *Lanice conchilega* tubes and those from areas of high tube densities (Figure 2.5; lower graph). In June 1993 and August 1993 significantly greater amounts of organic matter were present in the high tube density areas, but these amounts were still relatively small compared to the high levels previously found in February and March 1991.

The upper graph in Figure 2.6 shows the total organic content of sediment samples collected in June 1992 and September 1993 from areas containing different densities of *Lanice conchilega* tubes. All samples were collected from the mid-shore sampling site. Areas of sediment containing tube densities of between 0 and 66 per quadrat (i.e. 0 to 930m^{-2}) were sampled. Average organic content values were all within the range 0.93 - 1.26%, and there was no significant change in organic content with increasing tube density.

The lower graph in Figure 2.6 shows the total organic content of samples collected from the five transect sites. All sediment samples collected along the transect were taken from areas containing no visible *Lanice conchilega* tubes.

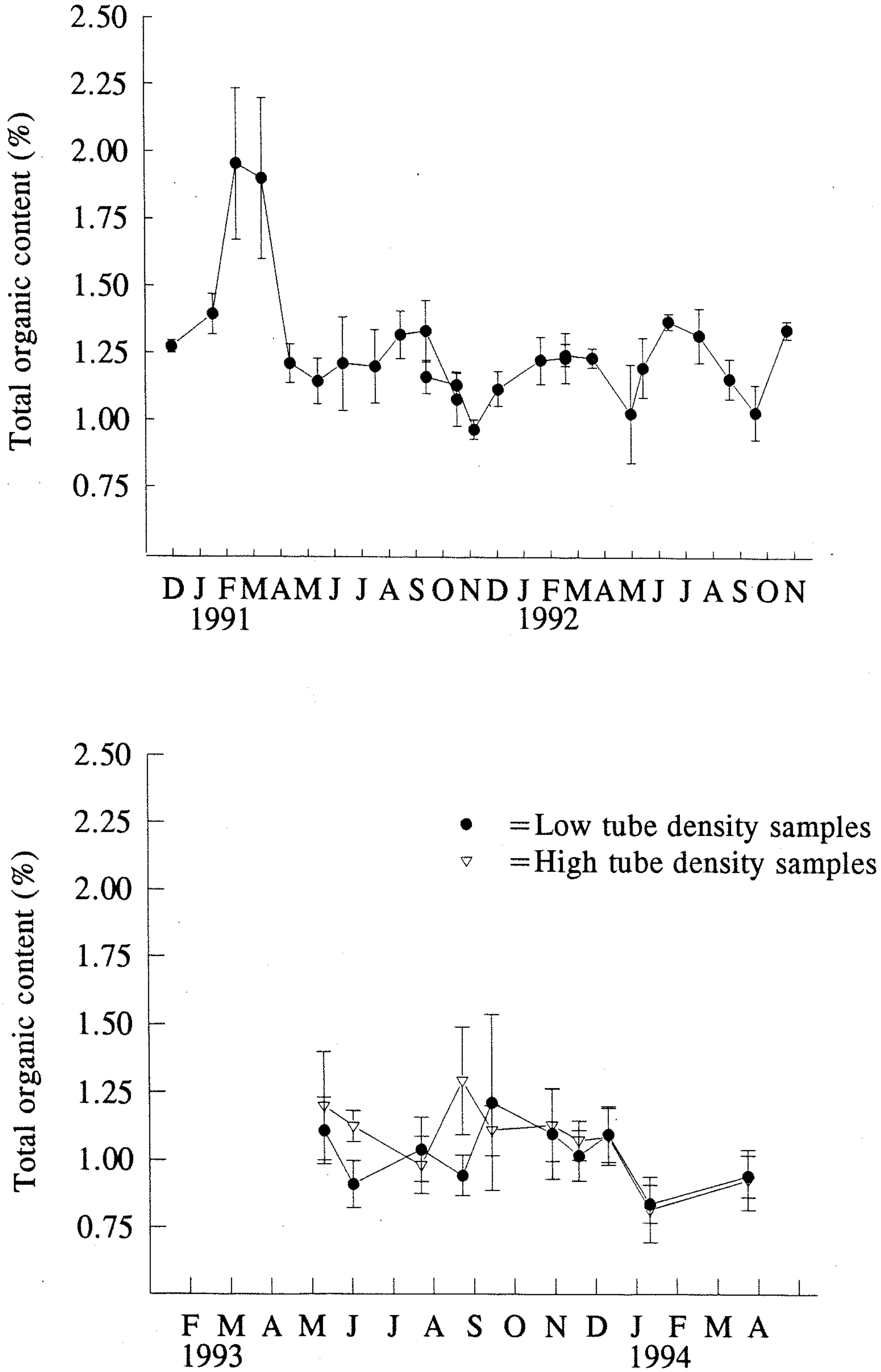
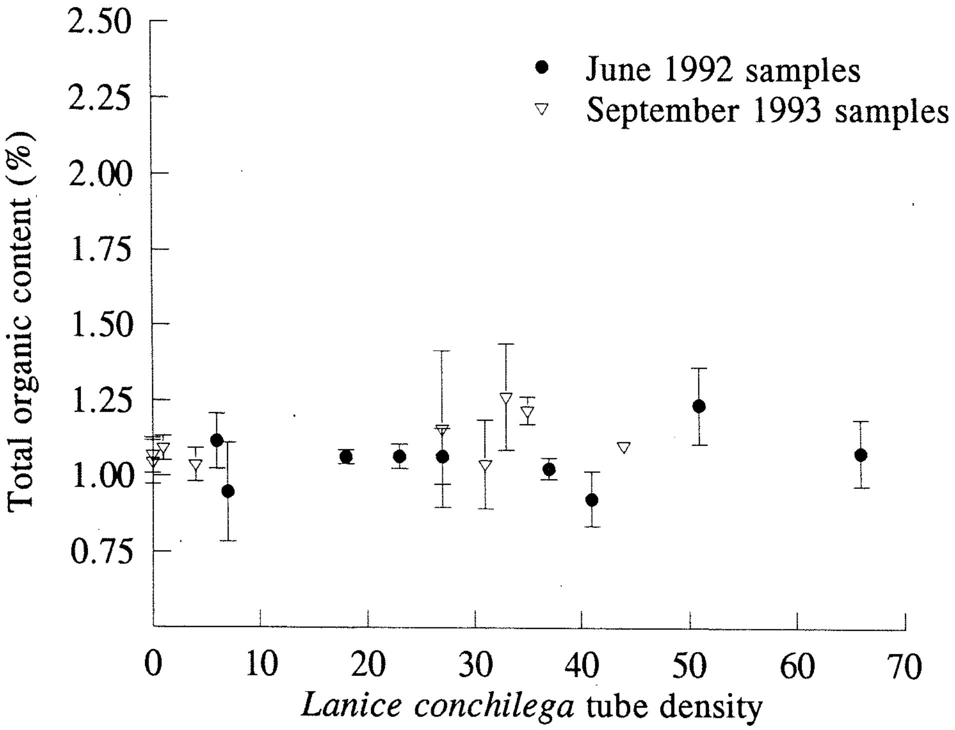


Figure 2.5 The Physico-Chemical Environment at Solent Breezes. The total organic content of surface sediment samples taken during monthly macrofaunal sampling visits (upper graph) and monthly meiofaunal sampling visits (lower graph). Mean values (± S.D.) shown.



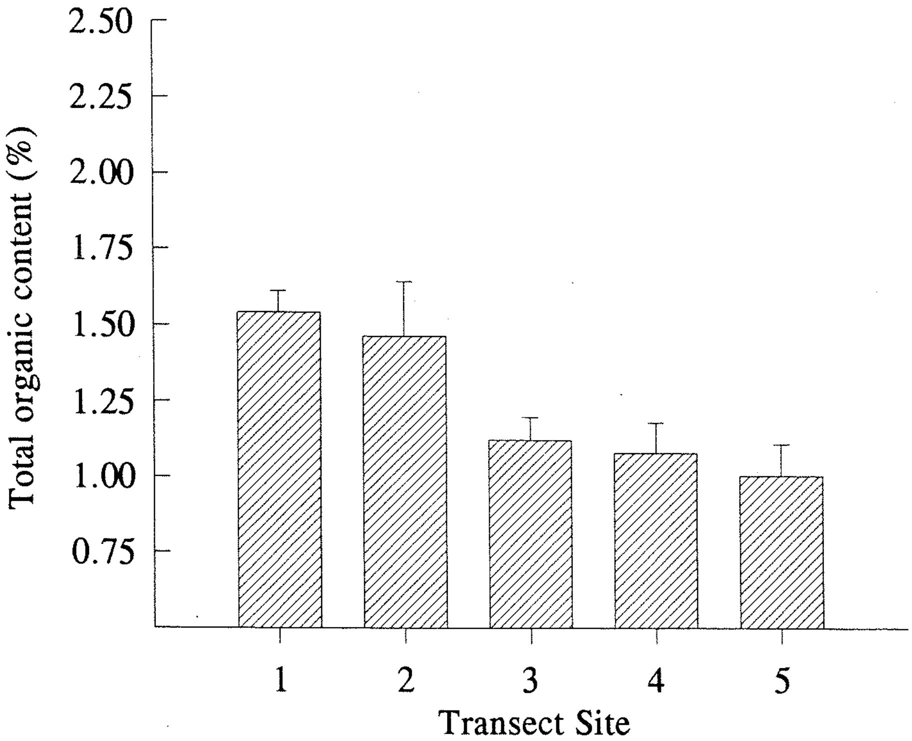


Figure 2.6 The Physico-Chemical Environment at Solent Breezes. The total organic content of surface sediment samples from different densities of *Lanice conchilega* tubes (upper graph) and from five transect sites extending from high tide (Site 1) to low tide (Site 5) (lower graph). Mean values (± S.D.) shown.

There were significantly greater amounts of organic matter in the samples collected from the top half of the shore (i.e. from Sites 1 and 2). The mid-shore sampling site (3) and the lower shore sites (4 and 5) contained similar average concentrations of organic matter (between 1.00 and 1.12%).

(ii) Particle size analysis

Particle size distributions were evaluated for all available surface sediment samples. Figures 2.7 to 2.10 present the results of the statistical analyses conducted on these particle size distributions. The percentage silt/clay fraction results are presented separately in Figures 2.11 and 2.12. Sediment samples collected in February 1993 and March 1993 were unfortunately lost during storage before the analyses were completed.

The Quartile Deviation (QDϕ) is a basic measure of sorting, more positive values indicating a lower level of sorting. The Phi Quartile Skewness is similarly a basic measure of skewness. Both these statistics have been criticised by Folk (1974) because they only take account of 50% of the particle size distribution. They must therefore be used in conjunction with the other three measures, which were developed by Folk, and which take account of up to 90% of the distribution.

Figures 2.7 and 2.8 show the statistical parameters calculated for sediment samples collected during the macrofaunal and meiofaunal sampling periods. There was a degree of variation in the level of sorting during the first six months of the study. Sediment sampled in February 1991 was poorly sorted ($\sigma_1 = 1.0$), and sediment sampled in March 1991 was moderately sorted ($\sigma_1 > 0.71$). Apart from January 1991 and May 1991 samples, which were moderately well sorted, **all** other regular monthly samples taken between June 1991 and March 1994 were well sorted ($\sigma_1 < 0.50$).

The Inclusive Graphic Skewness (Sk_1) shows that the distribution of sediment among the different size fractions was symmetrical for the majority of samples. Two months (November 1990 and October 1992) had sediment that was slightly fine skewed, and three months (February 1991, April 1991 and June 1991) were slightly coarse skewed.

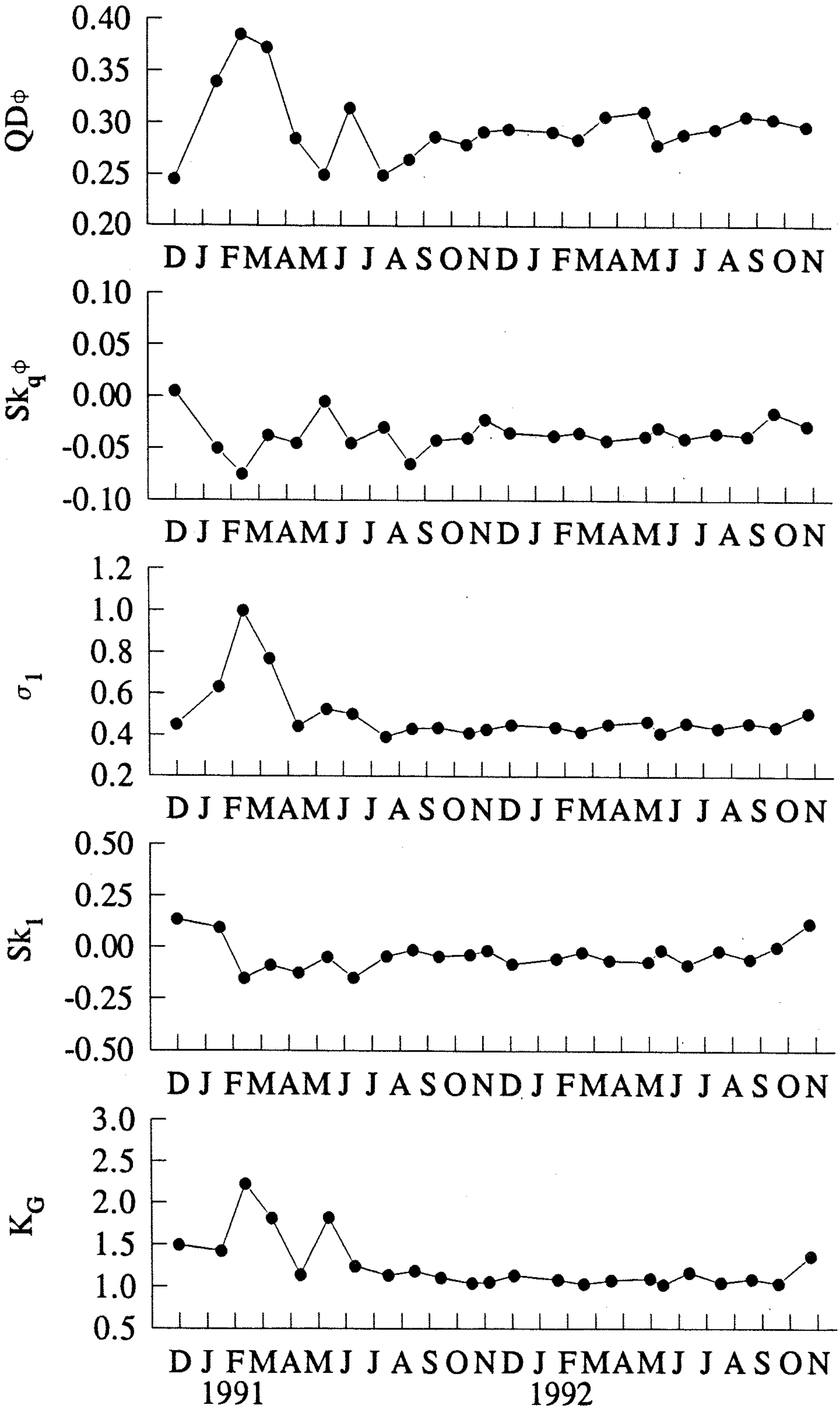


Figure 2.7 The Physico-Chemical Environment at Solent Breezes. Fluctuations in the five statistical measures derived from the particle size distributions of monthly sediment samples taken during the macrofaunal sampling period (November 1990 - October 1992).

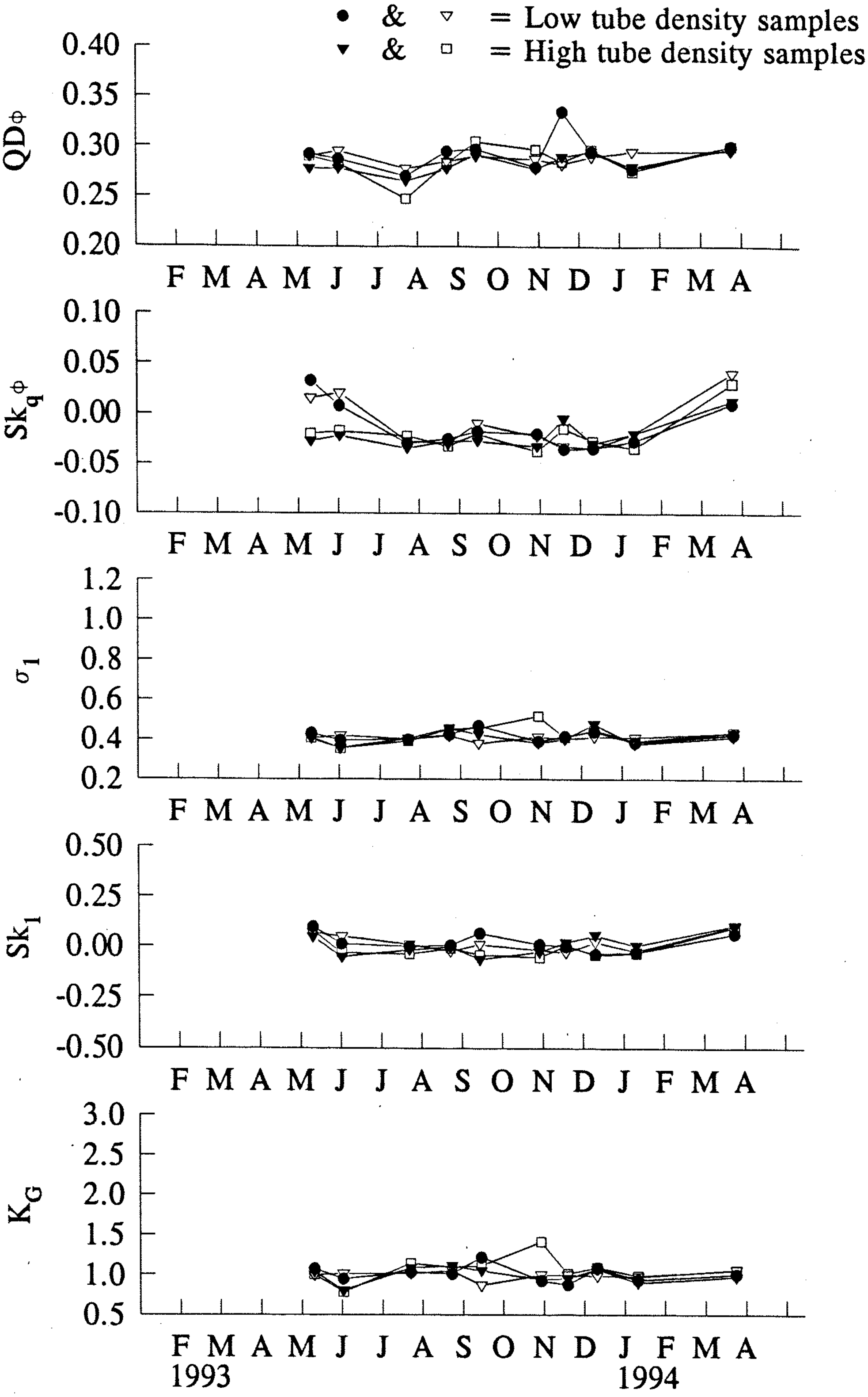


Figure 2.8 The Physico-Chemical Environment at Solent Breezes. Fluctuations in the five statistical measures derived from the particle size distributions of monthly sediment samples taken during the meiofaunal sampling period (February 1993 - March 1994).

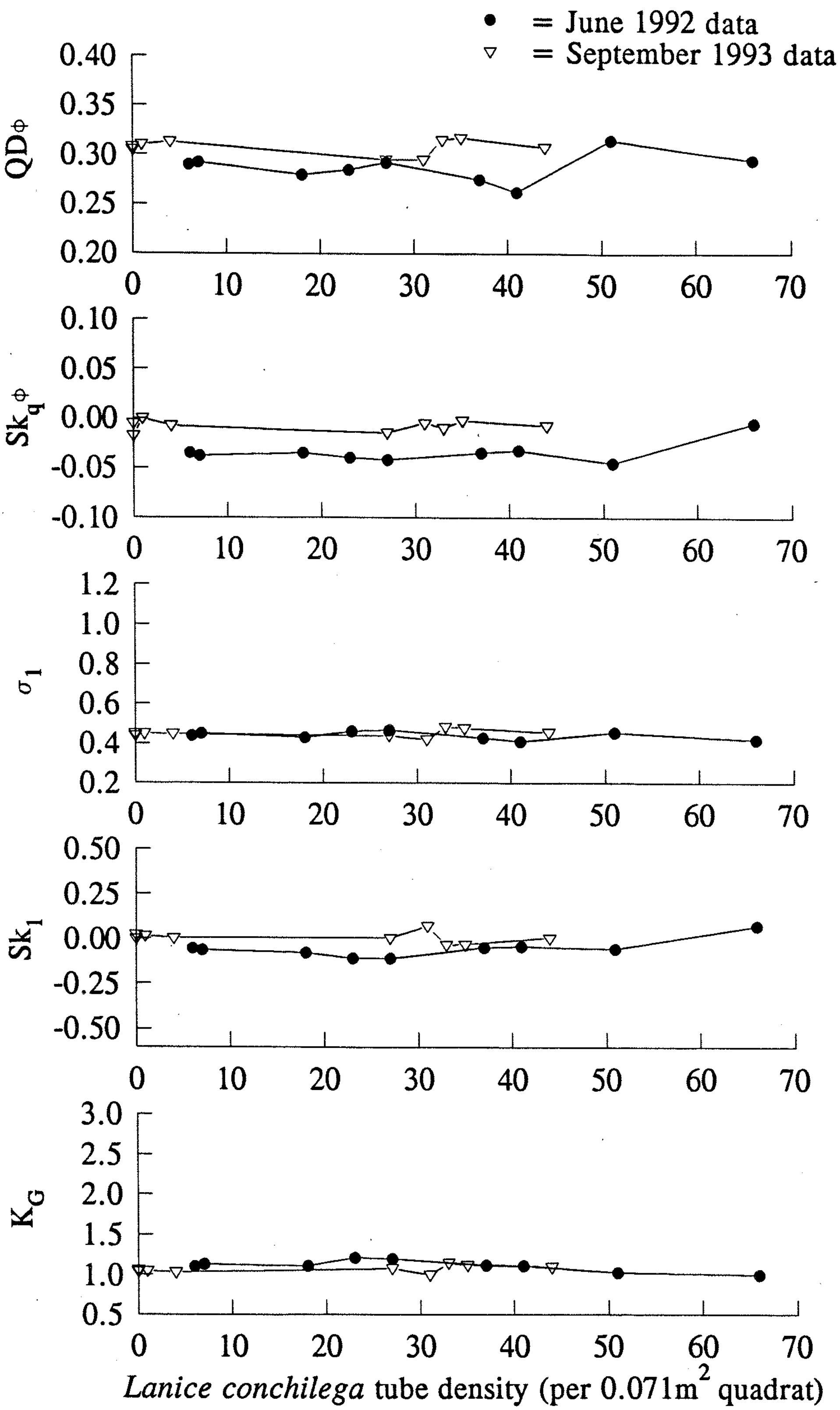


Figure 2.9 The Physico-Chemical Environment at Solent Breezes. Fluctuations in the five statistical measures derived from the particle size distributions of sediment samples taken from areas containing different densities of *Lanice conchilega* tubes.

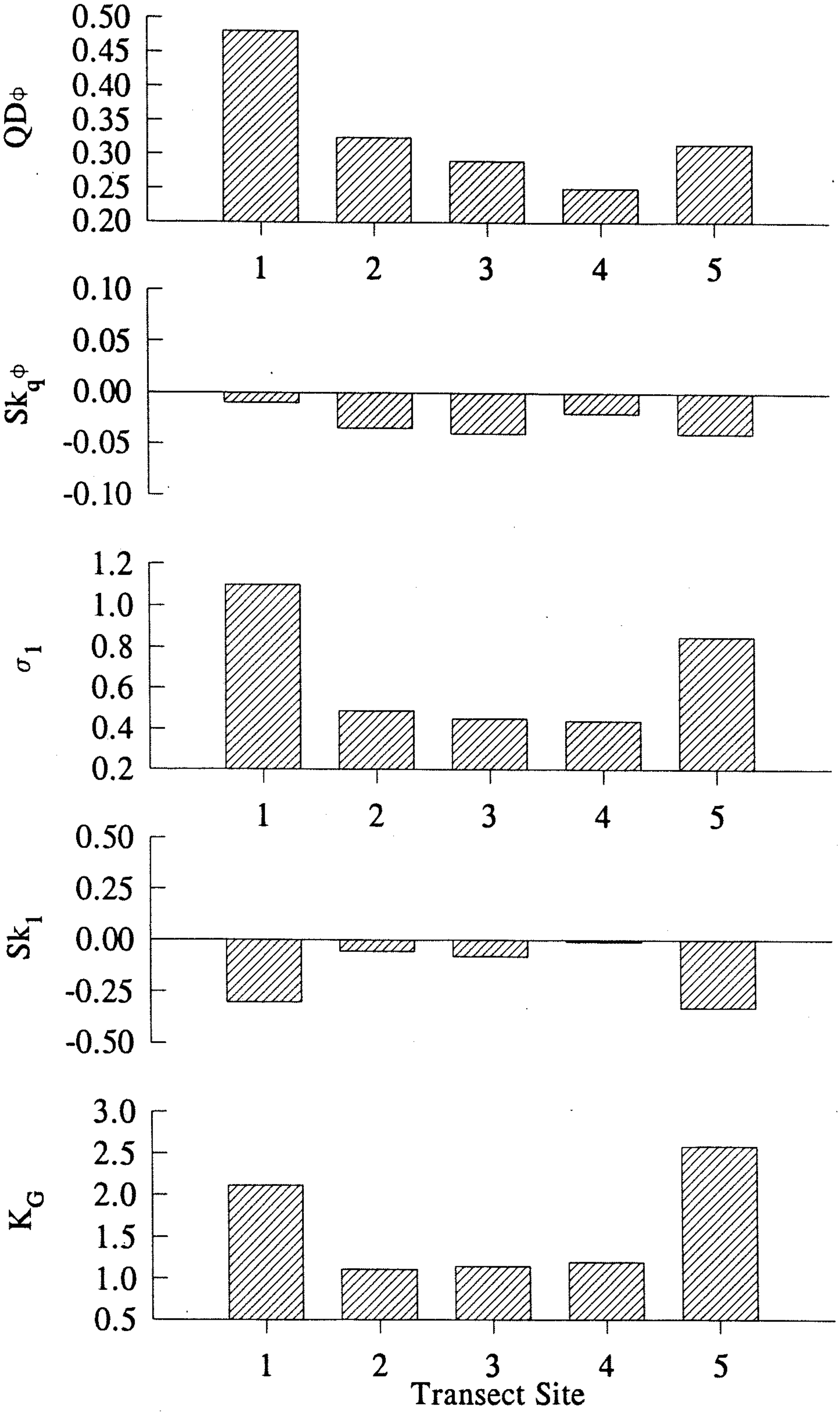


Figure 2.10 The Physico-Chemical Environment at Solent Breezes. Fluctuations in the five statistical measures derived from the particle size distributions of sediment samples taken from five sites along a transect between high water (Site 1) and low water (Site 5).

The particle size distributions of all monthly sediment samples analysed from the meiofaunal sampling period (i.e. from both zero tube density and high tube density areas) were symmetrical.

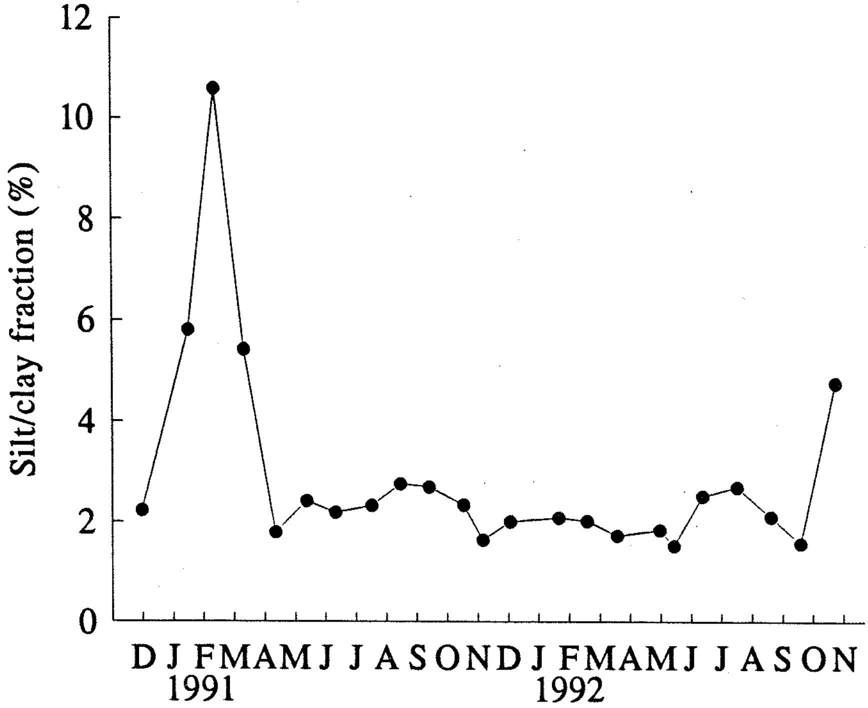
The Kurtosis statistic (K_G) shows that the only particle size distributions that deviated significantly from a normal distribution were from sediment collected in February 1991, March 1991 and May 1991 (all **very** leptokurtic, i.e. excessively peaked).

Figure 2.9 shows the statistical parameters calculated for sediment samples taken from areas containing different densities of *Lanice conchilega* tubes (June 1992 and September 1993). All sediment samples were well sorted ($\sigma_1 < 0.50$). Each sample also had a particle size distribution that was symmetrical (Sk_1 between - 0.1 and + 0.1), and was either mesokurtic or only slightly leptokurtic.

Figure 2.10 shows the statistical parameters calculated for sediment samples taken from the five transect sites. Particle size distributions evaluated for all transect samples were negatively skewed ($Sk_q\phi < 0$), and those from Sites 1 and 5 were strongly coarse skewed ($Sk_1 < - 0.30$). Site 1 sediment was poorly sorted and Site 5 sediment was moderately sorted and both were very leptokurtic.

The percentage silt/clay fraction results reveal obvious differences between the sediment samples collected early in 1991 and the subsequent samples taken during the macrofaunal sampling period (Figure 2.11). Between January and March 1991, the silt/clay content was above 5.40%, and a particularly high amount of silt/clay occurred in the February 1991 sediment (>10%). After this period, silt/clay fractions remained between 1.52 and 2.70%, until October 1992 when a relatively high silt/clay content was again observed (4.77%).

Sediment samples taken during the meiofaunal sampling period all contained silt/clay fractions that were lower than 4.50%, and the majority were below 3.50%. There was no consistent difference between sediment samples collected from areas of high tube densities and samples collected from areas containing no visible tubes. However, there appeared to be an increase in the variability between samples during late summer and autumn (between August and October 1993).



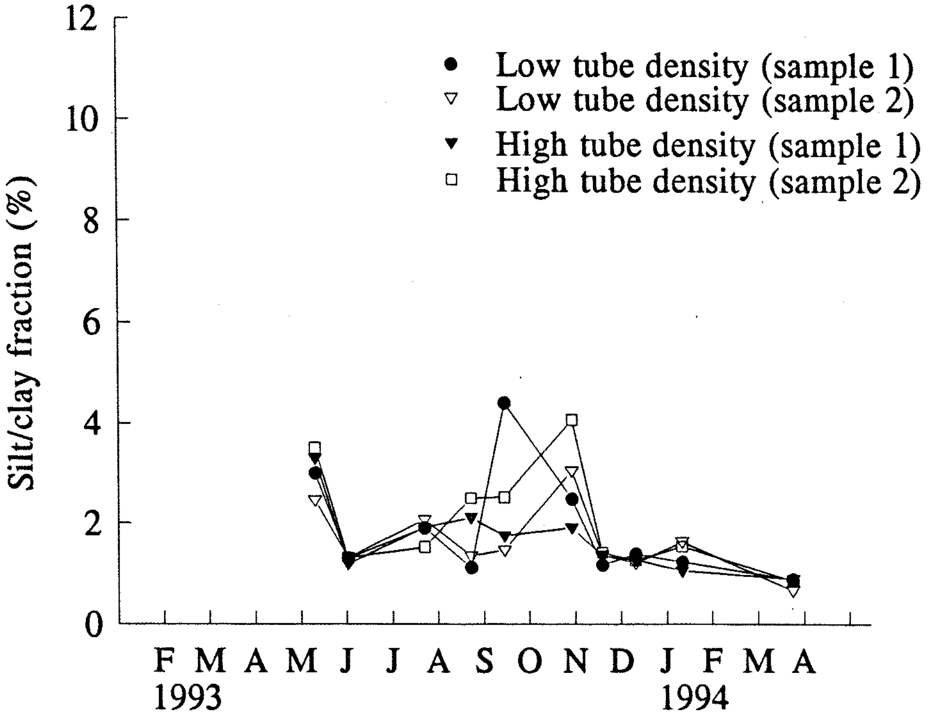


Figure 2.11 The Physico-Chemical Environment at Solent Breezes. The clay/silt content of sediment samples taken during monthly macrofaunal sampling visits (upper graph) and during monthly meiofaunal sampling visits (lower graph).

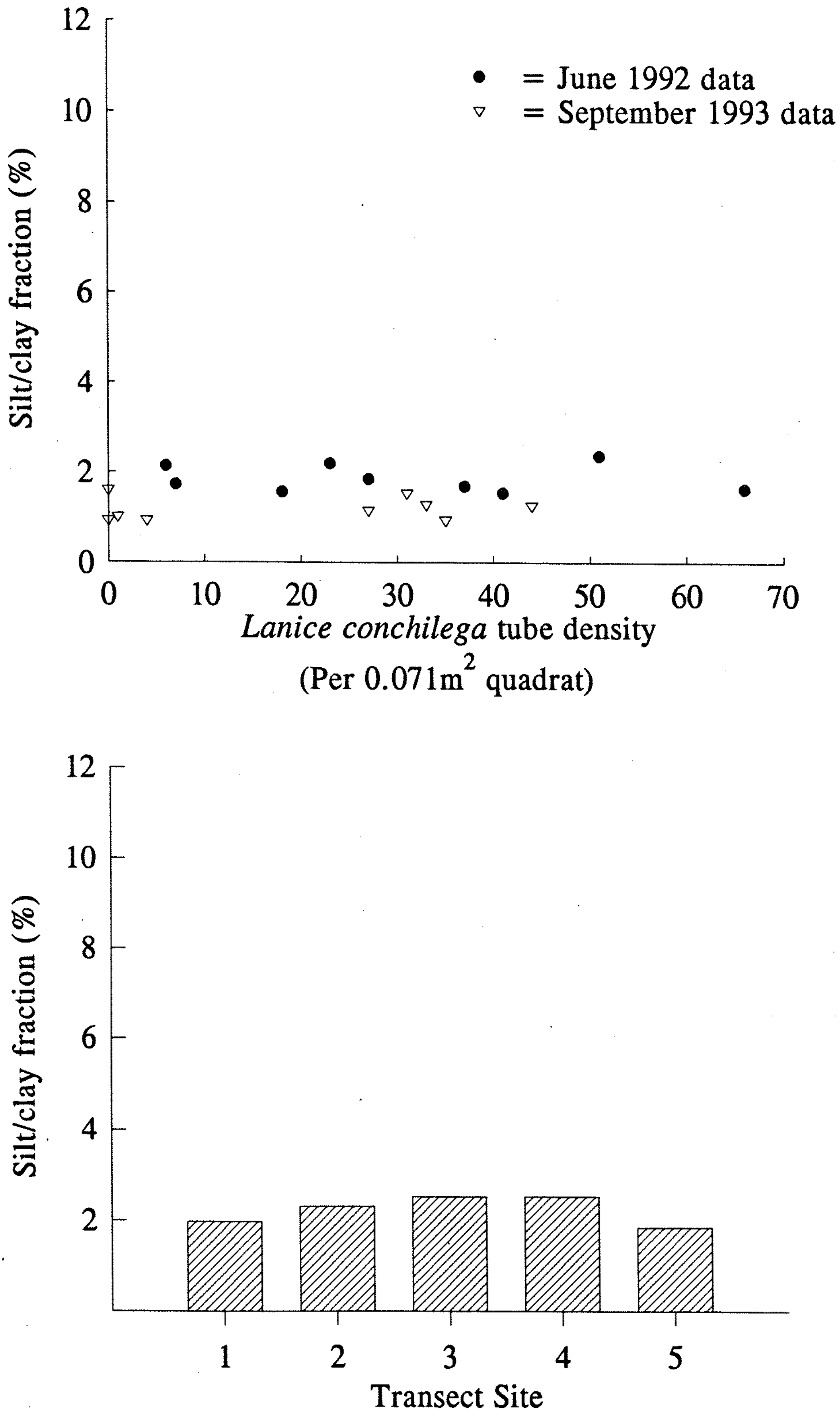


Figure 2.12 The Physico-Chemical Environment at Solent Breezes. The silt/clay content of surface sediment samples taken from areas containing different densities of *Lanice conchilega* tubes (upper graph) and from five transect sites between high tide (Site 1) and low tide (Site 5) (lower graph).

The top graph in Figure 2.12 shows the silt/clay fractions present in sediment samples collected in June 1992 and September 1993 from areas containing different densities of *Lanice conchilega* tubes. The bottom graph in Figure 2.12 shows the silt/clay fractions present in samples collected from the five transect sites. The scale used for both y-axes is identical to the previous graphs (Figure 2.11) for comparative purposes. The silt/clay fractions present in the June 1992 samples were slightly higher those present in the September 1993 samples. However, all values were relatively low (maximum value 2.36%). Similarly, the silt/clay fractions present in the transect sediment samples were all below 2.60%. Sediment taken from Site 5 contained the smallest silt/clay fraction (i.e. 1.85%).

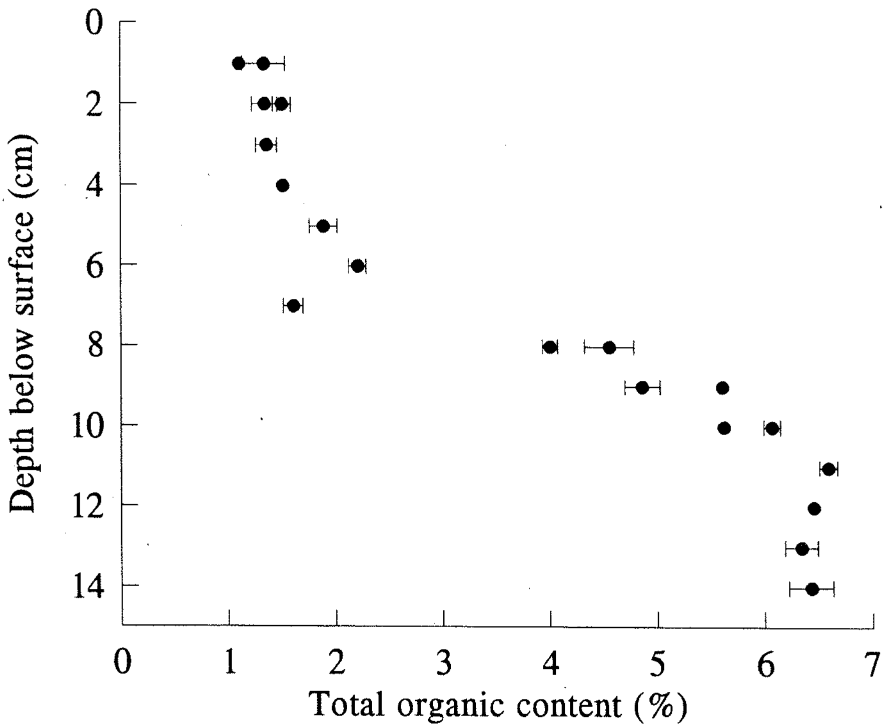
(iii) Changes in sediment characteristics with depth

The total organic content increased rapidly below a depth of 8cm (Figure 2.13), reaching a maximum at 11-12cm (approximately 6.5% of total sediment). Conversely, the bioavailable protein concentration decreased with depth from about 0.10% (0-3cm) to 0.04% (below 10cm). The majority of the organic matter that existed below the surface sediment was therefore refractory organic material.

(iv) Additional changes in sediment parameters with increasing tube density

The depth of sediment above the underlying clay layer was measured in areas containing different densities of *Lanice conchilega* tubes (Figure 2.14). Measurements were made at various stages throughout the sampling period. A significant positive correlation existed between tube density per quadrat and the depth of sediment above the clay layer ($p < 0.001$).

Finally, Mattin (1992) compared the bioavailable protein content of sediment collected from areas of high tube density and areas of zero tube density in October and November 1991. The bioavailable protein content of samples ranged between 0.7 and 1.3mg/g dry sediment, and on both occasions the mean value in high tube density areas was significantly greater than the mean value in zero tube density areas ($p < 0.05$).



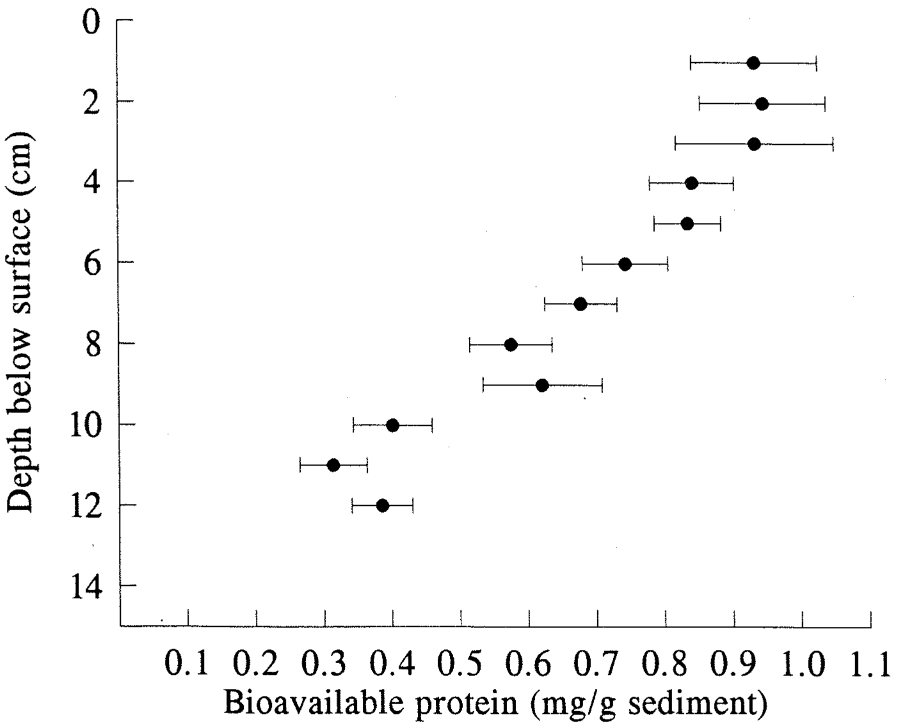


Figure 2.13 The Physico-Chemical Environment at Solent Breezes. Changes in the total organic content (upper graph) and the bioavailable protein content (lower graph) of Solent Breezes sediment with depth below the surface. Bioavailable protein data from Mattin (1992). Mean values (± S.D.) shown.

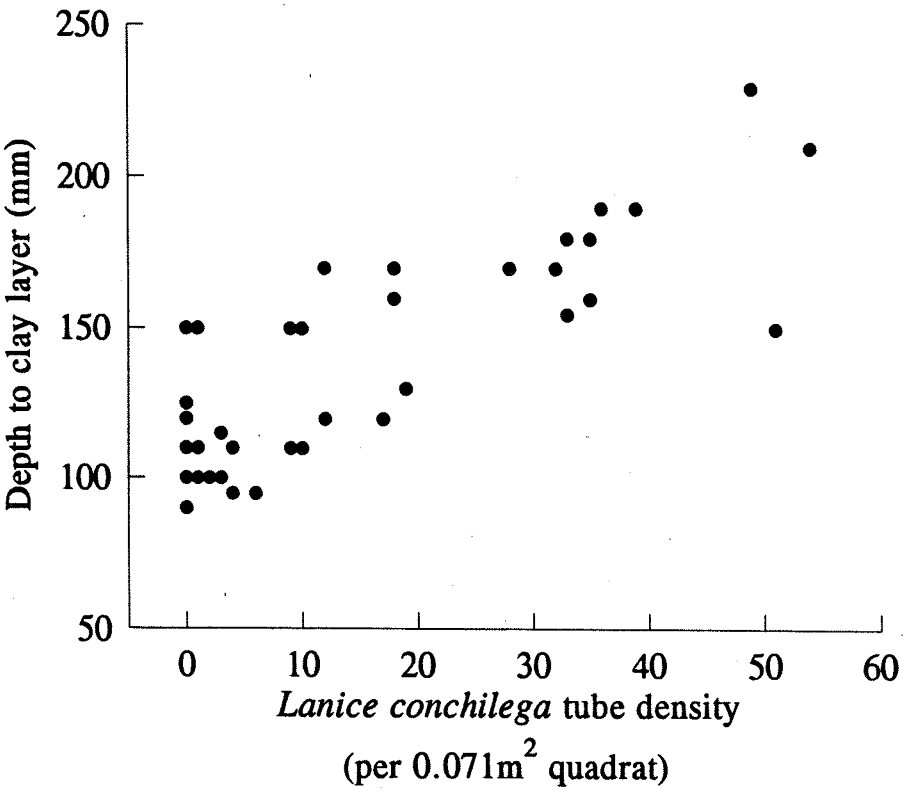


Figure 2.14 The Physico-Chemical Environment at Solent Breezes. The relationship between the density of *Lanice conchilega* tubes and the depth of the underlying clay layer.

2.4 Discussion

Benthic communities are affected by a wide range of physical and chemical parameters. The relative importance of these parameters to individual benthic species may vary and different species may be affected by environmental parameters in different ways. Physical and chemical parameters often exert a dominant influence on intertidal benthic communities, particularly in estuarine waters.

The following sections outline the main characteristics of the physico-chemical environment at Solent Breezes. Firstly, the temporal changes that occurred in meteorological and hydrological parameters are summarised. Secondly, the sedimentary environment at Solent Breezes is examined with particular reference to the changes that occurred along the sampling transect taken in June 1992. Thirdly, the mid-shore area used that was as the main sampling site is described in detail, and the temporal fluctuations observed in the sedimentary environment at this site are discussed. Finally, the characteristics of sediment taken from areas containing different densities of *Lanice conchilega* tubes are considered.

2.4.1 Meteorological and Hydrological Parameters

Both the air temperatures obtained from the Meteorological Office and the monthly seawater temperatures measured at Solent Breezes peaked and troughed in typical seasonal cycles. The particularly cold air temperatures recorded before the February 1991 sampling date were reflected in the seawater temperature measured during the February 1991 sampling visit. The extreme conditions during this period were liable to have adversely affected the infauna at Solent Breezes, particularly if very low air temperatures at night (frost conditions) coincided with periods of emersion.

Although air temperatures can fluctuate considerably more than seawater temperatures, the importance of the latter must not be underestimated. The sampling site at Solent Breezes is covered by seawater during a large part of each tidal cycle. Consequently, ambient seawater temperatures may also have significantly affected the infauna.

Low seawater temperatures have been also reported in the local area for the same period by Bamber (1993): winter minimum temperatures recorded at Stanswood Bay (approximately 6km from Solent Breezes) for the early part of 1991 were noticeably lower than those recorded for the previous two winters (i.e. 1988-1989 and 1989-1990). Similarly, winter minimum temperatures of intake seawater at Fawley Power Station (weekly mean values) were consistently above approximately 7°C during the period between January 1988 and October 1990 (Bamber, 1993).

The salinity of seawater may change dramatically in estuarine waters during periods of high freshwater input. However, no such dramatic fluctuations occurred in the monthly salinity readings taken throughout the project. It is possible that more significant changes occurred between sampling visits during extended periods of rainfall. In addition, high insolation levels or heavy rainfall during periods of emersion may have significantly changed the salinity of interstitial water in the surface layers of the beach. However, at the time of sampling each month, surface waters at the mid-shore sampling site were not noticeably different from the adjacent seawater.

2.4.2 Sediment Parameters

(i) The sampling transect

The sedimentary regime at Solent Breezes altered significantly along the sampling transect taken between the mean low water mark and the mean high water mark. Firstly, greater amounts of organic material were present at the top of the shore. At the time of sampling much of the upper shore (approximately 60%) was covered with fine, filamentous green macroalgae interspersed with patches of large fleshy green and brown macroalgal species. Although sediment samples were taken from areas of bare sediment, fragments of macroalgae (particularly the filamentous species) were impossible to avoid completely. Some fragments were inevitably included in the sediment samples, which would have significantly affected the organic content of these samples. Conversely, the macroalgae present on the lower parts of the shore (Sites 3-5) were predominantly fleshy species attached to small stones and shell fragments, and the total macroalgal cover was significantly lower (between approximately 10 and 30%). This resulted in fewer fragments being incorporated into sediment samples.

The particle size distributions of sediment samples also altered down the transect. Samples taken from the top and bottom of the shore (i.e. Sites 1 and 5 respectively) had sedimentary characteristics that were markedly different to those at the middle three sampling sites. These differences are discussed below with reference to the physical processes that influence sedimentary regimes.

Firstly, the sediment at Site 1 was poorly sorted and contained much greater amounts of coarse material than samples from the mid-shore region. It has already been stated that the size distribution of sediment particles in an area reflects both the hydrographic features and the geological history of that area. In purely physical terms, there are three basic types of beaches (Short and Wright, 1983). Dissipative beaches occur where there is fine sand and relatively high levels of wave action. They have shallow slopes and wide surf zones over which most of the wave energy is dissipated. Reflective beaches develop where there is coarse sand and relatively low levels of wave action. They have steep slopes that reflect wave energy and have harsh swash conditions. Between these extremes, intermediate beaches have fine to medium sands and moderate to high levels of wave action. Their intermediate slopes are characterised by bars, channels and rip currents.

The situation is more complicated in macrotidal environments, where a dissipative lower shore may be combined with a reflective upper shore (Wright *et al.*, 1982). Although tides in the Solent are not particularly large compared to other areas in the Channel (e.g. >12m in the Baie du Mont Saint Michel) and around the British Isles (eg. 12m in the Bristol Channel), the complex nature of the region's tides combined with the local geology of the land-sea interface have resulted in a distinct shore profile occurring at Solent Breezes and along the adjacent coastline between Hill Head and the mouth of the river Hamble (Holme and Bishop, 1980). The shore at Solent Breezes included a relatively narrow steep-sloping upper shore region of large boulders interspersed with pebbles and some sand. Below this region, the upper shore gave way to the wide expanse of shallow sloping muddy-sand. The gradient of the upper shore region changed quite abruptly as it merged with the main sediment flat region. However, there was a more gradual transformation in sedimentary characteristics across the interface between the two regions. Consequently, the sedimentary regime at Transect Site 1 was affected by its proximity to the steep upper shore region.

Transect Site 5 was positioned close to a small shingle bar that ran across the bottom of the shore at Solent Breezes. Coastal bars are formed as a result of the prevailing currents and wave action, and are consequently associated with increased water movement. Although Site 5 was positioned some 10m from the cross-sectional peak of the bar, the sediment characteristics at the site were markedly different from the mid- to lower-shore region (i.e. Sites 2, 3 and 4). The sediment was poorly sorted and contained greater amounts of coarse material than samples from higher up the shore. The increased amount of coarse material at Site 5 was clearly a reflection of its proximity to the shingle bar. In addition, the percentage silt/clay fraction was lower than at all other sites - indicating an increased level of water movement. (Higher water velocities result in an increase in the flux of suspended particles, a removal of fine material from the sediment and the prevention of fine particle deposition.)

The sediment of the wide, shallow sloping region encompassing Sites 2, 3 and 4 was physically relatively homogeneous. The main mid-shore sampling site chosen for the remainder of the current study was therefore unaffected by the variations in sedimentary characteristics that occurred at the top and bottom of the shore. It is suggested that the mid-shore sampling site was fairly representative of the large area of intertidal flat at Solent Breezes. In addition, the adjacent coastline extending north to the mouth of the Hamble and south to Hill Head was dominated by similar large areas of relatively homogeneous sediment flats (*pers. obs.*). Therefore, the mid-shore sampling site at Solent Breezes may also have been reasonably representative of much of this 3-4 mile stretch of the Solent's eastern shore.

(ii) The mid-shore sampling site

The surface sediment of the mid-shore sampling site was **generally** well sorted, with a silt/clay fraction of less than 5% and a total organic content of less than 1.5%. However, significant fluctuations occurred in the sedimentary regime during the study. The total organic content of the surface sediment remained relatively constant for the majority of the study, but in February and March 1991 large inputs of organic material coincided with considerable disruptions to the physical characteristics of the sediment.

Organic matter in near shore sediments is derived from both terrestrial and aquatic sources and organic content is often inversely proportional to sediment particle size. The total organic content was initially measured to allow an estimate to be made of the potential food resources that were available to deposit feeding animals. However, in general only a small fraction of sedimentary organic material (5-30%) is in a bioavailable form (Mayer, 1989). Sedimentary organic matter is made up of numerous types of non-living and living constituents. Many infaunal species are able to utilise non-living food resources (Taghon and Jumars, 1984; Lopez *et al.*, 1989; Tenore, 1983), but the physical state and the chemical nature of these resources in sediments are complex and poorly understood (Mayer, 1989).

Sedimentary organic matter concentrations are often highly dependent on grain size, i.e. finer sediments are generally associated with higher organic matter concentrations (Bordovskiy, 1965, Mayer *et al.*, 1981). This relationship has been attributed to the fact that finer sediments have a higher surface area to volume ratio, which results in a greater overall volume onto which organic matter can be adsorbed (Dale, 1974). In addition, larger particles of organic detritus (with low specific gravity) can act in a similar way to fine mineral grains in particular hydrodynamic conditions. This can result in an accumulation of organic detritus within fine sediments. The majority of non-living particulate organic matter is polymeric. The availability of this fraction to deposit feeders depends on its source and the level of polymerisation. Biopolymers are usually relatively labile. More refractory organic matter includes lignaceous and cellulotic material, along with geopolymers which can be formed during humification reactions. Organic molecules may also be adsorbed into the lattices of clay, making them unavailable to deposit feeding animals (e.g. Marshman and Marshall, 1981).

A strong inverse correlation has also been demonstrated between grain size and bacterial numbers, but this relationship is not necessarily a simple result of the increased specific surface area of finer sediments (e.g. Yamamoto and Lopez, 1985, Meadows and Anderson, 1966). Bacteria and their extracellular mucous coatings may form an important component of the living fraction of sedimentary organic matter (Mayer *et al.*, 1985). Other components include microalgae, protozoa, fungi and the meiofauna. The deposition of biogenic material from overlying waters may further increase the amount of potential food that is available to deposit feeders.

Some components of the bioavailable material present in sediments are potentially quantifiable, and it is acknowledged that the total organic content of a sediment does not necessarily reflect the amount of potential food available to the deposit feeders living within that sediment. The fundamental difference between the total organic fraction and the bioavailable protein fraction of a sediment was illustrated by the depth profiles shown in Figure 2.13. The pool of organic matter that existed below a depth of 8cm contained minimal amounts of bioavailable protein, and therefore contained considerable amounts of refractory material. It is possible that this refractory organic material was associated with the subsurface clay layer.

The marked increase in sedimentary organic material that occurred in February and March 1991 was **not** a result of significant inputs of bioavailable protein. Mattin (1992) found no significant change in the concentration of bioavailable protein in the surface sediment at Solent Breezes during this period. The increase in organic content was accompanied by an increase in the silt/clay fraction, particularly in February 1991. The actual source of the organic material and the fine sediment is unknown, but it is conceivable that a degree of physical disturbance may have caused subsurface material to be incorporated into usually well sorted surface sediment.

(iii) *Lanice conchilega* and the sedimentary regime

The physical characteristics of sediment taken from areas of different tube densities was relatively constant i.e. no significant changes occurred in the particle size distributions with increasing tube density. Similarly, sediment samples taken from areas containing relatively high densities of *Lanice conchilega* tubes did not contain significantly higher concentrations of total organic matter than areas with no tubes. However, data produced by Mattin (1992) indicated that bioavailable protein concentrations were significantly higher in areas containing dense aggregations of *Lanice conchilega* tubes. The mucus produced during tube building and feeding is one likely cause of this increased protein content in high density areas.

A significant increase was observed in the depth of sediment above the underlying clay layer with increasing tube density. This indicates that a degree of sediment accumulation occurred within dense patches of tubes. The physical presence of animal tubes significantly influences local hydrodynamics (e.g. Carey, 1983) and aggregations of tubes may be either stabilising or destabilising depending on the size and density of the tubes in question (Eckman, *et al.* 1981). The potential effects of *Lanice conchilega* tubes on sediment stability at Solent Breezes are discussed in more detail in Chapter 6. Hydrodynamic stabilisation is only likely to occur in exceptional circumstances and correlations between animal tubes and stabilised sediments are more often a result of sediment binding by mucus (Eckman *et al.*, 1981). Indeed, mucus binding is one of the most important biological mechanisms influencing sediment stability (Dyer, 1986). Stabilisation and net accumulation of sediment caused by mucus binding are therefore suggested as the controlling mechanisms that resulted in the significant increase observed in the depth of sediment above the underlying clay layer at higher tube densities.

CHAPTER 3

The Macrofaunal Sampling Transect

3.1 Introduction

A number of environmental gradients can occur on any shore and the faunal assemblages occurring at different locations on the shore often reflect these gradients. To enable the mid-shore area at Solent Breezes that was used for the majority of the macrofaunal sampling to be put into context on the shore, samples were taken from five sites along a transect between the mean high water mark and the mean low water mark. The results of this macrofaunal sampling transect were examined first and these are presented and discussed in this chapter.

3.2 Field Work and Laboratory Methods

To identify and quantify any changes in the fauna that occurred down the shore at Solent Breezes, samples were taken at five evenly spaced sites between the mean low water mark and the mean high water mark (sampling date: 5/6/92). The sampling sites were approximately 80m apart and the central site (3) coincided with the regular mid-shore monthly sampling area. Samples were taken using a corer with an internal diameter of 6cm (surface area approximately 0.003m^2). At each site, cores were taken at ten randomly chosen positions, and each core was taken to a depth of approximately 25cm. Core samples was transferred to individual labelled containers which were transported to the laboratory within two hours of collection. In the laboratory, a solution of 4% formaldehyde containing Phloxine B (C.I. No. 45410) at a concentration of 0.1g/l was added to fix and stain each sample (Phloxine B stains organic material red, thus facilitating sorting).

After at least 48 hours, the samples were carefully sieved through a 0.5mm mesh to eliminate mud and fine particles, and to rinse out all traces of formalin. The macrofauna was sorted from the remaining sediment of each sample and was retained in 70% ethanol. Animals were identified and enumerated using a binocular low power microscope and a high power compound microscope. The identified fauna from each sample was then stored in 70% ethanol. The identification keys used for different taxonomic groups are detailed in Table 3.1. In addition, several unpublished loose-leaf keys previously produced during national workshops and colloquia were used for the identification of various polychaete families.

TAXON	REFERENCES
Annelida: Polychaeta	Blake, 1991 Chambers and Garwood, 1992 Chambers and Muir, 1997 Eibye-Jacobsen, 1991 Fauchald, 1977 Fauvel, 1923, 1927 George and Hartmann-Schröder, 1985 Hartley, 1981 Hartmann-Schröder, 1971 Holthe, 1986 O'Connor, 1987 Pleijel, 1993 Rainer, 1990 Woodham and Chambers, 1994
Pycnogonida:	King, 1986
Crustacea: Amphipoda	Lincoln, 1979 Myers and Costello, 1984, 1986 Myers and Mcgrath, 1982, 1984
Crustacea: Isopoda	Naylor, 1972
Crustacea: Tanaidacea	Holdich and Jones, 1983a Holdich and Bird, 1986 Jones and Holdich, 1983
Crustacea: Cumacea	Jones, 1976
Crustacea: Decapoda	Ingle, 1983 Smaldon, Holthuis and Fransen, 1993
Mollusca:	Graham, 1988 Tebble, 1976
General texts:	Hayward and Ryland, 1990a, 1990b

Table 3.1. The taxonomic literature used to identify the macrobenthic fauna.

3.3 Data Analysis

The following sections describe the univariate and multivariate methods used to analyse both the transect faunal data (this chapter) and the monthly time series faunal data (Chapter 4).

3.3.1 Univariate analyses

Studies of benthic communities often use a simple index of species diversity to give an indication of how the total number of individuals is divided between the different species. The concept of community diversity incorporates two distinct components: species richness and equitability. The total number of species (s) can be used as a measure of species richness, but this is sample size dependent. **Margalef's index (d)** incorporates the total number of individuals (N), and thus eliminates sample size dependency (Margalef, 1951):

$$d = \frac{(s-1)}{\log N}$$

The equitability or evenness component of diversity indicates how the individuals of a community are distributed among the species. The most commonly used index of diversity is the **Shannon-Wiener diversity index (H')** (Shannon and Weaver, 1963). The equitability component can be isolated from the index by dividing the observed diversity (H') by the maximum possible value of diversity (H'_{max}) (Pielou, 1966). Shannon-Wiener's diversity index and **Pielou's evenness index (J)** were calculated for all individual core data sets and all total data sets, using the following equations:

$$H' = -\sum_{i=1}^{s} p_i \log_2 p_i \qquad\qquad J = H' / H'_{\max}$$

Where p_i is n_i/N (n_i is the number of individuals in the i^{th} species and N is the total number of individuals). H'_{max} is the maximum value of H' i.e. if each species has one individual ($= \log_2 s$).

Values of H' and J were calculated using a specifically designed Quattro Pro spreadsheet. It was later possible to check all calculated values using the PRIMER (Plymouth Routines in Multivariate Ecological Research) analysis package. PRIMER was also used to calculate values of **Caswell's *V*-statistic** for individual core data and summed replicates. Caswell's neutral model constructs an "ecologically neutral" community with the same number of species and individuals as the observed community (Caswell, 1976). Observed diversity (H') can then be compared against the predicted neutral model diversity ($E(H')$) and the deviation of the observed from the predicted is given as "the deviation statistic - V".

$$V = \frac{[H' - E(H')]}{S.D.(H')}$$

A value of zero indicates neutrality, i.e. the observed diversity is the same as the predicted diversity. A negative value of V indicates that the observed diversity is lower than predicted and a positive value indicates a higher diversity. In addition, V is essentially a measure of equitability, with more negative values indicating increasing dominance. Values greater than +2 or less than -2 indicate significant departures from neutrality.

3.3.2 Multivariate analyses

A number of multivariate methods were used to analyse the macrofauna. Cluster analysis, Non-metric Multi-Dimensional Scaling (MDS), the BIO-ENV procedure and Principal Component Analysis (PCA) were all performed using the PRIMER analysis package. The use of data transformations (e.g. square root or log) was avoided for all of the multivariate analyses presented in this chapter. Such transformations were considered to reduce the amount of information (particularly with respect to the dominance of important species) and inherently result in a departure from "reality".

Cluster analysis

Cluster analysis was conducted using a method of hierarchical agglomerative clustering, which aims to group together samples that are similar to each other. Hierarchical agglomerative methods are the most commonly used clustering techniques in ecological studies. They first identify samples with the highest mutual similarities and group them together, then connect these groups at gradually decreasing levels of similarity. The method used for the present study constructed dendrograms from Bray-Curtis similarity matrices using group average linking. One axis of a dendrogram represents the full set of samples, while the other defines the level of similarity. Cluster analysis attempts to group samples into distinct clusters, but does not display their inter-relationships on a continuous scale. Consequently, clustering must be used with care when there is a gradation in community structure, and it is often preferable to use cluster analysis in conjunction with an ordination technique.

Non-metric multi-dimensional scaling (MDS)

MDS is a popular ordination method used for the analysis of macrofaunal data. It utilises the matrix of similarity coefficients produced during cluster analysis to construct a 2-dimensional "map" of the samples (an ordination). Non-metric MDS is conceptually simple and makes few model assumptions about the form of the data or the inter-relationships between samples (Clarke and Warwick, 1994). Distances between sample points on an MDS ordination have the same rank order as the corresponding dissimilarities between samples. The computational procedure constructs a plot by refining the positions of sample points until they represent the similarities between samples as closely as possible.

The "stress" level calculated during the MDS procedure in PRIMER can be used to estimate how representative the resulting ordination is as a summary of the relationships between samples. If the stress is low (i.e. < 0.20), the ordination provides a useful 2-dimensional representation (Clarke and Warwick, 1994). The complementary use of MDS and cluster analysis can allow the adequacy of both methods to be checked.

BIO-ENV

The BIO-ENV procedure of the PRIMER analysis package attempts to select environmental variables that "best explain" faunal patterns. This is achieved by comparing a faunal similarity matrix (e.g. Bray-Curtis) with a similarity matrix produced from a set of environmental variables. All combinations of environmental variables are considered at increasing levels of complexity. The output from the programme produces a rank correlation coefficient for every possible combination of environmental variables. Therefore, the single variable that "best explains" faunal patterns can be determined, followed by the best 2-variable combination, followed by the best 3-variable combination, etc.

The use of a rank correlation coefficient to compare the biotic and abiotic similarity matrices is a logical step considering that accurate MDS ordinations are essentially functions of similarity ranks (Clarke and Ainsworth, 1993; Clarke and Warwick, 1994). The coefficient used in this analysis is the weighted Spearman rank correlation (ρ_w). Values of ρ_w around zero imply the absence of any match between the two similarity matrices, whereas values approaching 1.0 imply strong agreement between the two matrices.

The BIO-ENV approach relies on the following premise: pairs of samples which are similar with respect to physico-chemical variables are expected to have similar species compositions (Clarke and Ainsworth, 1993). In turn, the success of the analysis obviously requires the relevant physico-chemical variables (i.e. those that determine community structure) to be included in the analysis.

Finally, it must be noted that because of a lack of model assumptions underlying the procedure, it is difficult to support any conclusions with statistical significance tests. BIO-ENV must therefore be used simply as a guide to the relative importance of different environmental variables.

Principal Component Analysis (PCA)

Principal Component Analysis (PCA) was also conducted using the PRIMER analysis package to examine any correlations between faunal patterns and changes in environmental variables. PCA is a well established ordination method that is at least *conceptually* simple. The analysis starts with the original data matrix rather than a similarity matrix derived from the data. The data matrix is conceived as defining the positions of individual samples in multi-dimensional space. The axes of this space represent the species in the data matrix and consequently the number of dimensions is equal to the number of species.

As with all ordination techniques, a simple 2-dimensional representation produced from a PCA may not preserve distances between samples accurately. The degree to which a 2-dimensional PCA succeeds in representing the multi-dimensional picture is indicated by the percentage of the total variance accounted for by the first two principal components. Clarke and Warwick (1994) have suggested that a 2-dimensional ordination for which the first two principal components account for 70-75% of the variation gives an acceptable indication of the relationships between samples.

One important attribute of PCA is the potential interpretability of the ordination axes. Relationships between principal components and environmental variables can be examined using correlation coefficients, and the statistical significance of these relationships can be tested using Spearman rank order correlation.

PCA requires the exclusion of very rare species as these may have a distorting effect on the results. Some species are often represented by a single specimen and the exclusion of such species will not seriously affect the interpretation of results. However, deciding which species to exclude can be problematic when applying PCA to biotic data. Large data sets can be reduced to a manageable size by excluding those species that constitute less than a certain percentage of the total abundance. A guideline figure of 3% has been suggested by Clarke and Warwick (1994).

3.3.3 The Infaunal Trophic Index

The Infaunal Trophic Index (ITIUK) is a relatively recent development that can be used as part of the analysis of data from marine benthic surveys. It was originally developed as an aid to identifying changes in environmental conditions caused by organic pollution (Word 1978; 1990). The index is based on the allocation of species to one of four trophic groups and it has been used cautiously in this study to assess differences in the trophic groups present in macrofaunal samples.

A value of the Infaunal Trophic Index was calculated for each monthly data set using the following equation:

$$ITI = 100 - [33.33((0n_1 + 1n_2 + 2n_3 + 3n_4)/(n_1 + n_2 + n_3 + n_4))]$$

where n_{1-4} is the number of individuals in trophic groups 1-4 respectively.
For each data set, species were ordered in terms of their abundance and cumulative abundances were calculated. Only those species contributing the top 80% of the total abundance were used in the calculation. The trophic groups into which the species were categorised are summarised below (for further details see Codling and Ashley (1992)):

Group 1: Water Column Detrital Feeders.

Group 2: Interface Detrital Feeders and Burrowing Detrital Feeders.

Group 3: Deposit Feeders.

Group 4: Specialised Environment Feeders.

Most species could be categorised using information given in Codling and Ashley (1992). Other useful sources included Fauchald and Jumars (1979), Fish and Fish (1989) and Hayward and Ryland (1990a,b). ITI values range between 0 and 100. Low ITI values indicate degraded conditions.

ITI values close to 100 indicate the dominance of species feeding on detritus in the water column and values between 50 and 70 indicate the dominance of species feeding on surface detritus. Values between 30 and 50 indicate the dominance of surface deposit feeders, and values less than 30 indicate the dominance of sub-surface deposit feeders adapted for existence in highly anaerobic conditions. The index has also been used to classify faunal assemblages as 'normal' (ITI values 100 - 60), 'changed' (60 - 30) or 'degraded' (30 - 0).

3.4 Results

Complete lists of the fauna sampled from the five transect sites in June 1992 are presented in Appendix 2. A total of 32 species were present in the transect samples, and the greatest number of species (s) at any one site was 23 (at Site 3). The highest abundance (mean $N = 25.5$ per core) was found at the bottom of the shore at Site 5, although the total numbers of individuals at Sites 3, 4 and 5 were all similar (between 209 and 255). Total diversity (H') (i.e. the diversity of the pooled data set for each of the sites) ranged between 2.54 at Site 1 and 3.57 at Site 4. In contrast, the total evenness (J) was highest at Site 4, but was lowest at Site 5.

3.4.1 Univariate analyses

Figure 3.1 shows the mean values of the number of individuals (N), species richness (d), diversity (H') and evenness (J) at each of the five transect sites. Differences in the mean values were analysed using a standard one way analysis of variance (ANOVA) followed by the Student-Newman-Keuls Test for pairwise multiple comparisons. The mean number of individuals at the highest site on the shore (Site 1) was significantly lower than the mean values at Sites 3, 4 and 5 ($p \leq 0.002$). The mean value of N at Site 2 was also significantly lower than the mean value of N at both Site 3 and Site 4 ($p \leq 0.027$). Similarly, species richness (d) was significantly lower at Site 1 than at Sites 3, 4 and 5 ($p < 0.001$); and was significantly lower at Site 2 than at Sites 3,4 and 5 ($p < 0.05$).

Mean diversity also changed markedly down the shore. Samples taken from Site 1 at the top of the shore contained fauna with a mean diversity that was significantly lower than the mean diversity at the mid- and lower-shore sites (i.e. Sites 3, 4 and 5) ($p \leq 0.004$). In addition, the mean diversity at Site 5 was lower than at Sites 3 and 4 ($p \leq 0.032$).Changes in diversity down the shore were a reflection of both species richness and evenness (J). The latter was fairly consistent between Sites 1 and 4 (inclusive), but was lower at Site 5, which consequently affected the diversity at this site. Numerical dominance of one or a few species at Site 5 resulted in the mean evenness being significantly lower than at Sites 2, 3 and 4 ($p \leq 0.028$).

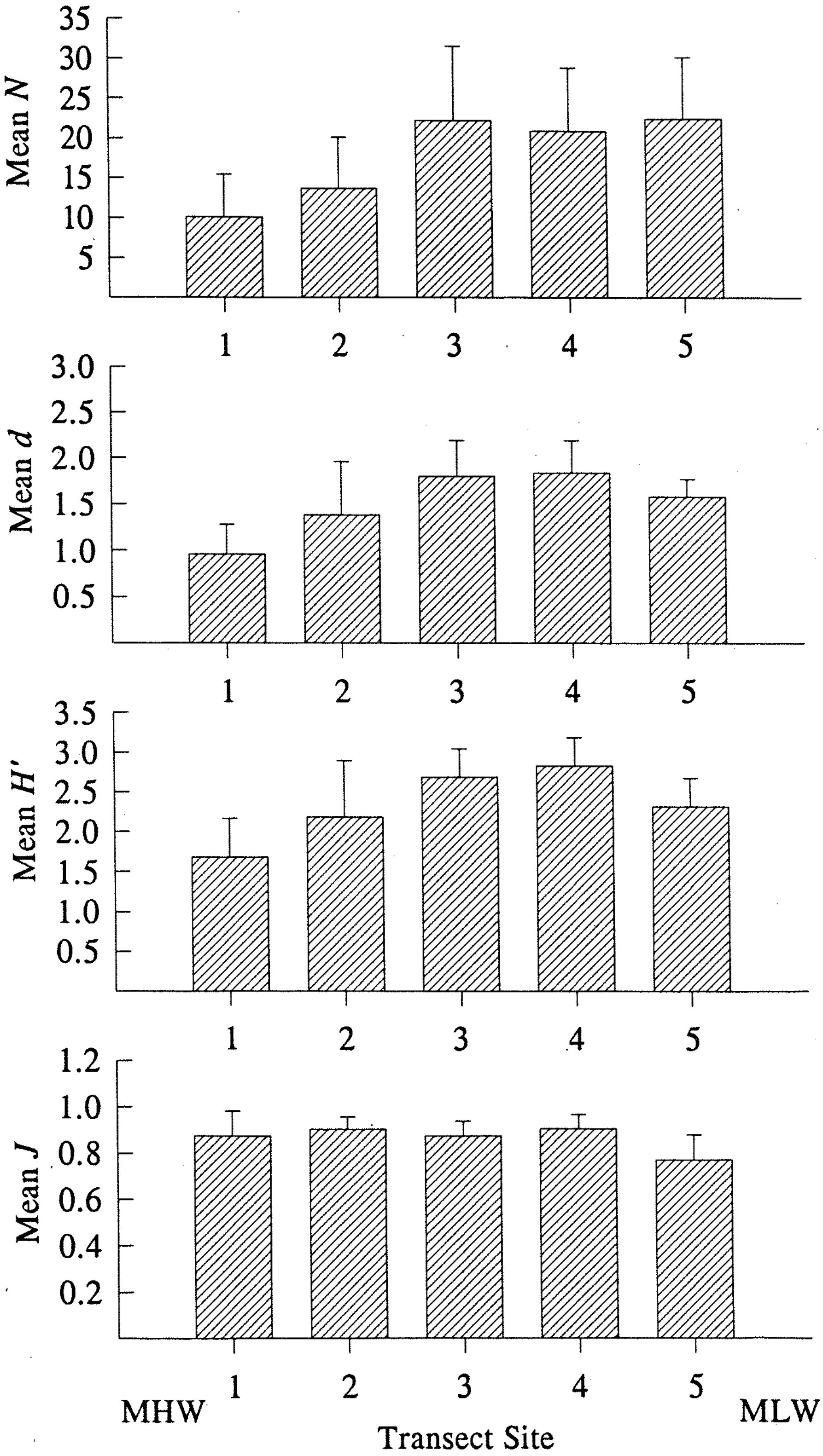


Figure 3.1 Transect Macrofauna. The number of individuals (*N*), the species richness (*d*), the diversity (*H'*) and the evenness (*J*) at the five transect sites. Each value shown is the mean of 10 sample values and standard deviations are shown as error bars.

Table 3.2 details the results of the *V*-statistic calculations conducted for the five transect sites. A value of *V* was calculated for individual cores and mean values were evaluated for each site. The PRIMER programme aborted during the calculation of *V* for four of the cores (2 from Site 1, 1 from Site 2 and 1 from Site 3). The mean values of *V* at Sites 1, 2 and 3 therefore had to be calculated without the inclusion of data from these cores. The number of cores (n) used in the calculation for each site is therefore also included in Table 3.2 (column 4). A value of *V* was also calculated for the total fauna (i.e. 10 samples combined) at each site (column 5).

	V-Statistic			
	Mean *V*	S.D.	n	Total Data Set *V*
^{MHW}Site 1	0.24	0.93	8	-0.47
Site 2	0.08	0.88	9	-0.32
Site 3	-0.36	1.26	9	0.02
Site 4	0.51	0.82	10	0.47
$_{MLW}$Site 5	-1.25	1.41	10	-1.55

Table 3.2. Values of the *V*-statistic calculated for Transect Sites 1 to 5.

None of the *V* values shown in Table 3.2 are either above +2 or below -2. Therefore these values indicate no significant departures from neutrality for all five transect sites. However, both the mean *V* value and the total data set *V* value calculated for Site 5 data were considerably further from zero (i.e. neutrality) than for any other site. In fact, nine of the Site 5 individual core data sets had negative *V* values, and 3 of these were below -2 (i.e. had significantly lower diversity than that predicted by the neutral model).

3.4.2 Multivariate analyses

Cluster analysis and MDS

Figures 3.2 and 3.3 present the results of the cluster analysis and the MDS analysis of the total fauna at the five transect sites. The similarity matrix used for the two analyses compared the total fauna data sets for the five sites (i.e. a large single "sample" from each transect site was used for the comparison). However, each of the single samples was made up of ten randomly positioned core samples taken at its respective site, and was therefore considerably more representative than a single large core sample would have been. The stress value calculated during the MDS analysis was less than 0.05, indicating that the ordination was an excellent representation with no prospect of mis-interpretation (Clarke and Warwick, 1994). The dendrogram produced by the cluster analysis, and the MDS ordination plot highlight similar patterns of groupings among the five sites:

Group 1: Sites 1 & 2

The fauna at each of these sites was dominated by *Spio martinensis*, *Pygospio elegans* and *Scoloplos armiger*. In addition, similar numbers of *Bathyporeia sarsi*, *Bodotria pulchella* and *Crangon crangon* occurred at each site. However, Site 2 contained notably more *Exogone hebes* and *Tanaissus lilljeborgi* than Site 1.

Group 2: Sites 3 & 4

The fauna at Sites 3 and 4 were the most similar - indicated by their proximity on the MDS plot and their level of clustering on the dendrogram. Most of the dominant species at the two sites were numerically similar (e.g. *Streptosyllis websteri*, *Exogone hebes*, *Aricidea minuta* and *Euclymene oerstedii*). In addition, several of the less dominant species were present at the two sites in similar numbers.

Group 3: Site 5

The fauna at Site 5 (i.e. at the bottom of the shore) was dominated by *Spio martinensis*. Although this characteristic would initially appear to be more analogous with Group 1 than Group 2, the significant presence of a number of other species (e.g. *Streptosyllis websteri*, *Exogone hebes* and *Aricidea minuta*) caused Site 5 to be clustered slightly closer to Group 2 (i.e. Sites 3 and 4).

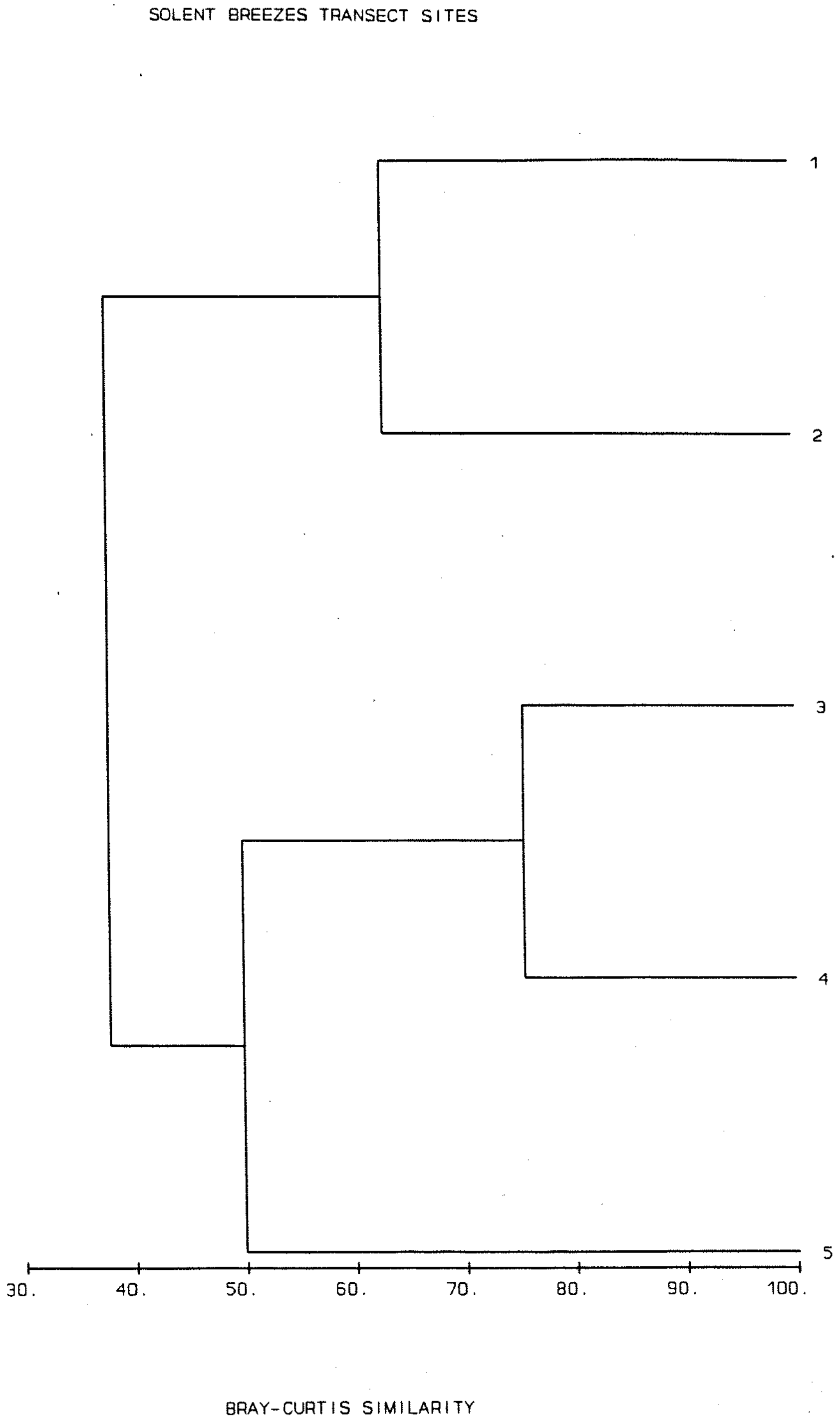
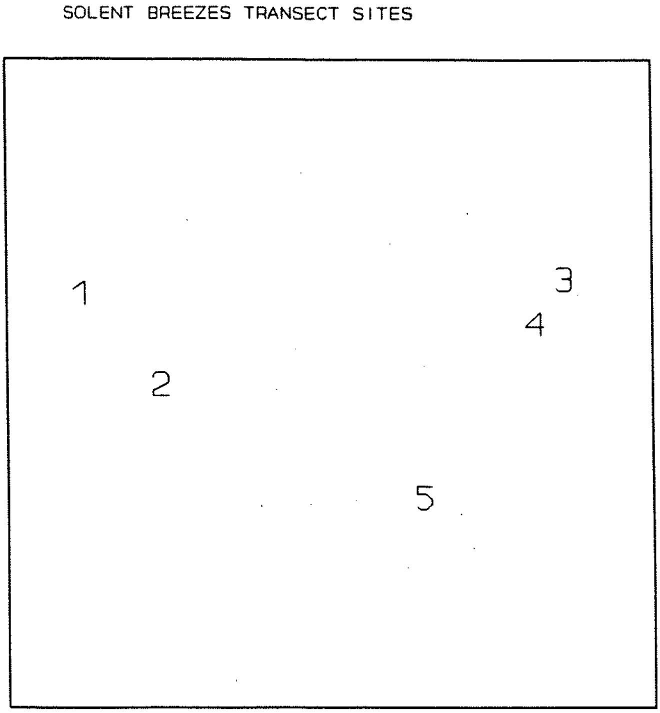


Figure 3.2 Transect Macrofauna. Dendrogram constructed for hierarchical clustering of the total fauna at the five transect sites using group-average linking of Bray-Curtis similarities.



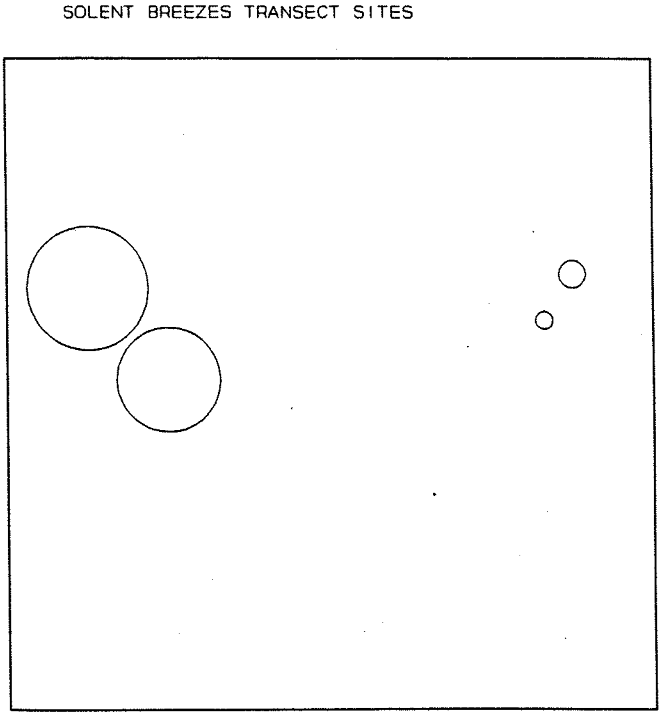


Figure 3.3 Transect Macrofauna. MDS plot of Bray-Curtis similarities for the total fauna at Transect Sites 1-5 (untransformed data). The upper plot shows the positions of the five sites, the lower plot is the same MDS with superimposed symbols representing total organic content at the five sites.

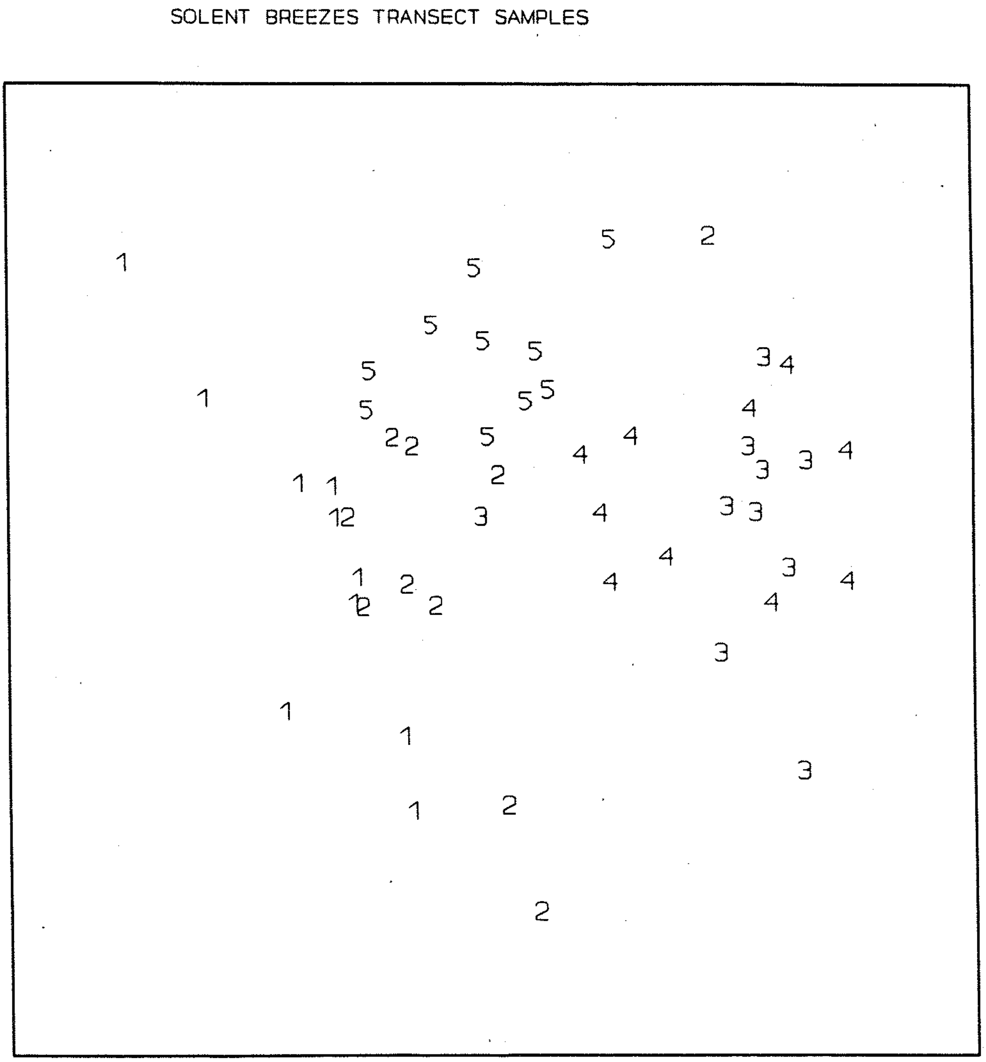


Figure 3.4 Transect Macrofauna. MDS plot of Bray-Curtis similarities for fauna in individual samples taken at Transect Sites 1-5 (untransformed data). The ten samples taken from each site are marked by their respective site number.

An MDS plot was also constructed for the 50 individual core data sets (Figure 3.4). The stress value calculated during the MDS analysis was 0.19, indicating that the ordination provided a "potentially useful" 2-dimensional representation (Clarke and Warwick, 1994). A large amount of variation existed between samples taken from each of the five sites. However, all Site 5 samples are grouped in moderately close proximity. Samples from Sites 3 and 4 are indistinguishable, reflecting the total fauna plot in which Sites 3 and 4 were very similar. Low numbers of individuals in the samples from both Site 1 and Site 2 resulted in the high level of scatter in these samples (the samples often only contained one or two individuals).

BIO-ENV

The BIO-ENV procedure of the PRIMER analysis package was used to examine which of the available environmental variables "best explained" changes in the benthic fauna along the sampling transect. A total of seven sedimentary parameters were available for input into the procedure as environmental variables, i.e. the total organic content, the Quartile Deviation, the Phi Quartile Skewness, the Inclusive Graphic Standard Deviation, the Inclusive Graphic Skewness, the Graphic Kurtosis and the percentage silt/clay fraction. However, the Inclusive Graphic Standard Deviation is essentially a more accurate method of measuring the level of sorting than the Quartile Deviation, and the Inclusive Graphic Skewness is a more accurate method of measuring the level of skewness than the Phi Quartile Skewness (see Chapter 2). Therefore the Quartile Deviation and the Phi Quartile Skewness were omitted from the analysis.

Table 3.3 details the combinations of the five sediment parameters giving the best matches between the transect faunal and abiotic matrices (the best single variable being organic content, the best 2-variable combination being organic content with silt/clay fraction etc.). The single abiotic variable that best matched changes in the fauna that occurred along the sampling transect was therefore the total organic content. This single variable was also the best match of all possible combinations of variables i.e. the addition of other variables only served to lower the correlation with the faunal similarity matrix.

n	ρ_w	Organic Content	Incl. Gr. S.D.	Incl. Gr. Skewness	Graphic Kurtosis	Silt/Clay Fraction
1	**0.81**	*				
2	**0.7**	*				*
3	**0.44**	*	*			*
4	**0.38**	*	*		*	*
5	**0.24**	*	*	*	*	*

Table 3.3. Results of the BIO-ENV procedure for the sampling transect. Combinations of the five sediment parameters giving the best matches between the faunal and abiotic matrices. Correlations were measured using weighted Spearman rank correlation (ρ_w).

The total organic content of sediment from each of the five transect sites was superimposed onto the previously constructed MDS plot (Figure 3.3; lower plot). The diameter of each circle is proportional to the total organic content measured at its respective site. Clearly, sediment from Group 1 sites (i.e. Sites 1 and 2) contained substantially more organic matter, and Group 3 (Site 5) contained relatively small amounts of organic matter.

Principal component analysis

A total of 32 species were present in the transect samples. Consequently, the species matrix constructed for Principal Component Analysis was of a manageable size and did not require reduction by the exclusion of rare species. The first two principal component axes explained 94.32% of the original variation in the data. The 2-dimensional PCA ordination (i.e. the plot of PC axis 1 against PC axis 2) therefore gave an acceptable indication of the relationships between samples. The groupings among the five samples were similar to those highlighted by the MDS plot (Figure 3.3), with Sites 1 and 2 positioned together, Sites 3 and 4 positioned together, and Site 5 in relative isolation.

The use of Spearman rank correlation revealed no significant relationships between either PC1 or PC2 and any of the environmental variables under investigation. However, using simple linear regression, a significant negative correlation was observed between PC1 and the silt/clay content ($p = 0.013$). In addition, PC2 was positively correlated with organic content ($p = 0.003$). The use of linear regression is perhaps statistically inappropriate here, as it requires one variable to be dependent on the other. However, the overall trends of: (a) a decrease in silt/clay content along PC axis 1; and (b) an increase in organic content along PC axis 2, could not be ignored.

3.4.3 The Infaunal Trophic Index

A single value of the Infaunal Trophic Index was calculated for each of the five transect sites, using the total fauna data set (Table 3.4).

TRANSECT SITE	ITI (UK) VALUE
MHW 1	81.13
2	68.45
3	59.92
4	65.69
MLW 5	86.67

Table 3.4. Values of the Infaunal Trophic Index for Transect Sites 1-5.

Although there was a degree of variation between sites, all five ITI values were greater than or approximately equal to 60, and were therefore within the range described as classifying areas of sediment as "normal" (i.e. unchanged). The ITI was originally developed as an aid to identifying changed and degraded conditions caused by organic pollution. As such the index was unlikely to indicate the presence of polluted conditions in the relatively clean littoral environment at Solent Breezes. ITI values approaching 100 indicate the dominance of species feeding on detritus present in the water column. The fauna at Sites 1 and 5 both had relatively high ITI values, primarily as a result of the dominance of *Spio martinensis* (categorised as trophic group 1) at these two sites. Conversely, ITI values calculated for the middle three sites indicate that the fauna at these sites was dominated by species feeding on surface detritus.

The potential limitations of the Infaunal Trophic Index are detailed in Chapter 4 (Section 4.4.4). However, two points require consideration here with specific reference to the transect macrofaunal data sets. Firstly, a potential problem arises when species have more than one mode of feeding. The allocation of *Spio martinensis* to trophic group 1 was based solely on information provided by Codling and Ashley (1992) but this allocation could not account for any facultative feeding behaviour potentially exhibited by this species. Although *Spio martinensis* is generally considered to be a suspension feeding species, spionids may also act as selective surface deposit feeders. It may be difficult to predict which mode of feeding is dominant in some species in a particular location, therefore potentially complicating the allocation of trophic groups.

A second problem arises when the fauna under consideration is not exclusively infaunal (see Section 4.4.4). By definition, the ITI deals with infaunal animals. The mobile scavenging isopod *Sphaeroma monodi* was categorised as trophic group 2 (interface detrital feeders) for the purposes this study. However, this species should perhaps have been excluded because it usually lives in crevices and under stones and is therefore not specifically infaunal. While it could be argued that epifaunal species are not necessarily permanent members of a faunal assemblage observed in a particular area, their occurrence in samples cannot be dismissed as incidental. For example, scavenging species are obviously more likely to occur in samples taken from areas where potential food items are more abundant. Although other environmental variables may also be important, the distributions of such species are potentially intimately linked to trophic factors. Consequently, any significant occurrence of epifaunal scavengers, carnivores or herbivores should perhaps be considered alongside the Infaunal Trophic Index.

3.4.4 Summary

The sampling transect was used to compare the main mid-shore sampling site with other areas of the shore at Solent Breezes. The faunal characteristics of the mid-shore site (i.e. Site 3) were indistinguishable from those at Site 4 lower down the shore. The lowest sampling site (i.e. Site 5) contained a similar faunal assemblage but high numbers of the dominant species *Spio martinensis* resulted in the evenness and consequently the diversity being relatively low. The sampling sites above the mid-shore area (i.e. Sites 1 and 2) contained fewer animals and fewer species. In addition, the diversity at the highest (i.e. the most exposed) site was significantly lower than at other sites further down the shore.

The environmental variable that "best explained" the changes in faunal characteristics along the transect was total organic matter (using the BIO-ENV analysis procedure). High levels of organic matter occurred in sediment samples taken from Sites 1 and 2. The exact nature of this organic matter was unknown but it has been previously suggested that the presence of relatively large amounts of macroalgae at the top of the shore influenced the organic content at these two sites (see Chapter 2). The use of PCA highlighted the importance of a second sedimentary parameter (the silt/clay content) which tended to decrease along the first principal component axis. This silt/clay content was relatively low at the top of the shore (Site 1), but was also particularly low at the bottom of the shore (Site 5).

3.5 Discussion

The transect sampling regime was primarily designed to put the main mid-shore sampling site into context on a local scale. In particular, it allowed any changes in the fauna that occurred down the shore at Solent Breezes to be quantified. It also facilitated the characterisation of both the sedimentary environment and the faunal assemblages at Solent Breezes in relation to other soft-sediment intertidal habitats.

Numerous ecological gradients may exist on a shore, and increasingly harsh physical conditions occur between the low water mark and the high water mark. Consequently, a shore represents an essentially unidirectional vertical stress gradient for the majority of marine organisms. The physical parameters that change along the vertical gradient on a shore are dominated by emersion factors such as temperature, relative humidity, and salinity. The risk of desiccation is increased by a combination of high air temperatures and low relative humidity. In addition, in cold temperate and polar regions animals may be exposed to extremely low temperatures during periods of emersion.

Macrofaunal species are arranged along the vertical gradient according to their respective capacities to cope with the physical stresses and with any accompanying biological interactions. Zonation of macrofaunal animals in intertidal soft sediments may not be immediately apparent, but it often occurs. Although this zonation is less distinct than on rocky shores, individual species may occur at specific levels on soft-sediment shores. For example, different species belonging to the amphipod genus *Bathyporeia* have been observed to predominate at different vertical positions on the shore (Watkin, 1939, 1941, 1942; Withers, 1977).

Zonation on sandy shores was first noted by Stephen (1929, 1930). Subsequently, various general schemes of zonation have been proposed for beaches and tidal flats. Dahl (1952) recognised three biological zones on beaches in cold-temperate regions, each characterised by different types of crustaceans. The top zone (the supra-littoral fringe) was characterised by talitrid amphipods (e.g. *Talitrus saltator*), the mid-littoral was characterised by cirolanid isopods (e.g. *Eurydice pulchra*) and the low shore region was characterised by haustoriid and oedicerotid amphipods. Salvat (1964, 1967) proposed an alternative zonation scheme based on the physical properties of beaches. The four zones of Salvat's scheme are defined on the basis of the hydrodynamics of the interstitial water at different levels on the shore. At the top of the shore, the "zone of drying" is characterised by dry sediment that is dampened intermittently by spray and particularly large waves. Below this is the "zone of retention" which is covered by water on every tide, but as the tide falls the sediment is left damp (rather than wet) through the retention of capillary water. The third zone recognised by Salvat is the "zone of resurgence". As the tide falls, gravitational water lost from the zone of retention above flows through the sediment in this zone and streams out across the sediment surface. Finally, the "zone of saturation" at the bottom of the shore is permanently saturated with water and consequently experiences a reduced level of groundwater circulation.

Although Salvat's scheme is based on physical parameters, some authors have suggested that distinct faunal assemblages may occur within the different zones (e.g. Bally, 1983; McLachlan, 1990; Withers, 1977). Furthermore, the two schemes outlined above are not entirely dissimilar as Dahl's supra-littoral fringe equates to Salvat's zone of drying, and Dahl's low shore region corresponds to Salvat's zone of saturation. Consequently, the middle two zones of Salvat's scheme are included within Dahl's mid-littoral zone.

The array of analyses conducted on the Solent Breezes transect data set revealed the presence of distinct faunal changes down the shore. The extent to which these changes were consistent with the zonation schemes outlined above is discussed in the following paragraphs.

Firstly, it must be noted that the sampling transect was restricted to the area of the shore below the mean high water mark. Consequently, the fauna within the area corresponding to both Dahl's supra-littoral fringe and Salvat's zone of drying was not formally investigated. However, the physical presence of a zone of drying was noted at Solent Breezes. Numerous large boulders were present at the top of the shore, interspersed with dry sand and pebbles. Identification of the fauna in this zone was not undertaken, but a gammaridean amphipod was often observed close to the strandline on the shore - which was presumably the common sand hopper (i.e. *Talitrus saltator*) or a related talitrid species. The distinct nature of this top zone makes it the easiest to detect on most beaches. Furthermore, McLachlan (1990) has suggested that the zone is simply characterised by air-breathing species. In fact, by definition, the zone is not truly intertidal, but represents the interface between terrestrial and intertidal conditions.

Chapter 2 has highlighted the complicating factors that arise in macrotidal areas with complex tidal features. The hydrodynamics of the region and the local geology has resulted in the shore profile at Solent Breezes incorporating two distinct physical zones. Although the uppermost sampling site (i.e. Site 1) was positioned within the lower muddy-sand region, its sedimentary regime was affected by the adjacent steep-sloping upper region of coarse material. The "universal" zonation schemes of Dahl and Salvat rely on a certain level of homogeneity in the sedimentary regime down the shore.

Site 1 might have equated to Salvat's zone of retention. It was covered by every tide and water of retention was conserved during periods of emersion. However, although no evidence of water movement across the surface was observed (as in Salvat's zone of resurgence), the sediment retained considerable amounts of water at low tide and could not realistically be defined as "damp" rather than "wet". The retention of water in the interstices between sediment particles is higher in fine deposits where the slope of the shore is shallow, and as a result the sediment may remain permanently wet. Under such conditions the zone of retention is more difficult to define.

True retention zone species are intertidal forms that are capable of surviving in "damp" conditions (McLachlan, 1990). However, the sediment moisture levels at Site 1 were not markedly different to those at lower sites, and species that can occur both intertidally and subtidally were present at the top of the shore (e.g. *Pygospio elegans* and *Spio martinensis*). Nevertheless, Site 1 was characterised by the absence of many species that were found further down the shore. The polychaete species *Streptosyllis websteri*, *Exogone hebes*, *Nephtys hombergii*, *Aricidea minuta*, *Euclymene oerstedii* and *Lanice conchilega* all reached their distributional limits below Site 1 and were consequently absent from the top shore samples. In addition, the isopod *Sphaeroma monodi* was found exclusively at Site 1 and was the fourth most dominant species at that site. Dahl's mid-littoral zone was characterised by cirolanid isopods on relatively exposed beaches, although other authors have been unable to validate his system on more sheltered shores. For example, Brown (1973) found that a sphaeromatid isopod replaced a cirolanid species on sheltered, fine-grained shores of the Cape Peninsula in South Africa.

While the presence of *Sphaeroma monodi* cannot be used to directly equate Site 1 with Dahl's mid-littoral, the occurrence of this species exclusively at Site 1 must be noted. In addition, Salvat's zones of retention and resurgence are both within Dahl's mid-littoral zone, and therefore a distinction between these two zones could not realistically be made at Solent Breezes.

Site 2 was more similar to Site 1 than any other site. However, many of the species absent from Site 1 were present (albeit in relatively low numbers) at Site 2 (e.g. *Streptosyllis websteri*, *Exogone hebes*, *Aricidea minuta*, *Euclymene oerstedii*, *Lanice conchilega*). Withers (1977) noted that the majority of polychaete species present on a number of beaches in South Wales were restricted to the zones of resurgence and saturation. In addition, he observed that only one species (*Scolelepis squamata*) was confined to the zone of resurgence, and most species reached their maximum abundance below MLWN in the zone of saturation. Similarly, the majority of polychaete species recorded by Raffaelli *et al.* (1991) on a beach in Aberdeenshire reached their maximum abundances in the zone of saturation, and only one polychaete species extended up the shore far enough to reach the zone of retention (*Nereis diversicolor*). Transect Site 2 therefore exhibited characteristics that could, to a limited extent, equate it with the zone of resurgence. However, this inference is based on the relatively low abundance of various species, rather than the distinct presence of any particular species.

Sites 3 and 4 were essentially indistinguishable with respect to their faunal composition. This mid- to low-shore region at Solent Breezes was inhabited by relatively large numbers of various species that can be found both intertidally and subtidally (e.g. *Streptosyllis websteri*, *Exogone hebes*, *Aricidea minuta* and *Euclymene oerstedii*). The area could not be directly related to Dahl's lower shore zone as it contained no characteristic haustoriid or oedicerotid amphipods. *Bathyporeia sarsi* (formally a haustoriid, and included in Dahl's original system) did not have a restricted distribution and occurred at all levels on the shore at

Solent Breezes. Withers (1977) previously recorded *Bathyporeia sarsi* from both the zone of retention and the zone of resurgence, and this species can also occur subtidally (Lincoln, 1979). Again, it seems Dahl's scheme using crustaceans to define major zones on beaches has limited use on more sheltered, fine-grained shores.

Conversely, the physical attributes of the sediment at Sites 3 and 4 suggest that this area of the shore equated to some extent to Salvat's zone of resurgence. The junction between the zone of resurgence and the zone of saturation below it can be difficult to observe precisely (Withers, 1977). However, the occurrence of anoxic conditions near the sediment surface indicates that the zone of saturation has been reached as the re-circulation of interstitial water in this zone is negligible. The mid- to lower-shore region at Solent Breezes (i.e. Sites 3 and 4) contained well sorted sediment with a silt/clay fraction of less than 5% (see Chapter 2), and anoxic conditions were never observed near the sediment surface.

The lowest sampling site (Site 5) contained a similar faunal assemblage to Sites 3 and 4, but with significantly more *Spio martinensis* individuals. Again, there was no evidence to suggest that anoxic conditions were prevalent near the sediment surface at Site 5, indicating that this area of the shore was comparable to Salvat's zone of resurgence.

However, the presence of a few particular species among the fauna at the bottom end of the shore (i.e. Sites 4 and 5) indicated that conditions were at least approaching those of Salvat's zone of saturation. McLachlan (1990) observed that saturation zone species are essentially subtidal species at the upper limits of their distribution. The four amphipod species *Pontocrates arenarius*, *Leucothoe incisa*, *Ampelisca brevicornis* and *Ericthonius* sp. all have predominantly subtidal distributions. Three of these species were present at Sites 4 and 5 and the fourth (*Ericthonius* sp.) was present exclusively at Site 5 (albeit in relatively low numbers).

The dominance of *Spio martinensis* at Site 5 is worthy of some comment at this point as this dominance was the primary reason for Site 5 being set apart from other sites by the multivariate analyses used in this study. Transect Site 5 was positioned close to a small shingle bar that ran across the bottom of the shore at

Solent Breezes (see Chapter 2). The increased amount of coarse material at Site 5 was a reflection of its proximity to the shingle bar. In addition, the percentage silt/clay fraction was lower than at all other sites - indicating an increased level of water movement. Higher water velocities result in an increase in the flux of suspended particles, a removal of fine material from the sediment and the prevention of fine particle deposition. Such conditions favour suspension feeders. Spionid polychaetes are generally described as selective surface deposit feeders (Fauchald and Jumars, 1979), but some species may also act as facultative suspension feeders (Taghon *et al.*, 1980; Word, 1990).

A distinct change in feeding behaviour has been observed in several spionid species with increasing water velocity and suspended particle flux (Taghon *et al.*, 1980; Miller *et al.*, 1992). At moderate water velocities, the tentacles are raised into the water column and are then coiled into tapering helices. As water velocity and the flux of suspended material increases further, the number of turns in each tentacle increases. Miller *et al.* (1992) described such detailed quantitative changes in the feeding behaviour of *Spio setosa*, and observed that other polychaetes with a crown of less muscular tentacles (including terebellid species) could not continue to feed in relatively high flow conditions. The ability of *Spio martinensis* to continue feeding in conditions of increased water velocity and sediment flux may therefore, at least in part, account for the dominance of this species at Site 5.

Spio martinensis was also abundant at Site 1, constituting over 45% of the total number of individuals. During periods of immersion, the fauna at Site 1 would be exposed to a higher level of wave action and swash conditions than lower areas of the shore. The facultative behaviour of *Spio martinensis* would allow this species to continue feeding in such conditions of increased water movement and sediment flux. Similarly, McLachlan (1990) noted the presence of another species of *Spio* (*Spio filicornis*) at the top of two relatively exposed beaches in Oregon, USA.

Alternatively, the key to the dominance of *Spio martinensis* both at the top of the shore and near to the shingle bar at Solent Breezes may lie in its possible ability to withstand longer periods of emersion. During the retreat of the tide, the bar became clearly visible above the water before much of the intertidal zone at

Solent Breezes. Exact emersion times at Site 5 were not formally quantified, but its proximity to the bar appeared to result in this site being emersed for relatively long periods during each tidal cycle. Although a definitive single cause for the dominance of *Spio martinensis* at Sites 5 and 1 cannot be ascertained, the prevailing hydrodynamic conditions and the associated sedimentary regime clearly placed this particular spionid at an advantage at these sites.

As the above discussion concerning the shingle bar at Solent Breezes has demonstrated, universal zonation schemes cannot account for local heterogeneity in the physico-chemical environment on a shore. In addition, the effects of unpredictable natural or anthropogenic pressures require consideration. While several features of the zonation schemes of both Dahl and Salvat have been recognised at Solent Breezes, the patterns of change in the fauna between the low water mark and the high water mark do not conform entirely to either scheme.

A number of exceptions to Dahl's zonation scheme have been documented (e.g. Dexter, 1972; Eletheriou and Jones, 1976). Furthermore, by definition, Salvat's scheme relies on the presence of distinct physical zones, but the degree to which any biological zonation coincides with these physical zones is not always clear. Other authors have critically assessed the validity of these universal zonation schemes (McLachlan, 1990; Raffaelli *et al.*, 1991; Wendt and McLachlan, 1985) and apart from the supra-littoral zone where air-breathers predominate, it appears that major biological zones are often difficult to define precisely (Allen and Moore, 1987; Brown and McLachlan, 1990; McLachlan, 1990; Raffaelli *et al.*, 1991; Wendt and McLachlan, 1985).

Clearly, vertical zonation is strongly influenced by the type and intensity of the physical processes that occur on a shore. The three basic types of beaches (i.e. reflective, dissipative and intermediate) have been described in Chapter 2. The changes that occur in grain size, wave action, beach slope and moisture content across this spectrum of beach types must significantly affect faunal patterns of zonation, abundance and diversity. McLachlan (1990) has suggested that faunal communities on exposed sandy beaches are generally structured by individual species reacting independently to the physical parameters rather than biological interactions. However, physical factors do not limit the distribution of infaunal species to the same extent on sandflats and mudflats (Raffaelli and Hawkins, 1996). The physical processes on shores towards the dissipative end of the spectrum are more conducive to macrofaunal life (McLachlan, 1990). The main intertidal sediment flat area at Solent Breezes was relatively homogeneous in physical terms, and the sheltered nature of the region further decreased the background level of physical control exerted on infaunal distributions.

The biological interactions that occur in soft sediment communities are considered in more detail in the next chapter. However, alongside the vertical physical gradient present at Solent Breezes between the low water mark and the high water mark, a possible gradient in predation pressure requires brief consideration. Most shorebirds feed on infauna during periods of emersion, and consequently, higher areas on the shore at Solent Breezes were potentially exposed to longer periods of bird predation. Feeding rates of shorebirds can be remarkably high, but the impact of this form of predation on infaunal populations varies from study to study (Raffaelli and Hawkins, 1996). Conversely, aquatic predators such as flatfish and crustaceans feed extensively on intertidal beaches and mudflats during periods of immersion. Therefore, higher areas on the shore were potentially protected from this source of predation for longer periods during each tidal cycle. The relative importance of different predators and the effects of predation on community structure can only be established using carefully designed exclusion experiments. Although, by definition, predation reduces the overall abundance of infauna, at least on the short term, the consequences of different levels of predation on community structure in soft sediment are complex and poorly understood.

Finally, it must be acknowledged that a group of samples taken at one point in time cannot necessarily provide specific information about temporal and spatial variations in environmental parameters that might have occurred prior to sampling. The sampling transect could only be used to compare faunal characteristics at the different sites and relate them to concurrent environmental characteristics. This potential shortcoming is highlighted by the apparent relationship between the total organic content and the faunal characteristics at the five transect sites. The relatively high organic content towards the top of the shore (i.e. Sites 1 and 2) may have been a permanent feature, and if this was the case, organic matter may well have significantly influenced the fauna. However, it has been suggested in Chapter 2 that fragments of the abundant macroalgae present at Sites 1 and 2 were unavoidably incorporated into sediment samples, and these fragments could have significantly affected the organic content of these samples. The short term occurrence of a macroalgal bloom may not have immediately influenced large scale infaunal distributions (i.e. between sites), but may have altered future infaunal patterns as fragments of algae became permanently incorporated into the pool of sedimentary organic matter.

A single-point-in-time sampling strategy is more suitable for analysing relatively permanent or predictable parameters such as emersion factors and levels of water retention. The use of a longer-term monitoring programme, however, may provide additional information on the dynamic and interactive nature of infaunal patterns and environmental variables.

In summary, the sampling transect revealed that a relatively consistent assemblage of infaunal species was present across the main mid-shore area of shallow-sloping sediment flat at Solent Breezes. Towards the top of this relatively homogeneous region, species abundance and diversity declined, presumably as a result of gradual changes in environmental conditions (e.g. emersion factors). The interacting physical parameters arising from the local geology and hydrodynamic conditions also potentially influenced the faunal assemblage found at the uppermost end of the sampling transect. Similarly, the sedimentary regime and the associated hydrodynamic processes close to the shingle bar at the bottom end of the shore are thought to have resulted in the observed increase in abundance of the facultative suspension feeder *Spio martinensis*.

CHAPTER 4

The Macrofaunal Monitoring Programme

4.1 Introduction

Infaunal communities are often characterised by conspicuous levels of temporal variability. The component populations of an infaunal community are potentially influenced by numerous abiotic and biotic parameters. An investigation into the dominant mechanisms that potentially control infaunal patterns requires longer-term monitoring of both the fauna and the environment.

The macrobenthic community of the mid-shore area at Solent Breezes was surveyed over a two year period. This chapter examines the temporal changes that occurred in the infaunal community in relation to the environmental parameters already described in Chapter 2. It also discusses some of the biotic interactions that may have influenced the structure of the infaunal community during the sampling period.

4.2 Field Work and Laboratory Methods

The macrofauna of the mid-shore sampling site was sampled each month for two years. The site was approximately 160m from the mean high water mark, and was at a tidal height of approximately 1.3m above the mean low water mark. Samples were collected using a corer with an internal diameter of 16cm (surface area approximately $0.02m^2$). Each core was taken at a randomly chosen position to a depth of 25cm. A total of ten cores were taken each month (total surface area approximately $0.2m^2$) within one hour of low tide. Individual cores were sieved *in situ* through a 0.5mm mesh sieve and the material retained was transferred to labelled storage jars. The samples were transported to the laboratory within two hours of collection. In the laboratory, a solution of 4% formaldehyde containing Phloxine B (C.I. No. 45410) at a concentration of 0.1g/l was added to fix and stain each sample (Phloxine B stains organic material red, thus facilitating the sorting procedure).

After at least 48 hours, the samples were carefully resieved through a 0.5mm mesh to eliminate mud and fine particles, and to rinse out all traces of formalin. The macrofauna was sorted from the remaining sediment of each sample and was retained in 70% ethanol. Animals were identified and enumerated using a binocular low power microscope and a high power compound microscope. The identified fauna from each sample was then stored in 70% ethanol. The identification keys used for different taxonomic groups are listed in Chapter 3 (Table 3.1). In addition, several unpublished loose-leaf keys previously produced during national workshops and colloquia were used for the identification of various polychaete families.

A reference collection of specimens was collated to facilitate the identification process. Accurate identification was essential, and each member of the reference collection was rechecked to provide a reliable species list for the area (see Appendix 1). The nomenclature used follows Howson and Picton (1997). The production of a comprehensive and accurate faunal list was considered important because of the relative scarcity of published material on the classification of the intertidal macrofauna within Southampton Water (see later).

4.3 Data Analysis

4.3.1 Univariate analyses

Details of the univariate indices used for the analysis of macrofaunal samples have been described previously in Chapter 3 (Section 3.3.1). Margalef's index (d), Shannon-Wiener's diversity index (H') and Pielou's evenness index (J) were calculated for all individual core data sets and all total monthly data sets. Values of d, H' and J were calculated using a specifically designed Quattro Pro spreadsheet. It was later possible to check all calculated values using the PRIMER analysis package. PRIMER was also used to calculate values of Caswell's V-statistic for individual core data and summed replicates. Details of the calculation and interpretation of Caswell's V-statistic are also given in Section 3.3.1.

In addition, Morisita's Index of Dispersion (I_δ) was calculated for each of the 15 most dominant species at Solent Breezes. This index gives an indication of the distribution of individuals among a set of samples (Morisita, 1962). It was used to determine the dispersion of individuals of a particular species among the ten cores taken each month.

Morisita's Index:

$$I_\delta = n\frac{\Sigma[x(x-1)]}{\Sigma x(\Sigma x-1)}$$

Where x is the number of individuals in each core and n is the number of samples. The index equals one for a random distribution, is greater than one for a contagious distribution and is less than one for a regular distribution.

Departures from randomness are judged to be significant when:

$I_\delta(\Sigma x-1) + n-\Sigma x$ is outside the appropriate significance of χ^2 for n-1 degrees of freedom (Elliott, 1971).

4.3.2 Multivariate analyses

A number of multivariate methods were used to analyse the macrofauna. Cluster analysis, non-metric Multi-Dimensional Scaling (MDS), the BIO-ENV procedure and Principal Component Analysis (PCA) were all performed using the PRIMER analysis package. All of these analytical procedures have been described in detail in Chapter 3 (Section 3.3.2). The use of data transformations (e.g. square root or log) was avoided for all of the multivariate analyses presented in this chapter. Such transformations were considered to reduce the amount of information (particularly with respect to the dominance of important species) and inherently result in a departure from "reality".

4.3.3 The Infaunal Trophic Index

A value of the Infaunal Trophic Index was calculated for each monthly data set using the equation given in Section 3.3.3.

4.4 Results

Macrofaunal samples were collected each month from the mid-shore sampling site (i.e. Transect Site 3) between November 1990 and October 1992. Faunal lists for all of the individual samples taken during this period are presented in Appendix 2. A grand total of 115 taxa were identified, although 35 of these only occurred once during the entire sampling period. A full list of the taxa that were recorded at Solent Breezes has been compiled in Appendix 1. Each species is listed with its authority and its designated code as given in the Species Directory of the Marine Fauna and Flora of the British Isles and Surrounding Seas (Howson and Picton, 1997). It was not possible to identify a small number specimens to species level, because of their size, sex or condition. As a result, it is conceivable that some of the specimens listed as "sp. indet." are simply juveniles or females of adjacent species. For example, female specimens of amphipods in the family *Aoridae* are notoriously difficult to identify and have been listed simply as *Aoridae* sp. indet. alongside the male specimens of *Aora gracilis*.

The total number of species collected each month varied between 25 (in March 1991) and 49 (in both June 1991 and August 1991), and the highest number of species present in single sample was 30 (in August 1991). Total monthly diversity (*H'*) ranged between 3.3 in October 1992 and 4.2 in September 1991, and all other monthly values were between 3.5 and 4.0.

4.4.1 Univariate analyses

Changes in the mean number of individuals, the mean species richness and the total species richness are shown in Figure 4.1. There was a distinct seasonal component to the changes in abundance of macrofauna (*N*). The lowest mean number of individuals occurred in March 1991, and the highest mean number of individuals occurred in August 1991. The latter was caused by high numbers of the amphipod *Gammarus locusta*. The second annual cycle in macrofaunal abundance (i.e. between November 1991 and October 1992) was considerably smaller in magnitude. Changes in the abundance of various dominant species significantly contributed to the observed patterns in overall abundance. These dominant species are considered individually later in Section 4.4.2.

Figure 4.2 shows the changes in mean diversity (*H'*) and mean evenness (*J*) that occurred over time. Mean diversity was generally above 3.0, but was considerably lower in March 1991 and October 1992. In September 1991, mean diversity was noticeably higher than in all other months, and the variation between samples was much reduced.

The majority of months had mean evenness values that were above 0.79. However, in August 1991 and October 1992 the mean evenness fell below 0.75. Variation between samples was high and consequently no other significant patterns in evenness were evident.

Figure 4.3 illustrates the results of the *V*-statistic calculations conducted for the 23 monthly data sets. The top graph shows mean values of *V* calculated for each month, and the bottom graph shows values of *V* calculated for the 23 monthly total data sets. The PRIMER programme aborted during the calculation of *V* for two of the samples (one from March 1991 and one from March 1992). Consequently, these two samples had to be omitted from the calculation of the corresponding monthly mean values.

Variation between samples each month was high, but none of the calculated values of mean *V* were either above +2 or below -2, indicating no significant departures from neutrality. The lowest mean *V* value occurred in August 1991, and this was the only value below -1.5.

A similar pattern was evident in the *V* values calculated for the total monthly fauna. However, two *V* values were below -2, indicating significantly lower diversity that that predicted by the neutral model. As a result of combining the ten samples, the fauna was heavily dominated by a single species both in June 1991 and August 1991 (*Lanice conchilega* and *Gammarus locusta* respectively).

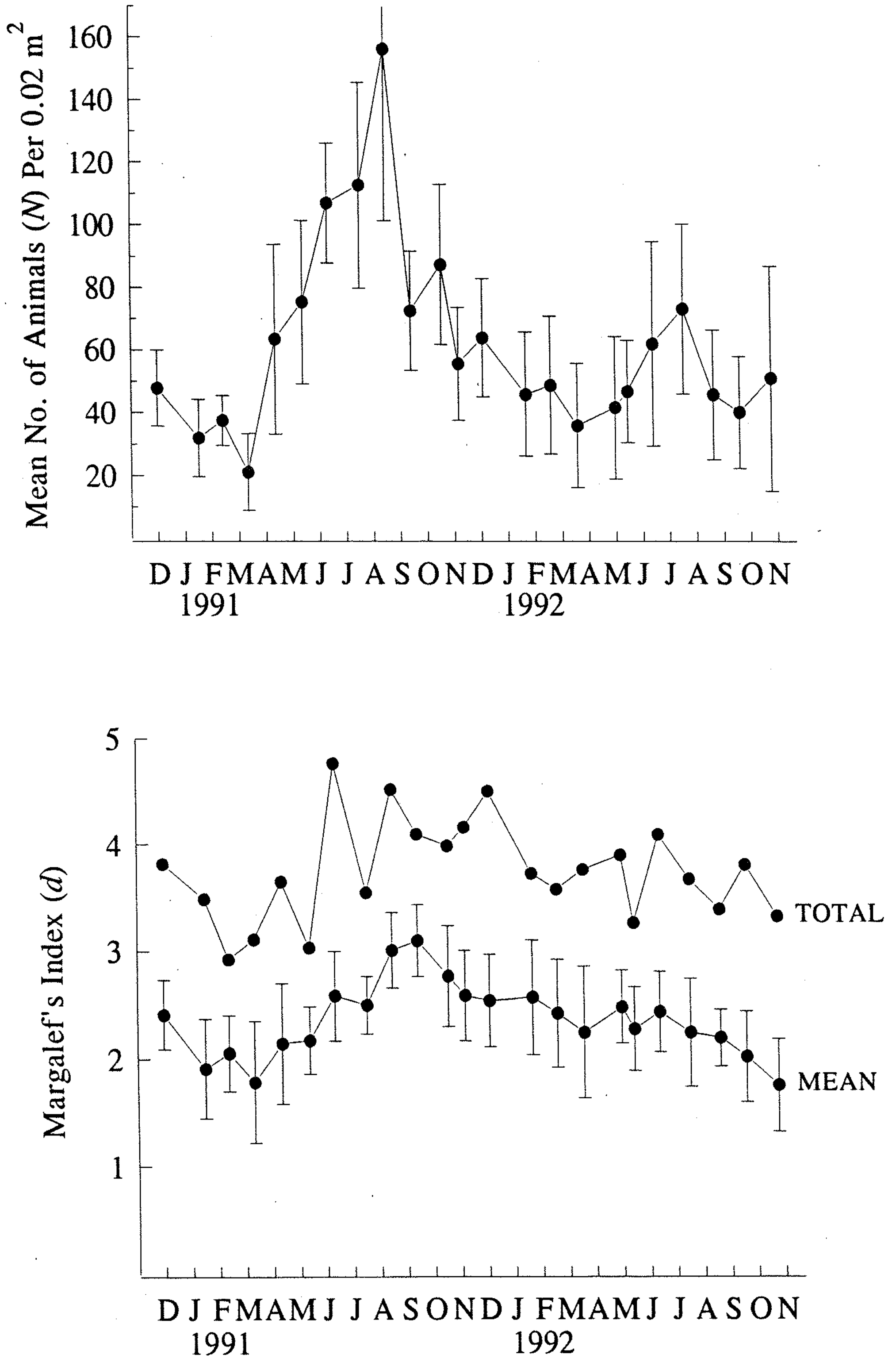
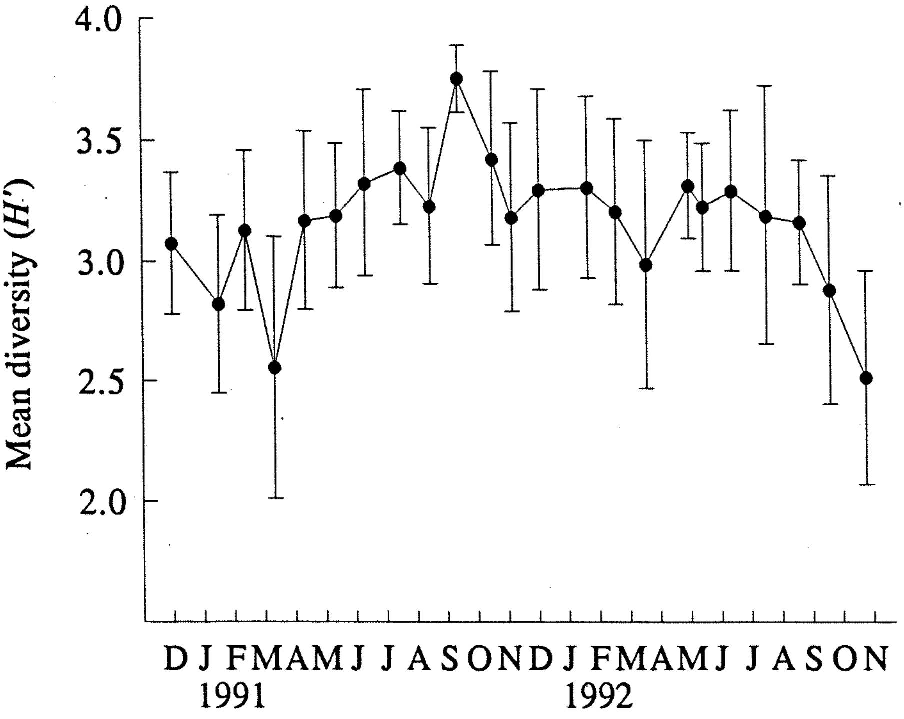


Figure 4.1 Monthly Time Series Macrofauna. Temporal changes in the number of individuals (*N*) and the species richness (*d*) over the two year sampling period. Mean values shown with standard deviations as error bars.



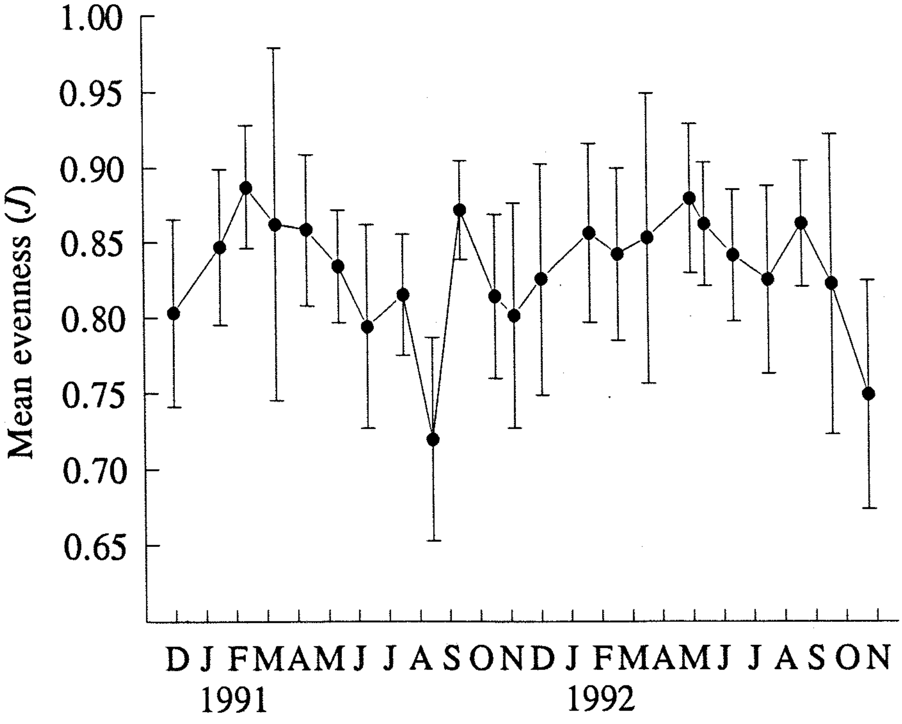
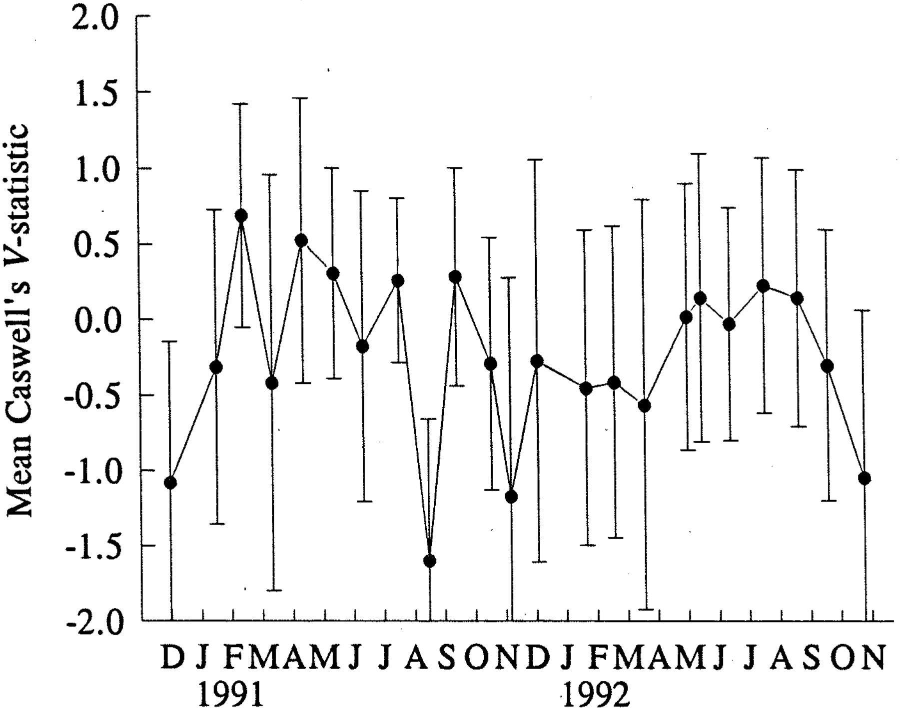


Figure 4.2 Monthly Time Series Macrofauna. Temporal changes in diversity (*H'*) and evenness (*J*) over the two year sampling period. Mean values shown with standard deviations as error bars.



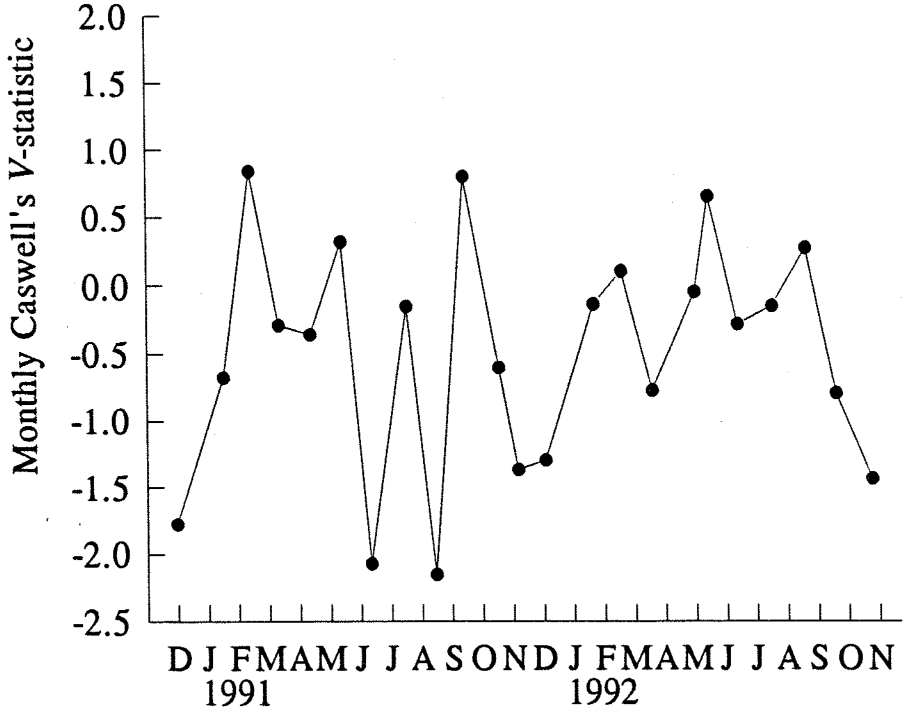


Figure 4.3 Monthly Time Series Macrofauna. Temporal changes in Caswell's *V* statistic over the two year sampling period. Mean values shown with standard deviations as error bars (upper graph). Lower graph shows values calculated for the 23 monthly total data sets.

4.4.2 The dominant species

Patterns of change in the overall abundance of animals (*N*) are usually controlled by changes in the abundance of a number of dominant species. The fifteen most consistently dominant species at Solent Breezes are listed in Table 4.1. To obtain this list, the top twenty species were ranked and scored from 20 (for the most dominant) down to 1 for each monthly data set, and the scores were summed to give the overall dominance rank score (column 2). This rank score gives a clearer indication of the more consistently dominant species. Column 3 shows the number of months in which each species appeared in the top ten species (maximum score = 23). Column 4 gives the total number of individuals per species in all samples taken over the two year sampling period.

Species	Rank Score	Top Ten Score	Total Number
Lanice conchilega	430	23	2,312
Euclymene oerstedii	428	23	1,934
Exogone hebes	396	22	1,688
Aricidea minuta	321	20	941
Pygospio elegans	304	20	674
Spio martinensis	303	20	593
Tanaissus lilljeborgi	288	17	772
Scoloplos armiger	245	12	434
Capitella capitata	217	9	488
Nephtys hombergii	197	7	219
Streptosyllis websteri	174	7	230
Spiophanes bombyx	160	3	174
Bathyporeia sarsi	158	9	476
Microprotopus maculatus	148	9	490
Gammarus locusta	147	8	972

Table 4.1. The dominant species at Solent Breezes.

The fauna was dominated by eleven polychaete species, three amphipod species and the tanaid crustacean *Tanaissus lilljeborgi*. *Lanice conchilega* was the most consistently numerically dominant species during the sampling period. *Euclymene oerstedii* had a very similar rank score and also had a maximum "top ten score". In terms of biomass, *Lanice conchilega* was significantly more dominant - being a much larger species. Although formal biomass calculations were not conducted for the Solent Breezes fauna, *Lanice conchilega* was the biomass dominant in the vast majority of samples. *Nephtys hombergii* was the only dominant species to have individual specimens that were similar in size to *Lanice conchilega* specimens. However, *Nephtys hombergii* was significantly rarer than *Lanice conchilega*. The remaining species in Table 4.1 are all relatively small, and consequently the biomass of *Lanice conchilega* was usually greater than the biomass of all the remaining fauna in individual core samples.

The following sections outline the general ecology of the dominant species at Solent Breezes. Patterns of change in the populations of these species over the two year sampling period are also described. Figures 4.4 to 4.9 show the mean number of individuals (± S.D.) present each month for the 15 species in Table 4.1. The figures also highlight months in which a species had a significantly contagious distribution. Morisita's Index of dispersion (I_δ) was used to calculate levels of contagion as described in Section 4.3.1. The level of significance of χ^2 selected was 5% for *n*-1 (i.e. 9) degrees of freedom. Months in which the distribution of individuals among the ten cores was significantly contagious are circled.

Lanice conchilega

Details of the ecology and reproduction of *Lanice conchilega* are not included here as these are described elsewhere in Chapter 1 and Chapter 5. Figure 4.4 shows the changes in both the mean number of individuals and the value of the dispersion index I_δ over time. The mean number of individuals varied considerably between a high of 25.8 per core (in June 1991) and a low of 2.2 per core (in October 1992). The peak in abundance that occurred in June 1991 was a direct result of an influx of large numbers of young individuals. The development of this cohort of young

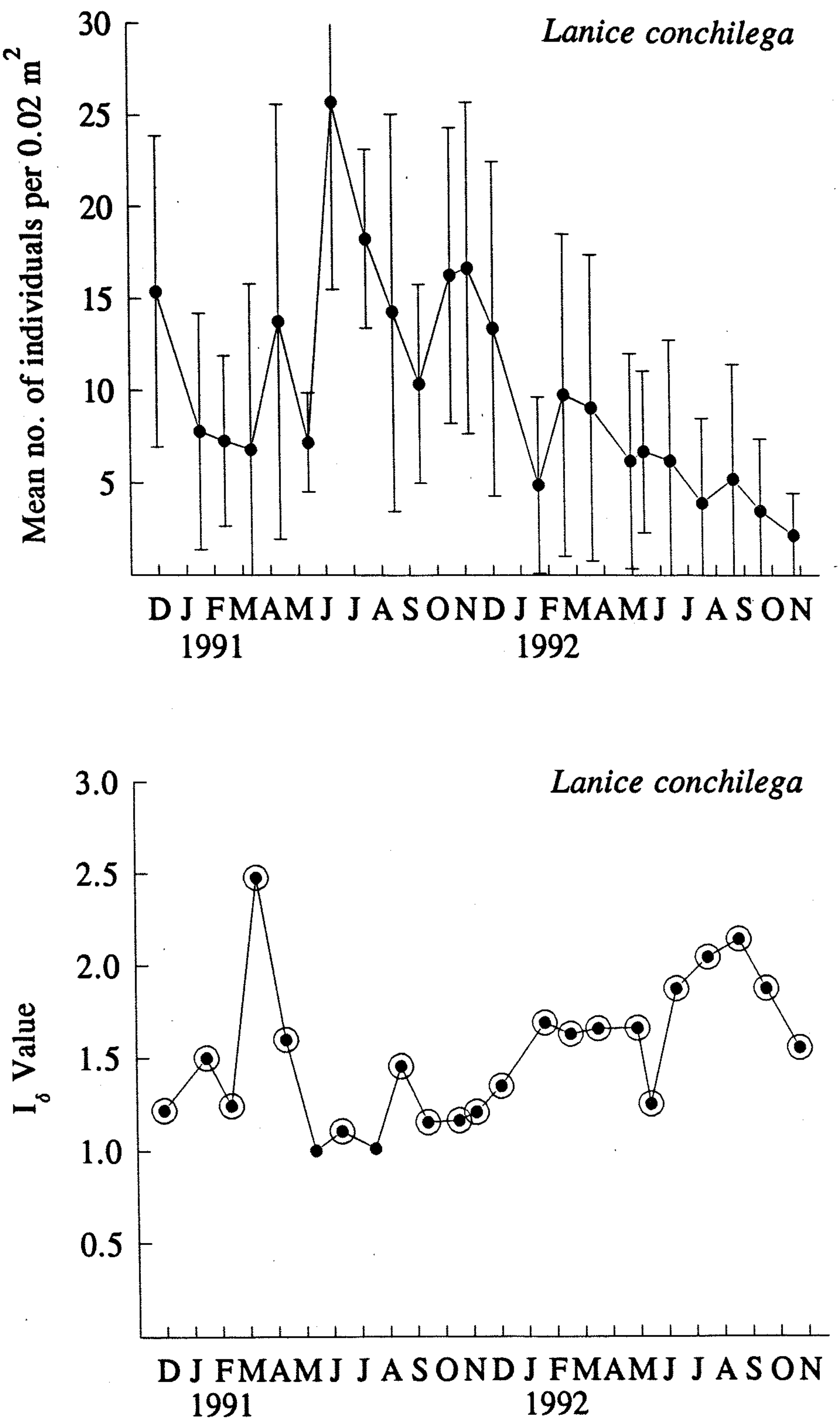


Figure 4.4 Monthly Time Series Macrofauna. Monthly mean densities of *Lanice conchilega* (upper graph) and values of Morisita's index of dispersion, I_δ (lower graph) calculated for the two year sampling period. Significant levels of contagion are indicated on lower graph (encircled points).

individuals and further details of the *Lanice conchilega* population at Solent Breezes are discussed in Chapter 5. There was no such influx of young individuals during the second year of sampling, and the overall numbers of *Lanice conchilega* continued to fall throughout the summer and autumn of that year.

Although the "patchiness" of *Lanice conchilega* varied over the sampling period, the distribution of individuals among the ten cores taken each month was usually significantly contagious. Values of Morisita's Index (I_δ) ranged between approximately 1.0 and 2.5, with 20 of the 23 sets of monthly cores having significantly contagious values (Figure 4.4, lower graph). The level of patchiness was particularly high in March 1991, and an almost random distribution of individuals occurred in samples taken in May 1991 and July 1991.

In June and July 1991 the population could be divided into two distinct cohorts (see Chapter 5), and in both of these months members of the older cohort had a significantly contagious distribution while the smaller individuals of the new cohort were randomly distributed across the shore. The implications of this are discussed in Chapter 5.

Euclymene oerstedii

The Maldanid polychaete *Euclymene oerstedii* is a sedentary tube dweller that inhabits intertidal and subtidal soft substrata. Maldanids are head-down deposit feeders with an eversible sac-like pharynx that is used to ingest detrital material (including protozoa and diatoms). The pygidium plugs the entrance of the tube, which is relatively fragile in species of *Euclymene*. Reproduction in *Euclymene oerstedii* has been observed to occur in only a fraction of a population (Clavier, 1983). Eggs are incubated in mucus cocoons attached to the burrow entrance and the larvae emerge at a relatively late stage of development (Day, 1967). A swimming prototrochophore develops into a benthic larva within three days.

At Solent Breezes, the average density of *Euclymene oerstedii* ranged between 2.1 and 16.8 per core sample (equivalent to between approximately 105 and 840 m^{-2}). The maximum mean density of *Euclymene oerstedii* occurred in June 1991 samples (Figure 4.5). The minimum mean density occurred in March

1991 samples, and recruitment during the spring and early summer of 1991 was followed by a general decline in numbers until March 1992. A small increase in numbers was evident during the spring and early summer of 1992, but the level of recruitment was significantly lower than that of the previous year. The distribution of individuals among samples was either random ($I_\delta = 1.0$) or contagious ($I_\delta > 1.0$), with 15 of the 23 monthly data sets having distributions that were significantly contagious (Figure 4.5).

Exogone hebes

Exogone hebes occurs intertidally or in shallow subtidal areas. It inhabits sand, shell gravel or sea-grass beds and can be found on most British coasts (Hayward and Ryland, 1990a). A typically small member of the family Syllidae, it is a free-living, active polychaete with an eversible pharynx and an obvious, muscular proventriculus. All members of the subfamily Exogoninae are most probably highly selective surface deposit feeders (Fauchald and Jumars, 1979). They are also both carrion-feeders and carnivorous when the opportunity arises. Sexually mature *Exogone hebes* males develop swimming chaetae, and the fertilised eggs develop attached to the parapodia of mature females (Garwood, 1991). In addition, fertilised eggs have been observed inside females, which subsequently develop internally into fully differentiated juveniles (Pocklington and Hutcheson, 1983). This second, viviparous mode of development was observed in a population from Newfoundland and was a very successful reproductive strategy.

Exogone hebes was present at the mid-shore sampling site in mean densities of between 0.5 and 21.0 per core sample (i.e. between 25 and $1050m^{-2}$). An extremely low mean density occurred in March 1991, but the subsequent high mean densities that occurred in July 1991 and October 1991 resulted in *Exogone hebes* being the numerically dominant species in both these months. The relatively high mean density value shown for October 1992 was a result of one sample containing a very high number of individuals (equivalent to $3150m^{-2}$). The patchiness of *Exogone hebes* was evident throughout the sampling period. All monthly I_δ values were greater than 1.0, and 21 of the 23 months had significantly contagious distributions of individuals (Figure 4.5).

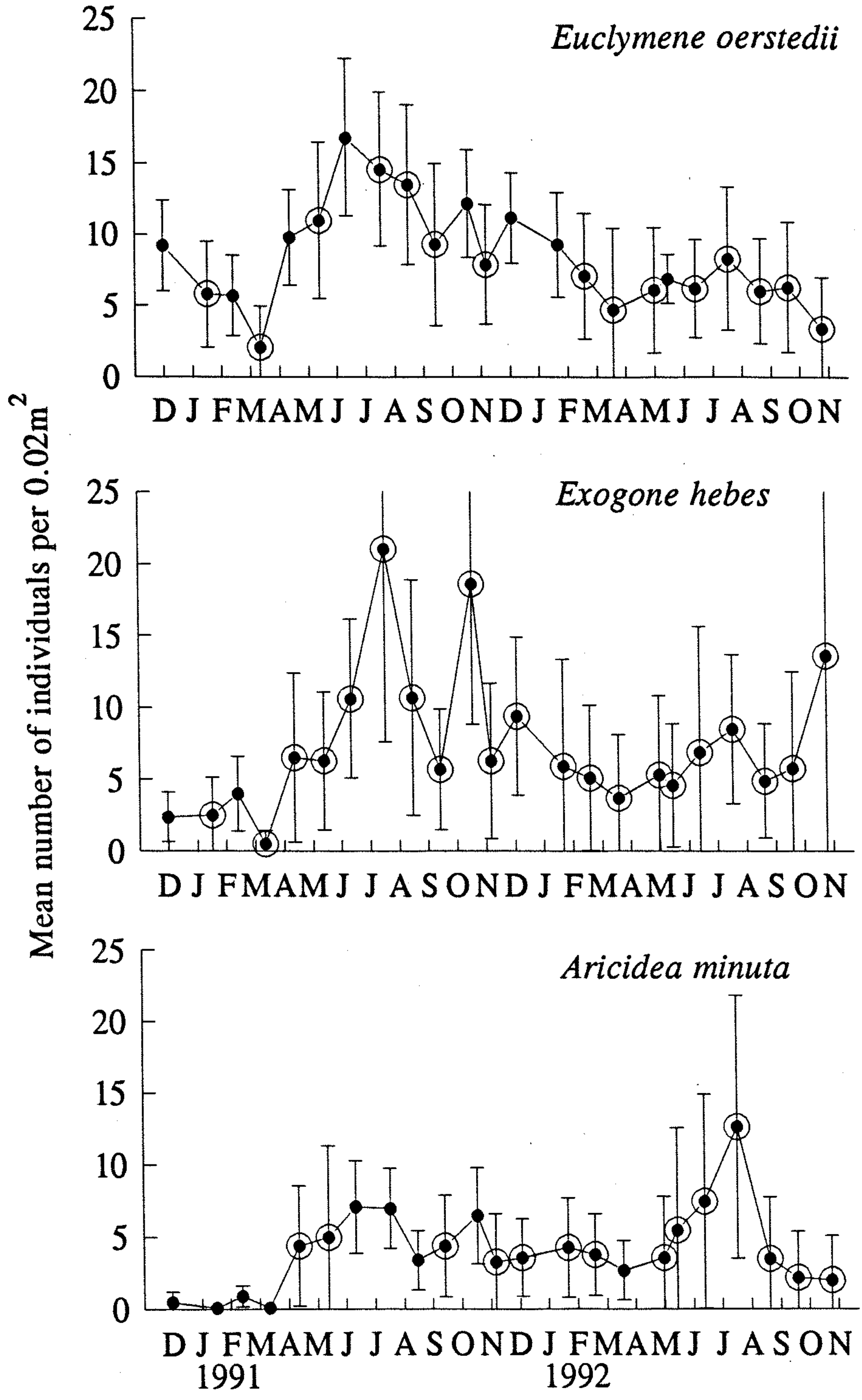


Figure 4.5 Monthly Time Series Macrofauna. Monthly mean densities of *Euclymene oerstedii*, *Exogone hebes* and *Aricidea minuta* during the two year sampling period. Months in which the distribution of individuals among samples was significantly contagious are outlined with a circle.

Aricidea minuta

Aricidea minuta (Polychaeta, Paraonidae) has been widely recorded from British and European waters. It has been collected from a range of depths from the intertidal zone to below 60m (Hartmann-Schröder, 1971). Paraonids live on or near the surface of sandy or silty sediments (Strelzov, 1973). A short eversible pharynx allows paraonids to ingest surface deposits, and they feed mainly on the microorganisms inhabiting the surface layers (Fauchald and Jumars, 1979; Strelzov, 1973). The level of selectivity is uncertain as the feeding biology of only one species of paraonid (*Paraonis fulgens*) has been described (Fauchald and Jumars, 1979). Little is known about the reproduction of paraonids, and details of the reproductive strategy of *Aricidea minuta* remain undocumented.

Although initial densities during the first four months of sampling were very low, *Aricidea minuta* was present at Solent Breezes throughout the sampling period (Figure 4.5). Mean densities varied between 0.1 and 12.7 per core sample (equivalent to 5 and 635m^{-2} respectively). The high densities that occurred in July 1992 resulted in *Aricidea minuta* being the numerically dominant species in this month. The distribution of individuals during the initial period of low densities was either random or regular (i.e. $I_\delta \leq 1.0$). However, values of I_δ for all subsequent months were greater than 1.0, and 14 of these months had significantly contagious distributions of *Aricidea minuta*.

Pygospio elegans

Pygospio elegans is a cosmopolitan spionid polychaete species that occurs on many north-east Atlantic coasts, including Britain, and extends into the Mediterranean and the North Pacific. It is found in intertidal and subtidal areas in rock crevices or among shell fragments (Hayward and Ryland, 1990a). On some European shores, *Pygospio elegans* can occur in extremely dense aggregations, forming large mats of tubes (e.g. Batten, 1994) or forming bundles of tubes filling rock crevices (Gudmundsson, 1985). Individuals feed on surface deposits or catch plankton with their palps. In addition, *Pygospio elegans* is able to filter feed by building a net of mucus (Fauchald and Jumars, 1979). Reproduction can occur sexually or asexually. Egg capsules laid inside the tubes of the females initially contain up to 300 eggs, but only two eggs per capsule develop into larvae (Gudmundsson, 1985). These larvae remain inside the capsules until they hatch as 14 to 20 setiger juveniles. An alternative mode of larval development involves all the eggs within capsules developing into three-setiger planktotrophic larvae which hatch into the water column (Gudmundsson, 1985). Asexual reproduction may also occur through the regeneration of fragmented adults.

Pygospio elegans occurred at Solent Breezes in mean densities of up to 13.8 per core sample (Figure 4.6). Monthly mean density values were generally below 6.0 per core (i.e. $300m^{-2}$), but numbers were markedly higher in June 1991 samples. The distribution of individuals among cores was significantly contagious in every month with a mean density greater than $125m^{-2}$. Below this density, the distribution of *Pygospio elegans* was random, contagious or occasionally regular.

Population densities were generally lower than those documented for a northern U.K. estuarine sandy mudflat (Gudmundsson, 1985). However, both these populations were significantly smaller than dense populations occurring in particular areas of the Somme estuary, which were estimated to reach densities of approximately $150\ 000m^{-2}$ (Batten, 1994).

Spio martinensis

Species of the genus *Spio* (Polychaeta, Spionidae) are commonly found in coastal benthic samples. However, accurate identification of *Spio* species has often been hindered by a degree of ambiguity and a lack of clarity in taxonomic literature. *Spio martinensis* is a small and characteristically thread-like species which is found in intertidal and subtidal sediments. It builds a delicate tube but remains discretely mobile. Spionids are generally described as selective surface deposit feeders (Fauchald and Jumars, 1979). Food particles are selected from the surrounding area by the tentacles and may also be filtered from the water column. Female *Spio martinensis* lay eggs in flattened egg-cylinders and the developing larvae remain in these egg-cylinders until they emerge as pelagic three-setiger larvae

(Gudmundsson, 1985). During the pelagic phase the larvae develop into juveniles (with approximately 30 setigers) which subsequently settle and burrow.

Spio martinensis was present at Solent Breezes throughout the sampling period (Figure 4.6). Mean densities were generally below approximately 4.0 per core sample ($200m^{-2}$), but a pulse of higher numbers occurred in a single summer month each year (i.e. July 1991 and June 1992). Maximum mean densities at Solent Breezes ($\leq 375m^{-2}$) were significantly lower than maximum mean densities previously observed in a mudflat at Black Middens, North Shields (Gudmundsson, 1985). The population at Black Middens was at its maximum size during August and September, reaching mean densities of over $7500m^{-2}$. In addition, the two annual pulses of recruitment observed at Solent Breezes both occurred considerably earlier than the main population increase observed by Gudmundsson at Black Middens.

Tanaissus lilljeborgi

Tanaissus lilljeborgi is the only tanaid crustacean that is common in both intertidal and subtidal sediments around Britain, and it has also been recorded from northern Europe and Canada (Holdich and Jones, 1983a, 1983b; Jones and Holdich, 1983; Withers, 1979). This species burrows in the surface layers of sandy sediments, feeding on detritus and its associated microorganisms. Sexual dimorphism is pronounced and eggs develop in a marsupium on the underside of the ovigerous female. Juveniles (or mancas) are released at a late stage of development and the subsequent stage has fully formed appendages. Adult densities of up to $600m^{-2}$ have previously been reported in the Solent area (Withers, 1979).

The maximum mean density of *Tanaissus lilljeborgi* at Solent Breezes during the macrofaunal sampling period was $610m^{-2}$ (Figure 4.6). Individuals were all of a sufficient size to be retained on the 0.5mm mesh used for macrofaunal sampling, and were therefore all likely to be adults. The maximum mean density occurred in May 1991, and particularly low numbers were present at the end of the sampling period between July and October 1992.

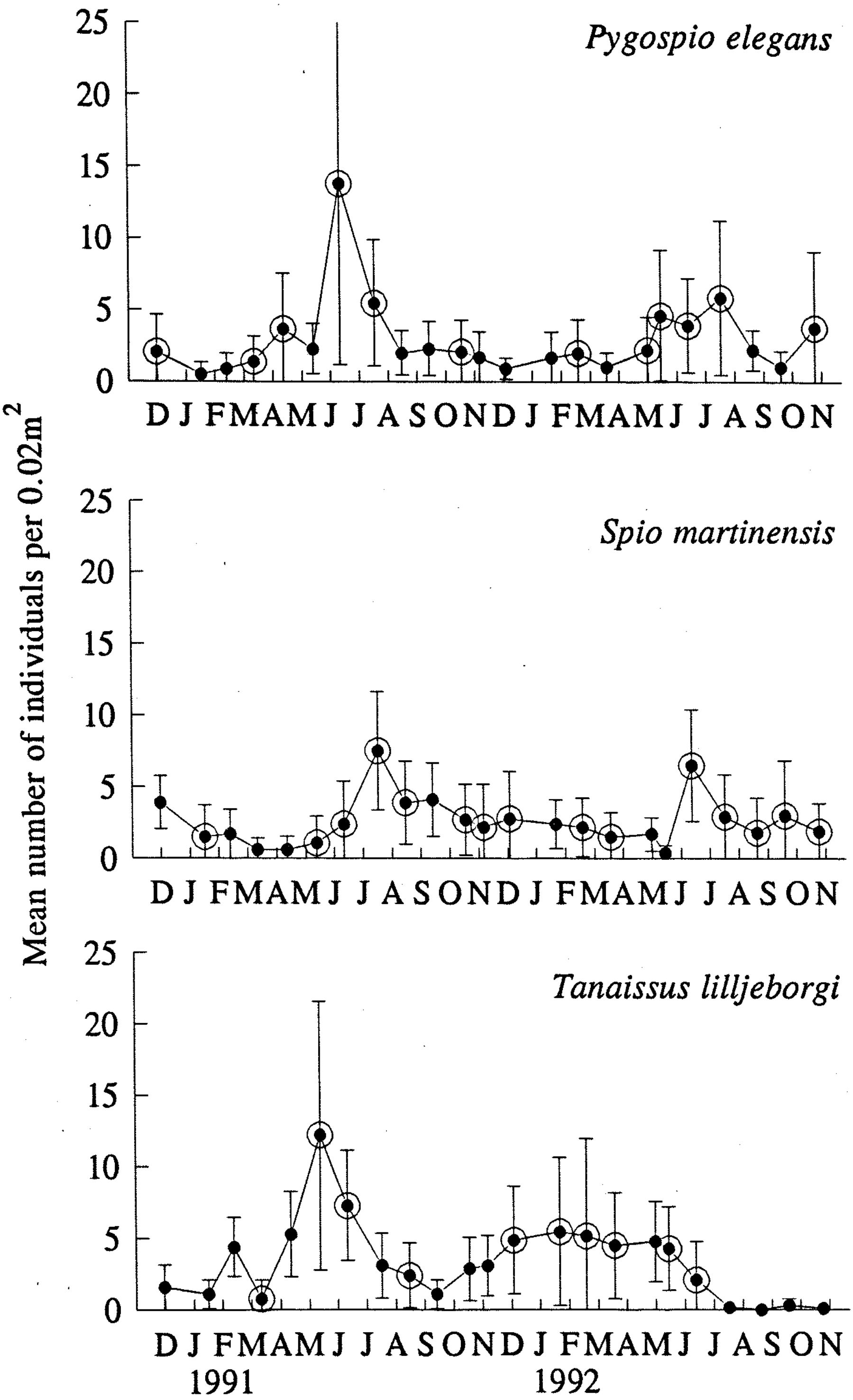


Figure 4.6 Monthly Time Series Macrofauna. Monthly mean densities of *Pygospio elegans*, *Spio martinensis* and *Tanaissus lilljeborgi* during the two year sampling period. Months in which the distribution of individuals among samples was significantly contagious are outlined with a circle.

Scoloplos armiger

Scoloplos armiger is a widely distributed and often common orbiniid polychaete. It has been recorded from intertidal and subtidal sediments around Britain and from north-west Europe, the Arctic, the Indian Ocean, the Pacific Ocean and the Antarctic (Hayward and Ryland, 1990a). As it burrows in muddy sands, it feeds on subsurface deposits using a sac-like eversible pharynx. The level of selectivity remains unconfirmed, although most authors describe orbiniids as non-selective (Fauchald and Jumars, 1979).

The sexes in *Scoloplos armiger* are separate and breeding has been recorded in early spring, synchronised with spring tides (Fish and Fish, 1989) or temperature (Plate and Husemann, 1992). Eggs are deposited in a cocoon on the sediment surface and a hollow stalk connects each cocoon to the sediment. These larvae are entirely benthic, hatching at two or three weeks and migrating down the stalk to emerge in subsurface layers. An alternative mode of development has been described by Plate and Husemann (1992), in which larvae are entirely planktonic and settlement occurs at about the ten-setiger stage. *Scoloplos armiger* individuals live for approximately four years and breeding first occurs at two years.

Between November 1990 and September 1992 *Scoloplos armiger* was present at Solent Breezes in mean densities of between 0.1 and 4.2 per core sample (Figure 4.7). Numbers were relatively stable during the first 10 months of sampling, after which there was a general decline. The higher mean values recorded in February 1992 and June 1992 were each a result of a single core sample containing a relatively high number of individuals. Apart from these two samples, densities were markedly lower throughout the second year of sampling and in October 1992, *Scoloplos armiger* was completely absent from all core samples.

Capitella capitata

Capitellid polychaetes have a widespread distribution and can occur in extremely large densities, particularly in areas of organic enrichment. *Capitella capitata* is known to be a species complex, the component species of which have not been adequately described. Members of the species complex occur intertidally and offshore, in areas of rich mud or muddy sand. The distribution of these tubiculous polychaetes includes areas of the Arctic, Atlantic and Pacific coasts and the Mediterranean (Hayward and Ryland, 1990a). Feeding is achieved by everting a sac-like pharynx to ingest sedimentary material. The level of selectivity remains uncertain but some selection of organic particles and associated microorganisms is conceivable (Fauchald and Jumars, 1979, Fish and Fish, 1989). Members of the *Capitella capitata* species complex have been described as dioecious and hermaphroditic, and as having pelagic and benthic larvae. Other studies have also revealed that the component species of the complex can be found in the same sample and have similar adult morphologies but distinct reproductive modes (Grassle and Grassle, 1976; Wilson, 1991a).

Capitella capitata was present at Solent Breezes throughout the sampling period (Figure 4.7). During the first 19 months, mean densities were between 0.3 and 2.1 per core sample (equivalent to between 15 and 105m^{-2}). After June 1992, mean densities increased significantly and reached a maximum of 700m^{-2} in October 1992. The distribution of individuals among cores during each of the last 4 months was significantly contagious (Figure 4.7). The final mean density was sufficiently great to cause *Capitella capitata* to become the numerically dominant species in October 1992.

Nephtys hombergii

Nephtys species (Polychaeta, Nephtyidae) are widely distributed in north-west Europe. They are generally considered to be active predators, feeding on molluscs, crustaceans and smaller polychaetes (Hayward and Ryland, 1990a, Fish and Fish, 1989). The superficial similarity of species of this genus has created much confusion (e.g. Rainer, 1989) and consequently the distribution of *Nephtys hombergii* is difficult to describe accurately. This species is one of several species usually found in different combinations of sand and mud. It is found in both intertidal and shallow subtidal sediments, and it is able to tolerate fluctuations in salinity. There appear to be certain morphological differences between some intertidal specimens and some subtidal specimens and the taxonomic status of these

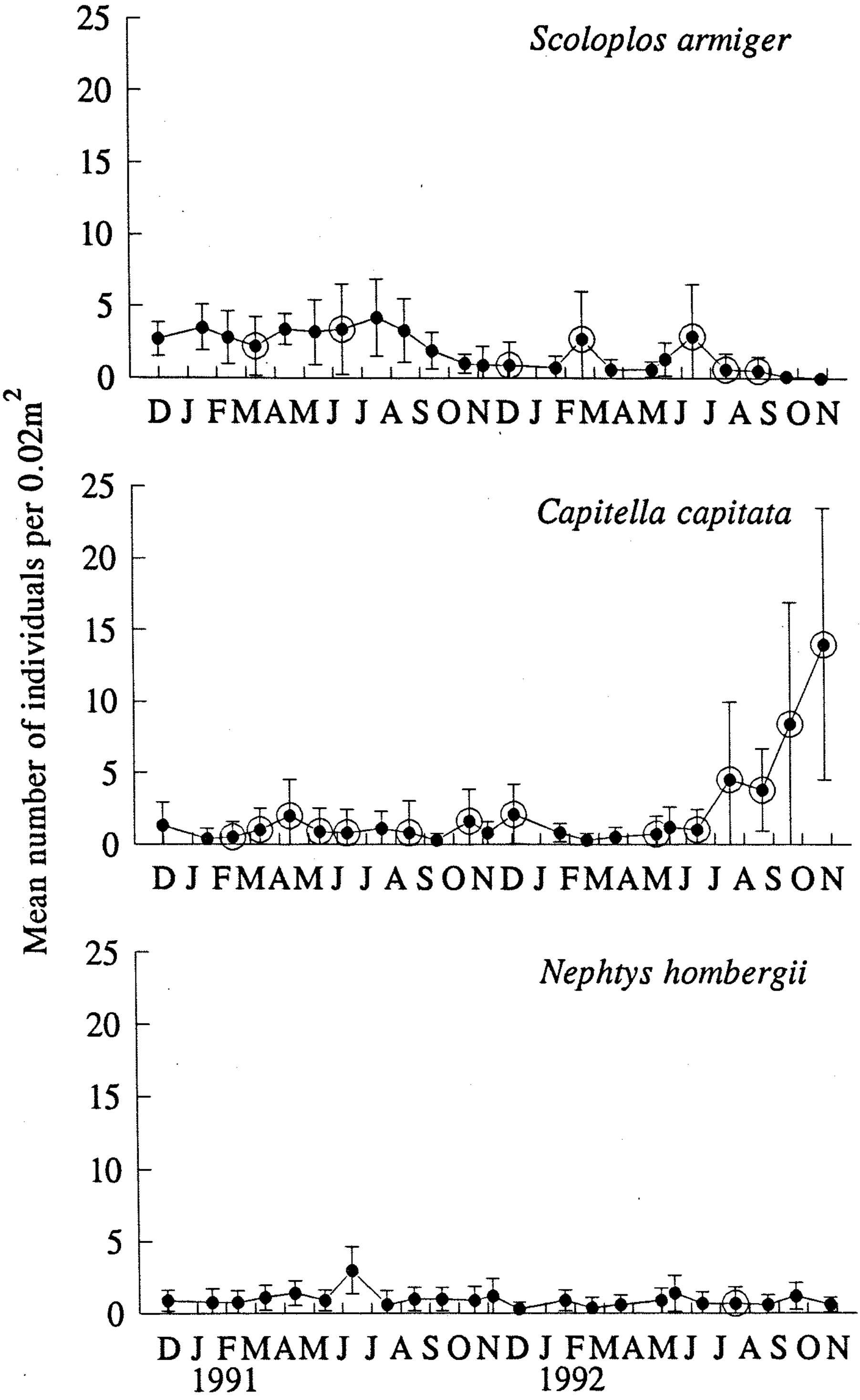


Figure 4.7 Monthly Time Series Macrofauna. Monthly mean densities of *Scoloplos armiger*, *Capitella capitata* and *Nephtys hombergii* during the two year sampling period. Months in which the distribution of individuals among samples was significantly contagious are outlined with a circle.

subtidal specimens requires clarification (Garwood, 1992). Mature *Nephtys hombergii* have been observed to breed during April and May producing gametes during low tide which are mixed as the tide rises. Larvae are pelagic and adult specimens may live up to six years (Fish and Fish, 1989).

Nephtys hombergii occurred at the Solent Breezes sampling site in relatively low numbers throughout the sampling period (Figure 4.7). Mean densities were between 0.3 and 3.0 per core sample (i.e. between 15 and 150m^{-2}). The peak in abundance that occurred in June 1991 was caused by an influx of relatively small individuals. This pattern of recruitment was not repeated the following year. The distribution of individuals was predominantly regular ($I_8 < 1.0$) and was significantly contagious in only one month (July 1992). The distribution of this relatively large motile polychaete was clearly different to many of the other smaller and often sedentary species.

Streptosyllis websteri

Streptosyllis websteri is a small errant polychaete belonging to the family Syllidae (subfamily Eusyllinae). It has been recorded from the North Atlantic and the North Sea (Hartmann-Schröder, 1971). It occurs both intertidally and subtidally, and it is known to feed on diatoms (Garwood, 1982; Hartmann-Schröder, 1971). The epigamous reproduction of *Streptosyllis websteri* has been described by Garwood (1982) for an intertidal population from a Northumberland beach. Spawning was observed between April and July and larval development was principally benthic, with any prolonged truly pelagic phase being unlikely (Garwood, 1982).

Mean densities of *Streptosyllis websteri* at Solent Breezes were between 0.0 and 4.1 per core sample (Figure 4.8). The relatively small size of this species may have caused inaccuracies to have arisen in the estimation of population densities, as some specimens were potentially small enough not to have been retained on a 0.5mm mesh. However, a distinct pulse of relatively high numbers was identified in samples taken in May 1991. Population densities were significantly lower than densities previously observed in an intertidal sandy beach in Northumberland (Garwood, 1982). The maximum mean density than occurred at

Solent Breezes during the macrofaunal sampling period (i.e. 205m^{-2}) was at least one order of magnitude smaller than densities found at the two sampling stations studied by Garwood. In addition, peak numbers in the Northumberland samples were not reached until August or September each year.

Spiophanes bombyx

The spionid polychaete *Spiophanes bombyx* occurs on most British coasts. It has been recorded from the Atlantic, the Mediterranean and the north Pacific (Hayward and Ryland, 1990a), and its distribution extends into the South Atlantic, the South Pacific and further into sub-Antarctic regions (Hartmann-Schröder, 1971). It occurs both intertidally and subtidally, constructing a thin tube using secreted mucus and surrounding fine particles. Spionids are generally described as surface deposit feeders, selecting food particles from the surrounding area using their tentacles (Fauchald and Jumars, 1979).

Spiophanes bombyx occurred at Solent Breezes throughout the sampling period (Figure 4.8). Mean densities were consistently below 1.5 per core sample (i.e. 75m^{-2}), and the distribution of individuals among samples varied between regular, random and contagious, with no apparent pattern emerging.

Bathyporeia sarsi

The amphipod genus *Bathyporeia* is well represented throughout Britain and Europe. *Bathyporeia sarsi* has been frequently recorded from Norway to the English Channel (Lincoln, 1979). It occurs intertidally below mean high water (neaps) and extends sublittorally to a depth of approximately 20m. It lives below the surface in sandy sediments where it feeds by removing organic matter from the surface of individual sand grains (Fish and Fish, 1989). Emerging into surface waters during spring tides, individuals are able to move up and down the shore in large numbers. Males and females also pair while swimming. Females produce several broods of eggs in succession and development of the young takes approximately two weeks.

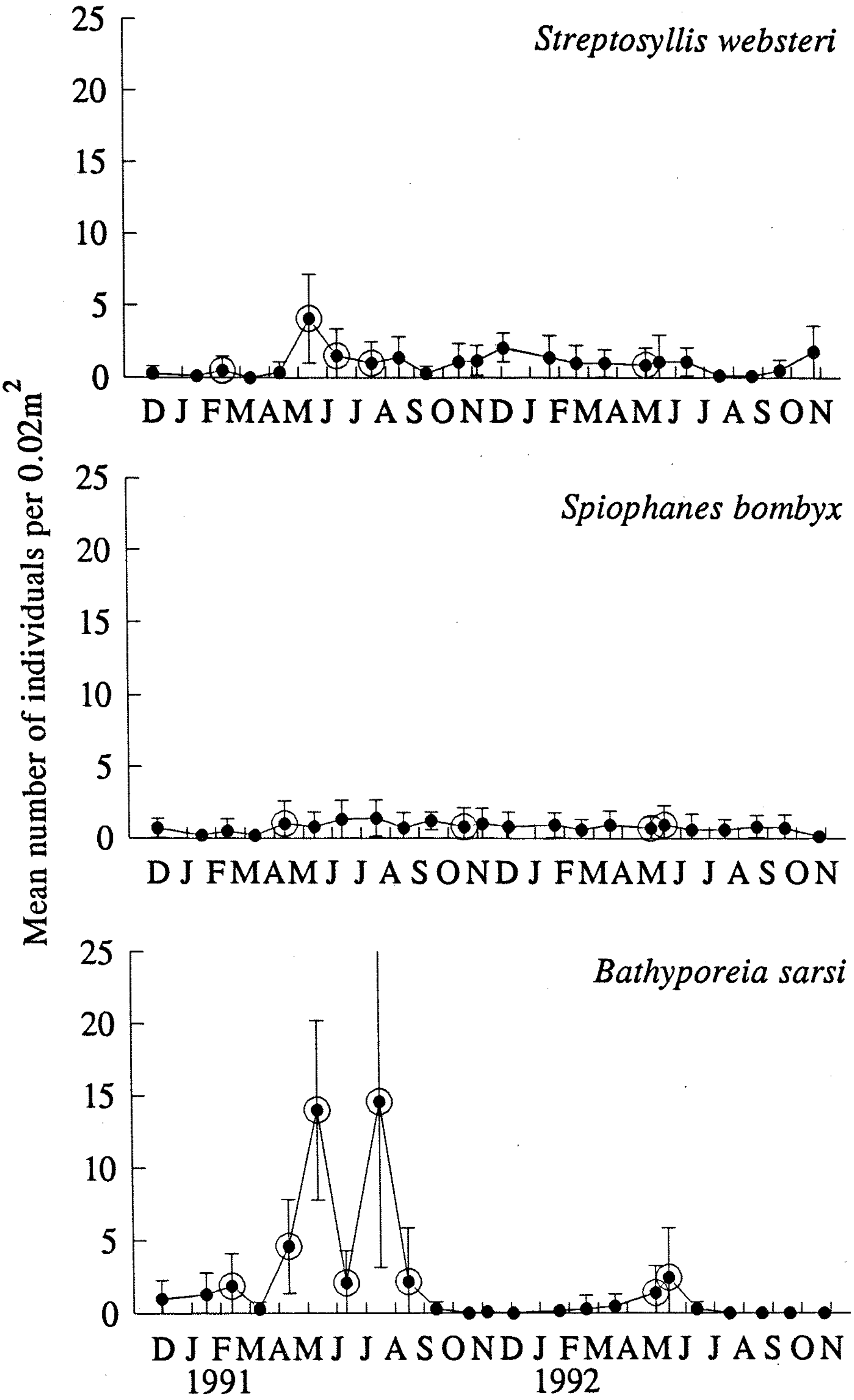


Figure 4.8 Monthly Time Series Macrofauna. Monthly mean densities of *Streptosyllis websteri*, *Spiophanes bombyx* and *Bathyporeia sarsi* during the two year sampling period. Months in which the distribution of individuals among samples was significantly contagious are outlined with a circle.

Bathyporeia sarsi occurred in the monthly samples taken from Solent Breezes in vastly differing densities during the sampling period (Figure 4.8). Mean densities varied between zero and 14.6 per core sample (equivalent to between zero and $730m^{-2}$). The ability of this species to move up and down the shore probably caused the significant variation that occurred between consecutive months (particularly high densities were present in May 1991 and July 1991, but not in June 1991). Mean densities were often extremely low, and *Bathyporeia sarsi* was completely absent from samples taken in 6 of the 23 months. The distribution of individuals among samples was consistently significantly contagious when the mean density was above 1.3 per core sample.

Microprotopus maculatus

Microprotopus maculatus (Amphipoda, Gammaridea) has been recorded from the north-east Atlantic, the North Sea, the Mediterranean and on European coasts from Norway to the Adriatic (Lincoln, 1979). It occurs among algae and on sandy substrates both intertidally and in the shallow subtidal zone. It has a relatively small, pigmented body and sexual dimorphism is marked. In particular, adult males have extremely large second gnathopods. Details of the feeding ecology of *Microprotopus maculatus* have not been documented, but it seems likely that this species typically feeds on organic detritus, particularly fragments of the algae within which it is commonly found.

Microprotopus maculatus occurred in significant densities at Solent Breezes during the summer and early autumn (Figure 4.9). Mean densities during the two year sampling period varied between zero and 13.2 per core sample (equivalent to between zero and $660m^{-2}$). The high numbers that occurred in August 1991 gradually decreased over the subsequent months. This pattern was repeated the following year, although the initial increase in numbers occurred a month earlier in July 1992. The annual pattern in population density observed at Solent Breezes was probably a result of the association between *Microprotopus maculatus* and surface macroalgae that was present on the shore during summer months.

Gammarus locusta

The amphipod genus *Gammarus* contains a large number of species from both freshwater and marine habitats. *Gammarus locusta* is described as a fully marine species that is very widespread around Britain, frequently recorded and often locally abundant (Hayward and Ryland, 1990a, Lincoln, 1979). It is found from the middle shore down to a depth of approximately 30m, living amongst algae and under stones, and feeding on seaweed and organic detritus (Fish and Fish, 1989, Spooner, 1947). During reproduction, the male accompanies the female for several days before fertilisation. Embryos develop within a brood chamber and gravid females carrying embryos have been recorded throughout spring and summer (Fish and Fish, 1989).

Mean densities of *Gammarus locusta* at Solent Breezes varied between zero and 59.8 per core sample (i.e. $2990m^{-2}$). Extremely high numbers were present on the shore in August 1991 (Figure 4.9). *Gammarus locusta* was markedly dominant in this month and the high densities caused a significant peak in overall macrofaunal abundance. The association between *Gammarus locusta* and abundant surface macroalgae resulted in these exceptional densities of both mature and immature individuals. There were significantly less immature individuals in samples taken during the summer of 1992 and consequently the second annual peak in abundance was much smaller. However, the presence of macroalgae again resulted in relatively high densities of *Gammarus locusta*.

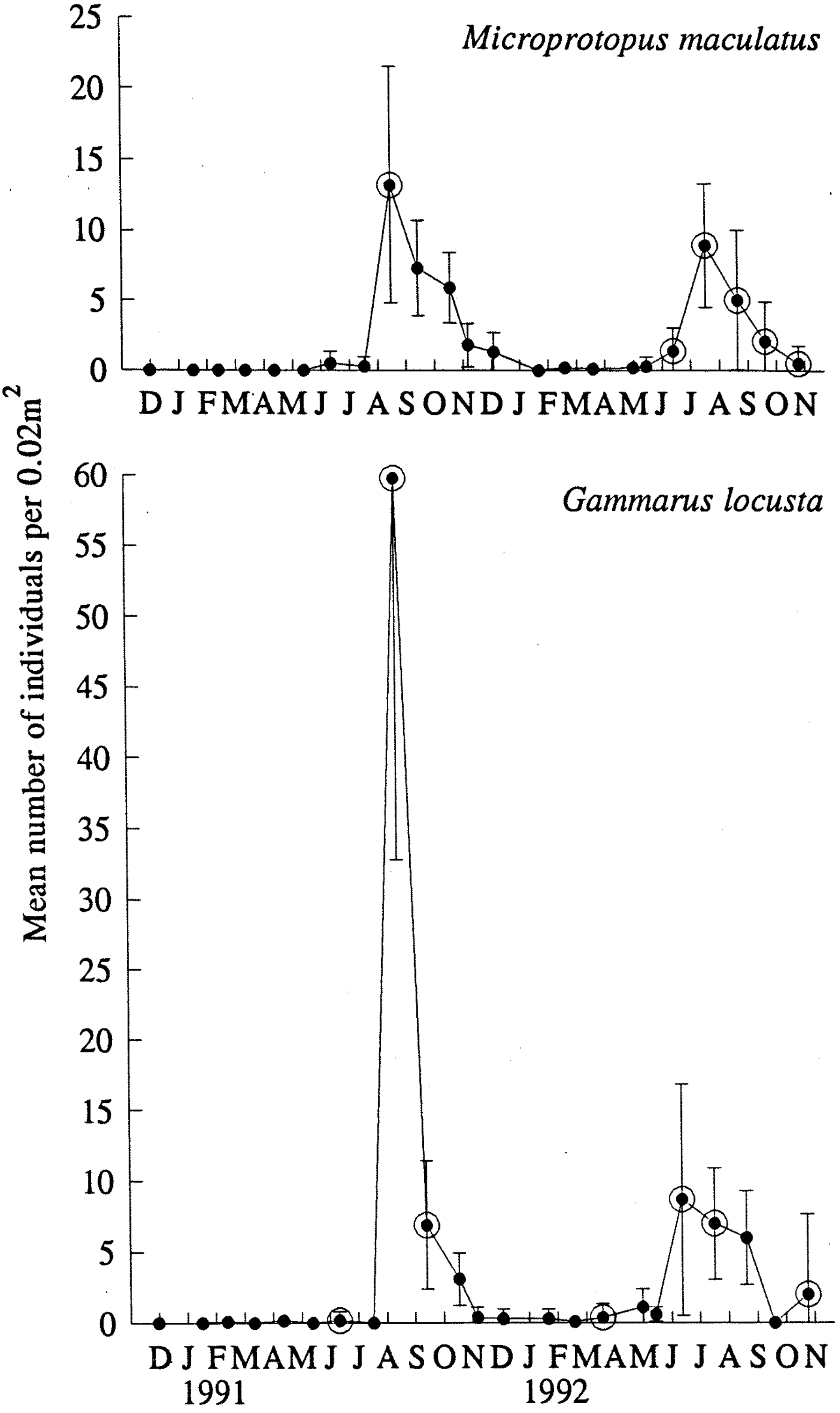


Figure 4.9 Monthly Time Series Macrofauna. Monthly mean densities of *Microprotopus maculatus* and *Gammarus locusta* during the two year sampling period. Months in which the distribution of individuals among samples was significantly contagious are outlined with a circle.

4.4.3 Multivariate analyses

Figure 4.10 presents the results of the cluster analysis performed on the total fauna of the monthly time series data sets. The similarity matrix produced for the analysis compared monthly total fauna data sets. Monthly totals were used for this analysis because of the large number of samples taken over the two year sampling period (i.e. 230), and because of the level of variation that occurred between individual samples each month. Consequently, a large single "sample" from each month was used, but each of these single samples was made up of the ten randomly positioned core samples taken in that month. Each sample was therefore considerably more representative than a single large core sample would have been. The use of monthly totals gave an acceptable indication of the changes that occurred in the fauna at Solent Breezes over the sampling period.

Cluster analysis

The dendrogram produced by the PRIMER cluster analysis programme highlighted six clusters at the 60% level:

Group 1: Aug 1991

The fauna in this single month was very heavily dominated by the amphipod *Gammarus locusta*. In addition, both *Microprotopus maculatus* and *Atylus swammerdamei* featured in uniquely high positions in the dominance rank of this month. Total numbers of most of the other dominant species were similar to many other monthly totals, but the presence of *Gammarus locusta* in such high numbers caused this month to be separated at the highest level.

Group 2: Mar 1991

The fauna in this month was characterised by particularly low numbers of individuals. The dominant species included *Lanice conchilega*, *Euclymene oerstedii* and *Pygospio elegans*, but the presence of *Scoloplos armiger* in a high position in the dominance rank (i.e. second) was unique to this month. In addition, two species that usually featured highly in monthly dominance ranks (i.e. *Aricidea minuta* and *Exogone hebes*) were absent from the top ten species in March 1991.

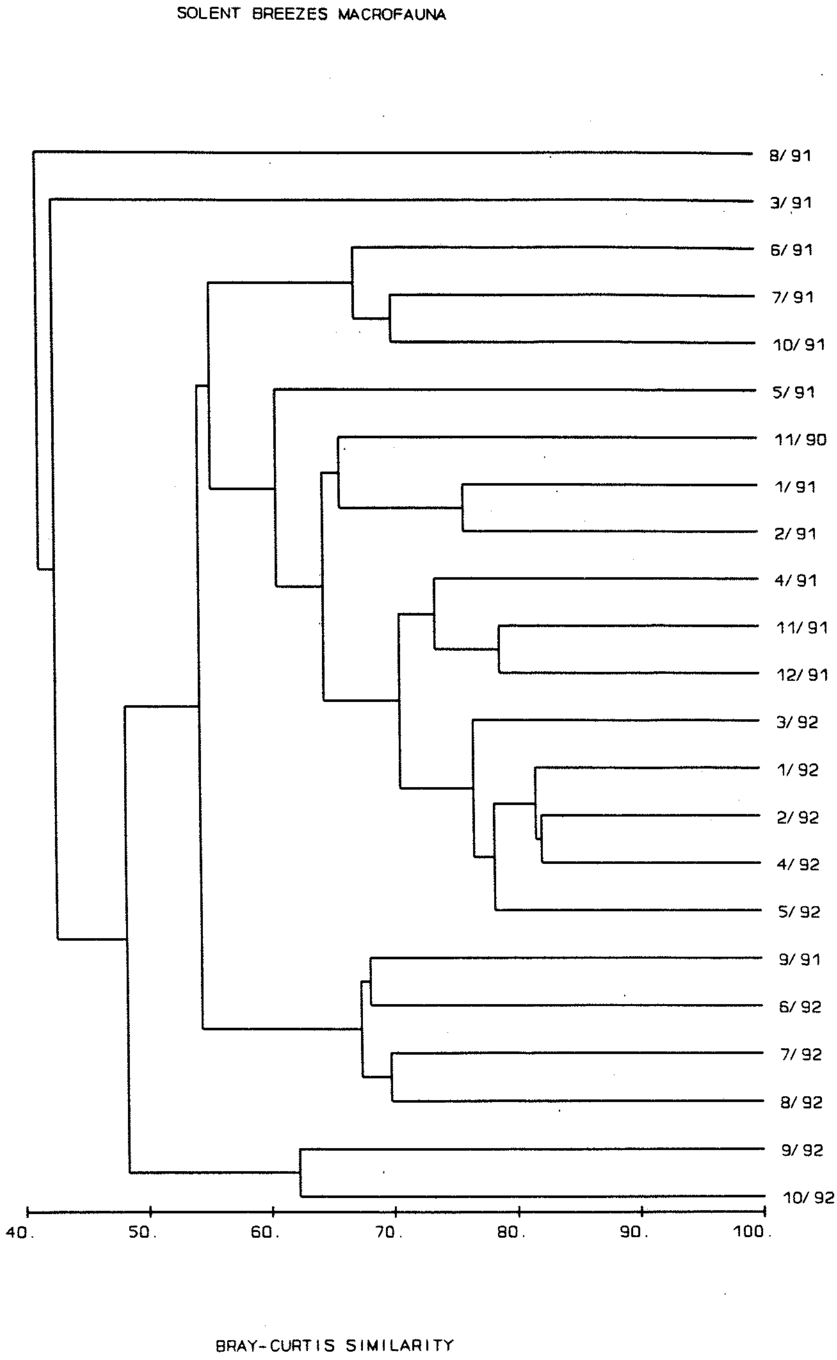


Figure 4.10 Monthly Time Series Macrofauna. Dendrogram constructed for hierarchical clustering of monthly total data sets using group-average linking of Bray-Curtis similarities (untransformed data).

Group 3: Jun 1991, Jul 1991 and Oct 1991

This group contained three months in which *Lanice conchilega*, *Euclymene oerstedii* and *Exogone hebes* were all present in relatively high numbers (n > 100). In addition, the density of *Aricidea minuta* was very similar in all three months, and a number of other species consistently occurred in the top ten species of each dominance rank (i.e. *Pygospio elegans*, *Tanaissus lilljeborgi* and *Spio martinensis)*.

Group 4: Nov 1990-Feb 1991, Apr 1991, May 1991, Nov 1991-May 1992

This group contained a large number of the "more typical" monthly faunal assemblages. Four species were consistently among the ten most dominant species (*Lanice conchilega*, *Euclymene oerstedii*, *Exogone hebes* and *Tanaissus lilljeborgi*). *Lanice conchilega* was the most dominant species in the majority of the months in this group, and *Euclymene oerstedii* was invariably one of the three most dominant species.

Within this group, May 1991 was clustered separately because of the relatively high numbers of *Bathyporeia sarsi* that occurred in this month.

Group 5: Sep 1991, Jun 1992, Jul 1992, Aug 1992

The faunal assemblages in Group 5 were similar to the Group 4 assemblages in many respects. *Lanice conchilega*, *Euclymene oerstedii*, *Exogone hebes*, *Aricidea minuta*, *Pygospio elegans* and *Spio martinensis* were consistently among the ten most dominant species in each of the Group 5 months. However, the presence of *Gammarus locusta* in relatively high numbers ($n \geq 60$) resulted in these months being clustered separately from Group 4.

Group 6: Sep 1992, Oct 1992

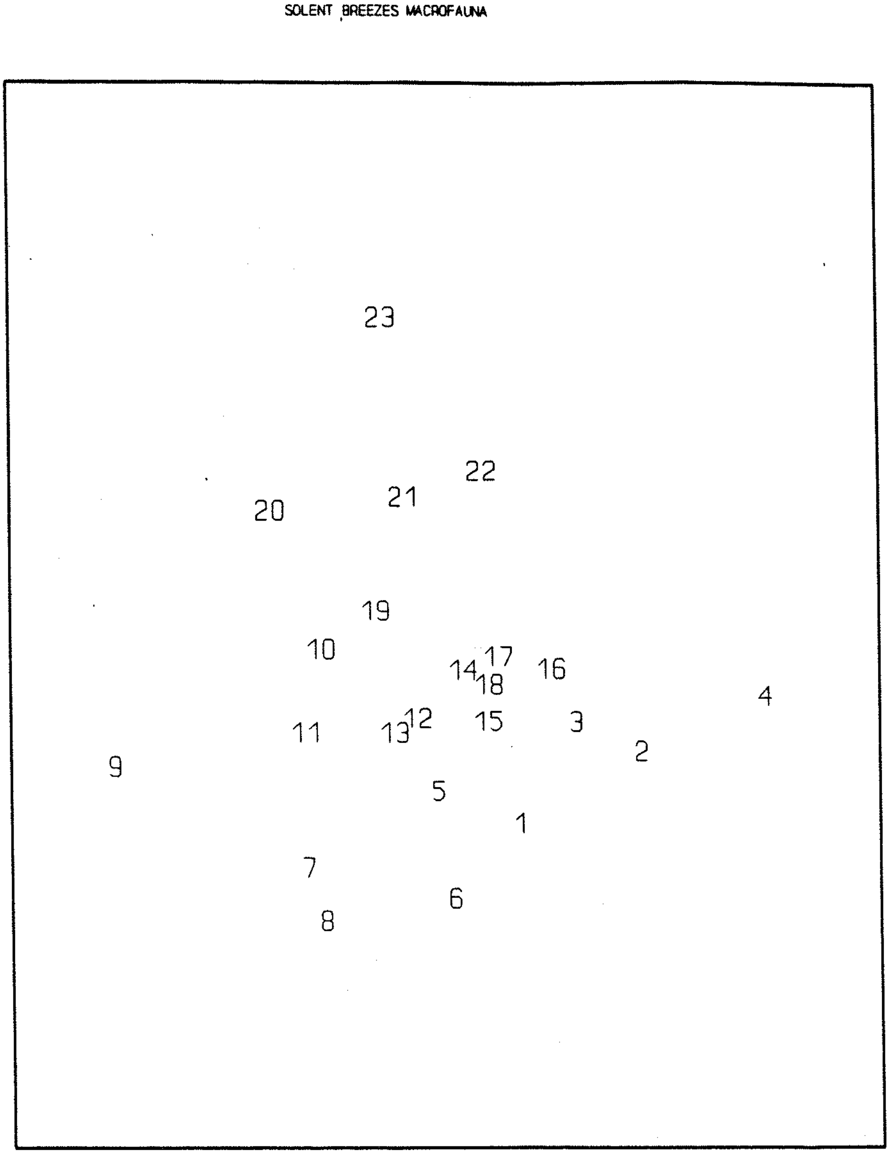
Capitella capitata was the most dominant species in both September 1992 and October 1992. This unique characteristic caused these two months to be clustered together in Group 6. Total numbers of *Lanice conchilega* were also relatively low compared to other monthly totals.

MDS

The similarity matrix used for the cluster analysis described above was also used to produce an MDS plot for the total fauna of the monthly data sets (Figure 4.11). The stress value calculated during the MDS analysis was 0.12, indicating that the ordination provided a useful 2-dimensional representation of the data (Clarke and Warwick, 1994). The MDS analysis re-emphasised some of the patterns of change previously highlighted by the cluster analysis. For example, both August 1991 (i.e. Group 1 of the cluster analysis) and March 1991 (i.e. Group 2) were in isolation on the MDS plot because of the individual characteristics of their respective faunal assemblages.

June 1991 and July 1991 were again grouped closely together, but October 1991 was positioned closer to the main group of "more typical" monthly data sets. The high numbers of *Bathyporeia sarsi* that occurred in May 1991 caused this month to be plotted in a relatively isolated position.

However, the changes that occurred in the fauna towards the end of the sampling period produced a pattern of groupings on the MDS plot that differed from the cluster analysis groups. As a result of the particularly high numbers of *Aricidea minuta* that occurred in July 1992, this month was clearly isolated from adjacent months on the MDS plot. Although *Capitella capitata* was the top dominant in September 1992 and October 1992, differences in the absolute numbers of this and other dominant species caused October 1992 to be plotted in relative isolation. September 1992 was positioned closer to August 1992 despite the actual order of the dominant species in these months being markedly different.



Key:

1 = Nov 90
2 = Jan 91
3 = Feb 91
4 = Mar 91
5 = Apr 91
6 = May 91

7 = Jun 91
8 = Jul 91
9 = Aug 91
10 = Sep 91
11 = Oct 91
12 = Nov 91

13 = Dec 91
14 = Jan 92
15 = Feb 92
16 = Mar 92
17 = Apr 92
18 = May 92

19 = Jun 92
20 = Jul 92
21 = Aug 92
22 = Sep 92
23 = Oct 92

Figure 4.11 Monthly Time Series Macrofauna. MDS plot of Bray-Curtis similarities for the monthly total data sets (untransformed data).

BIO-ENV

The BIO-ENV procedure of the PRIMER analysis programme was used to examine which environmental variables best explained changes in the monthly data sets. The environmental variables used for the analysis are given in Table 4.2. In addition to sedimentary parameters, temperature data and wind speed data, percentage algal cover data was derived from estimations made during each sampling visit. The meteorological variables included in the analysis (i.e. mean temperature, minimum grass temperature and wind speed) were "between sampling" means, allowing conditions before each sampling date to be quantified (see Section 2.2.1).

The single environmental variable that best matched changes in the fauna that occurred during the sampling period was percentage algal cover. The addition of other variables initially decreased the correlation with the faunal similarity matrix, but the maximum correlation occurred with the inclusion of six variables (i.e. grass minimum temperature, inclusive graphic standard deviation, inclusive graphic skewness, graphic kurtosis, silt/clay fraction and percentage algal cover).

The values of ρ_w produced by the BIO-ENV programme were all relatively low and within a restricted range of between 0.427 and 0.477 (cf. values for the transect data shown in Table 3.3). Therefore no single variable or combination of variables was sufficiently able to explain the faunal changes that occurred at Solent Breezes over the sampling period (using the BIOENV analysis procedure).

n	ρ_w	Mean Temp.	Min. Grass Temp.	Wind Speed	Organic Content	Incl. Gr. S.D.	Incl. Gr. Skewness	Graphic Kurtosis	Silt/Clay Fraction	% Algal Cover
1	0.454									*
2	0.427					*				*
3	0.449					*			*	*
4	0.463		*			*			*	*
5	0.473		*			*	*		*	*
6	**0.477**		*			*	*	*	*	*
7	0.47		*		*	*	*	*	*	*
8	0.468		*	*	*	*	*	*	*	*
9	0.463	*	*	*	*	*	*	*	*	*

Table 4.2. Combinations of the nine environmental parameters giving the best matches between the faunal and abiotic similarity matrices (the best single variable being percentage algal cover, the best 2-variable combination being percentage algal cover with inclusive graphic standard deviation, etc.). Correlations were measured using weighted Spearman rank correlation (ρ_w).

The multivariate analyses presented above did not reveal any particularly distinct correlations between the fauna and the abiotic factors considered. However, the presence or absence of macroalgae predictably influenced the numbers of weed associated animals in the samples. High densities of the amphipods *Microprotopus maculatus*, *Atylus swammerdamei* and, in particular, *Gammarus locusta* significantly affected both the univariate and the multivariate analyses. As a result, the cluster analysis, MDS and BIO-ENV were repeated on a reduced data set from which these species had been omitted. In justification for the extraction of *Gammarus locusta*, *Microprotopus maculatus* and *Atylus swammerdamei* it can be argued that these amphipods were not truly infaunal and were only transient members of the shore community at Solent Breezes. The following analyses were therefore conducted to re-examine the changes that occurred in the infaunal community.

Cluster analysis, MDS and BIO-ENV with weed-associated fauna excluded

Figure 4.12 presents the results of the repeated cluster analysis conducted using the PRIMER analysis package. The dendrogram highlights five clusters at the 60% level. The unique characteristics of the faunal assemblage found in March 1991 again resulted in this month being clustered independently from all the other months. June 1991 and July 1991 were again clustered together, but October 1991 returned to the main group of "more typical" months. A significant change did occur in the positions of the data sets of the last four months of the sampling period (i.e. July 1992 - October 1992). These months were clustered separately, probably as a result of increasing numbers of *Capitella capitata.* In addition, samples taken during these months contained relatively low numbers of *Lanice conchilega* and extremely low numbers of *Tanaissus lilljeborgi*.

Within the main group of "more typical" faunal assemblages, three sub-groups were evident. April 1991 and May 1991 were clustered together mainly because of the relatively high numbers of *Bathyporeia sarsi* that occurred in these months compared to all the other months in the group. This grouping occurred despite the fact that May 1991 samples contained substantially more *Bathyporeia sarsi* than April 1991 (the total numbers were 140 and 46 respectively).

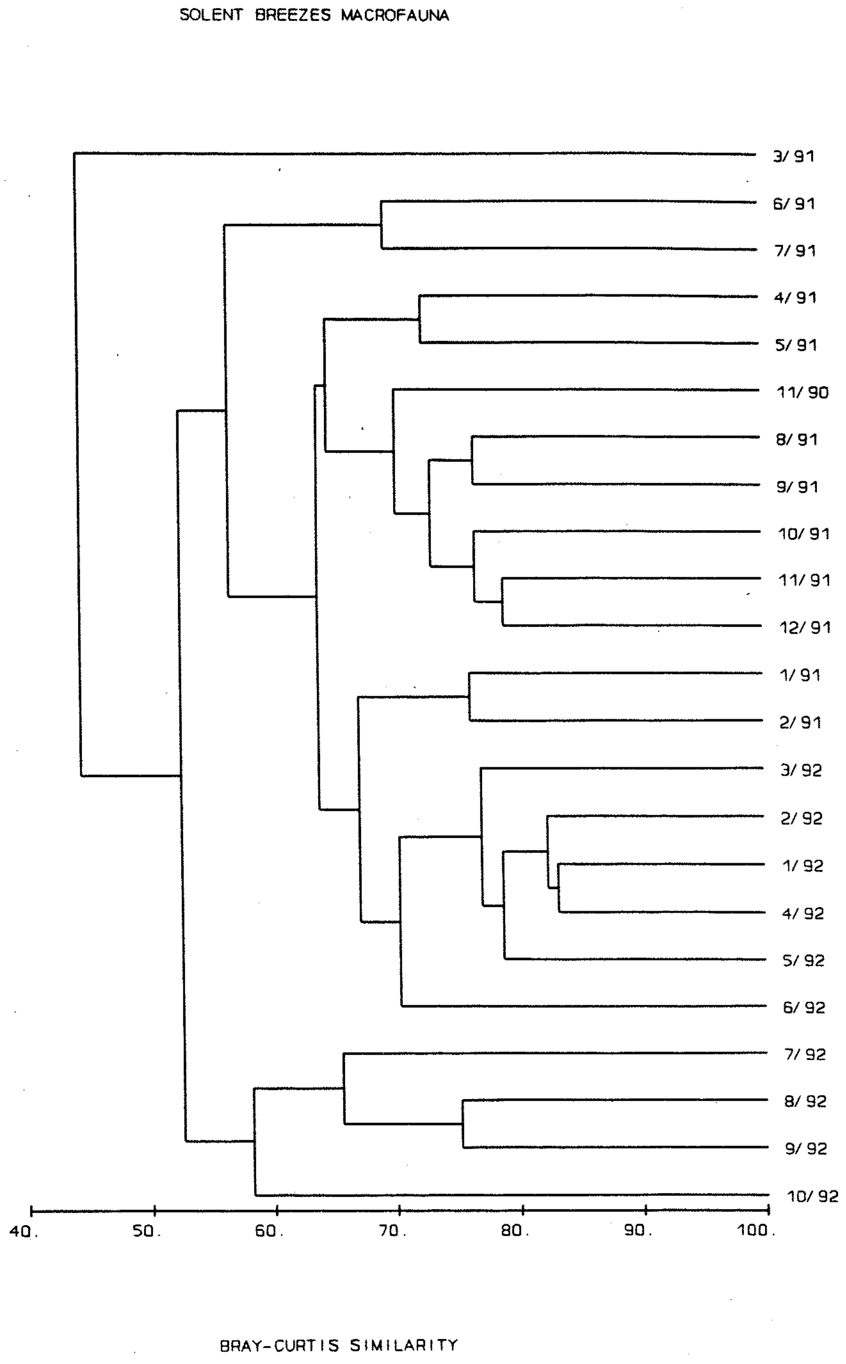


Figure 4.12 Monthly Time Series Macrofauna. Dendrogram constructed for hierarchical clustering of monthly total data sets with the weed associated species *Gammarus locusta*, *Microprotopus maculatus* and *Atylus swammerdamei* removed (untransformed data).

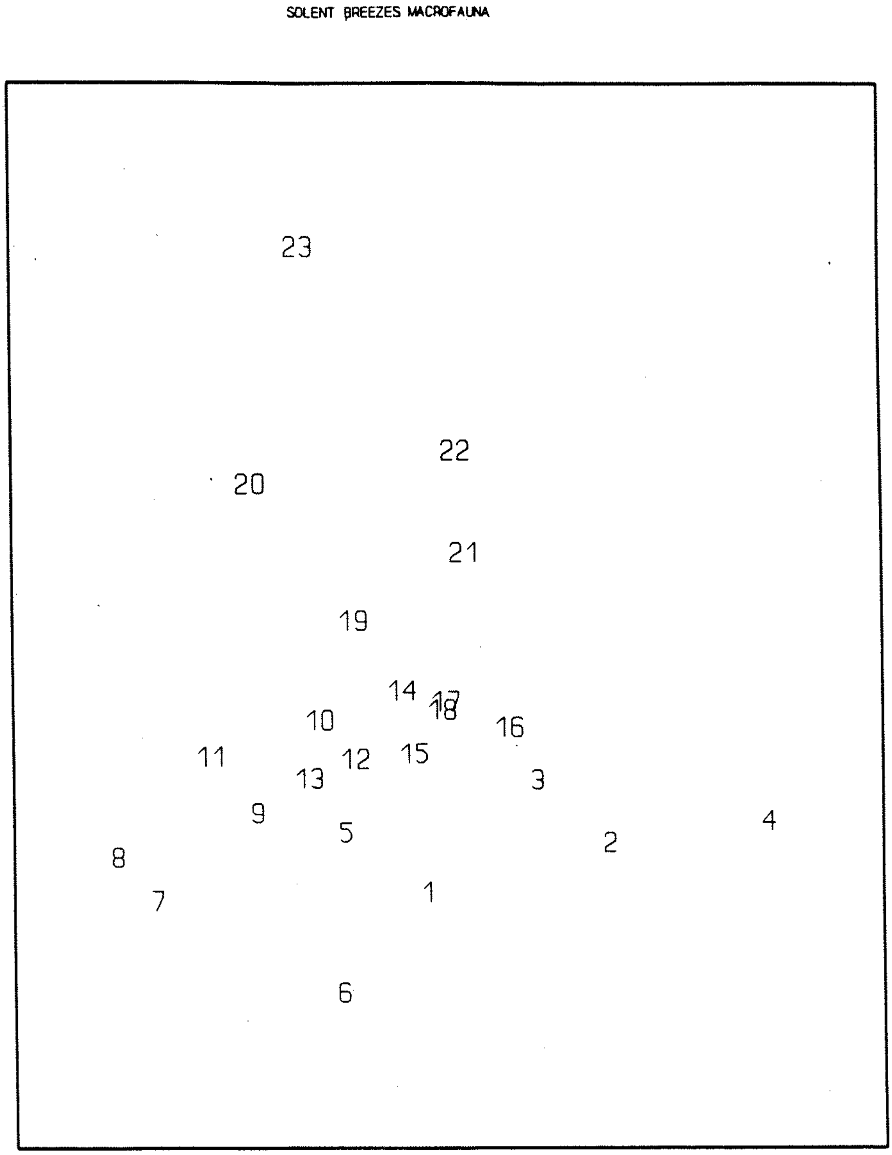


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Figure 4.13 Monthly Time Series Macrofauna. MDS plot of the Bray-Curtis similarities for monthly total data sets with the weed associated species *Gammarus locusta*, *Microprotopus maculatus* and *Atylus swammerdamei* removed (untransformed data).

The second sub-group contained late summer/autumn and early winter months (i.e. November 1990 and August 1991 to December 1991). The third sub-group contained late winter and spring months from 1992 (i.e. January to June) along with late winter months from 1991 (i.e. January and February).

The stress value calculated during the MDS analysis was 0.11, indicating that the ordination provided a useful 2-dimensional representation of the data (Clarke and Warwick, 1994).

The changes that occurred in the fauna over time were again reflected in the MDS plot constructed from the respective similarity matrix (Figure 4.13). In particular, the changes that occurred towards the end of the sampling period and the distinct nature of the October 1992 fauna were highlighted. March 1991 was again placed in isolation, and June and July 1991 were again placed together in a relatively isolated group. In addition, the MDS analysis emphasised the individual nature of the May 1991 data set more clearly than the cluster analysis (caused by the presence of particularly high numbers of *Bathyporeia sarsi* in this month).

The BIO-ENV procedure was also repeated using the reduced data set, but the resulting ρ_w values were markedly lower than those previously shown in Table 4.2. Again, no single variable or combination of variables were sufficiently able to explain the changes that occurred in the infauna over the sampling period.

Principal Component Analysis

The complete species matrix constructed for the monthly time series data contained 115 species. Consequently the matrix needed to be reduced in size by the exclusion of rarer species. Those species that never constituted more than 1% of the total abundance in any sample were removed. The figure of 1% was a fairly arbitary selection, but was much less than the guideline figure of 3% suggested by Clarke and Warwick (1994). This figure also successfully reduced the data set to a manageable size without excluding any of the important dominant species. The resulting species matrix, containing only 35 species, was much more suitable for Principal Component Analysis.

The first two principal components produced by the analysis accounted for 76.3% of the original variation between samples. Spearman rank order correlation was used to examine any relationships that existed between either of these first two principal components and any of the available environmental variables. The first principal component (PC1) explained 56.3% of the variation, and four environmental variables were significantly correlated with this component. Mean temperature, minimum grass temperature and percentage algal cover were all negatively correlated with PC1 ($p < 0.005$). These three seasonal parameters were obviously closely related to each other and were strongly correlated with each other ($p < 0.005$). PC1 was therefore primarily a reflection of the dominant seasonal changes in the fauna that occurred over the two year sampling period. In addition, a single sedimentary parameter (the Inclusive Graphic Standard Deviation) was positively correlated with PC1 ($p = 0.024$). However, this correlation was markedly weaker, and was perhaps more a result of the inverse relationship between the Inclusive Graphic Standard Deviation and the three seasonal parameters.

The second principal component (PC2) explained a further 20.0% of the variation between samples. The Inclusive Graphic Standard Deviation was the only environmental variable that was significantly correlated with PC2 ($p = 0.021$). PC2 was therefore essentially related to the degree of sorting (measured by the Inclusive Graphic Standard Deviation) in the monthly sediment samples taken at Solent Breezes.

As with the previous multivariate analyses, PCA was repeated on a reduced data set from which the weed associated species *Gammarus locusta*, *Microprotopus maculatus* and *Atylus swammerdamei* had been excluded. This allowed changes in the infaunal community to be re-examined in the absence of these transient and essentially epifaunal species.

The first two principal components produced by the repeated analysis accounted for 66.1% of the variation between samples. This percentage was lower than that of the previous analysis, but was still approaching the "acceptable" level given by Clarke and Warwick (1994). PC1 explained 45.9% of the variation and a strong positive correlation existed between PC1 and the Inclusive Graphic

Standard Deviation ($p = 0.009$). No other environmental variables were significantly correlated with PC1. Conversely, PC2 was significantly negatively correlated with the three seasonal variables - mean temperature, minimum grass temperature and percentage algal cover ($p < 0.005$).

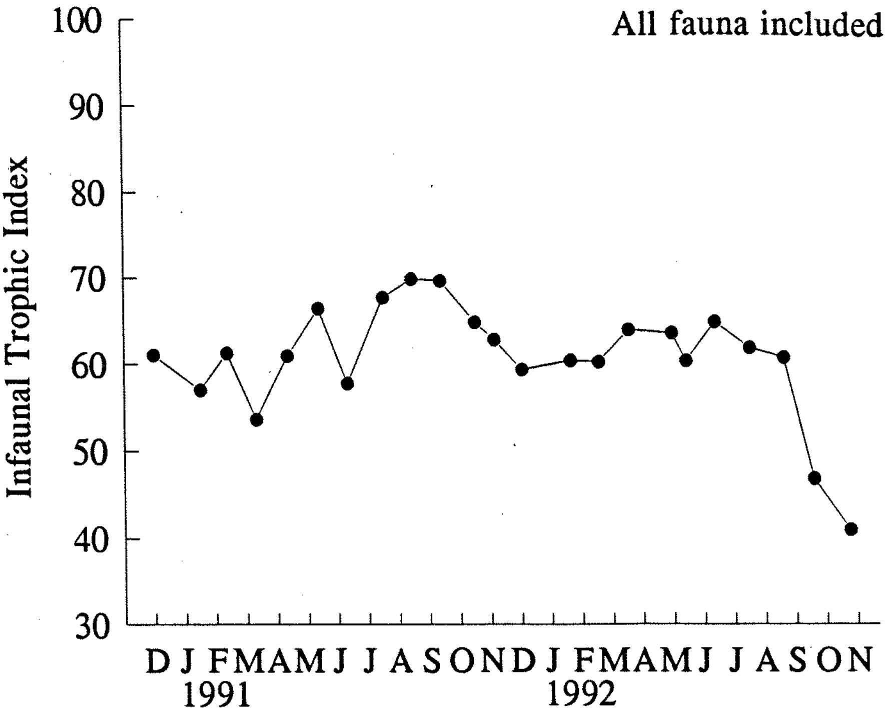
The removal of the weed associated species reduced the relative importance of the seasonal component. Consequently, the level of sorting assumed a more dominant position in relation to the faunal changes that occurred during the sampling period.

4.4.4 Infaunal Trophic Index

Finally, a single value of the Infaunal Trophic Index (ITI) was calculated for each of the monthly total data sets (Figure 4.14; upper graph). The majority of ITI values were greater than 60.0, and the remaining values were between 41.1 and 59.4. Consequently, the faunal assemblages could be classified as either "normal" or "changed". The highest ITI value (70.0) was observed in August 1991, and index values remained above 57.0 for the first 21 months of the study period. Such values indicate the dominance of species feeding on surface detritus.

As the ITI is concerned with infaunal animals, the major weed associated epifaunal species (*Gammarus locusta*, *Microprotopus maculatus* and *Atylus swammerdamei*) were removed from the faunal lists and the analysis was repeated. The ITI values presented in the lower graph of Figure 4.14 therefore give a more accurate representation of the changes that occurred in the infauna over time. The majority of values were between 52.3 and 66.5, again indicating the dominance of species feeding on surface detritus.

Both graphs in Figure 4.14 highlight the decreases in ITI values that occurred towards the end of the sampling period. The faunal assemblages present in samples taken in September 1992 and October 1992 could not be classified as "degraded" (i.e. the ITI values were not less than 30). However, the presence of *Capitella capitata* (trophic group 4) in increasing numbers resulted in ITI values falling considerably.



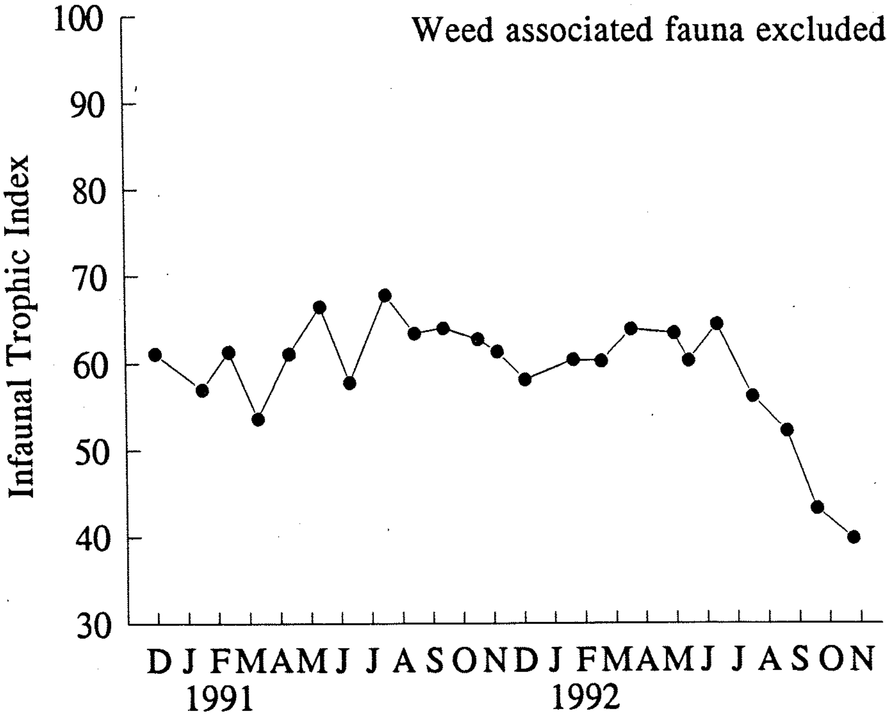


Figure 4.14 Monthly Time Series Macrofauna. Changes in the Infaunal Trophic Index over the two year sampling period, both with and without the weed associated species *Gammarus locusta, Microprotopus maculatus* and *Atylus swammerdamei*.

The use of the Infaunal Trophic Index in the current study highlighted a number of problems associated with its determination and application. Firstly, the allocation of species to trophic groups relies on the availability of accurate literature on feeding modes. Many species can currently only be allocated by referring to generalised descriptions of feeding modes documented for families or genera. Whilst an increasing amount of species specific information is becoming available, the categorisation of some species can be difficult. A further problem arises when a species has more than one mode of feeding (e.g. a surface deposit feeder that is also a facultative suspension feeder). It may be difficult to predict the dominant mode of feeding in such a species in a particular location, which potentially complicates the allocation of its trophic group.

By definition, the ITI only deals with infaunal animals. While it could be argued that mobile epifaunal species are not necessarily permanent members of the faunal assemblage observed in a particular area, their occurrence in samples cannot be dismissed as incidental. The distributions of such species are potentially intimately linked to trophic factors (although other environmental variables may also be important).

Finally, the inclusion of only those taxa contributing the top 80% of the total abundance in the ITI calculation, could lead to a degree of misrepresentation of the overall trophic composition. Hypothetically, all or most of the animals excluded from the calculation could be members of the same trophic group. The inclusion of these taxa could therefore significantly influence the ITI value. Although it could be time consuming or perhaps impractical to include all minor taxa, it must be recognised that collectively these animals may constitute an important trophic component. In addition, taxa that were just outside the top 80% in the dominance ranks constructed for Solent Breezes data sets often contained only 1 or 2 individuals less than those taxa just above the 80% cut off point. Therefore, it would perhaps be more appropriate to include species that constitute more than a certain percentage (e.g. 1%) of the total abundance in the ITI calculation. This would result in only very minor taxa being excluded.

4.4.5 Summary

A comprehensive and accurate list of the fauna at Solent Breezes was compiled during this study. The production of this list was considered to be important because previously published surveys of the intertidal macrofauna within Southampton Water were found to be relatively scarce.

A sequence of monthly samples were taken from the main mid-shore sampling site over a two year period. There was a distinct seasonal pattern in both the number of animals and the number of species occurring during the sampling period. The first winter minimum in faunal abundance was particularly low and a subsequent period of recruitment occurred in many of the dominant species during the summer. In particular, the *Lanice conchilega* population increased dramatically in June 1991 as a result of an influx of young individuals (see also Chapter 5). The dominance of *Lanice conchilega* in June 1991 caused a significant deviation from neutrality to occur in Caswell's V-statistic calculated for this monthly data set. In August 1991 the fauna at Solent Breezes was heavily dominated by *Gammarus locusta*. This dominance again caused Caswell's V-statistic to decrease and also resulted in the lowest mean value of Pielou's evenness (J). The presence of such large numbers of *Gammarus locusta* was attributed to their association with surface macroalgae which was particularly abundant in August 1991.

Multivariate analyses conducted on the monthly time series data highlighted the impact that the weed associated animals had on the characteristics of the fauna at Solent Breezes. Consequently, *Gammarus locusta* and two other weed associated species were removed from subsequent multivariate analyses to allow changes that occurred specifically in the infaunal community to be examined. The multivariate analyses highlighted the following faunal patterns:

(i) Relatively low densities of most species occurred in March 1991;

(ii) Relatively high densities of several of the dominant species occurred in both June and July 1991;

(iii) Distinct changes occurred in the fauna towards the end of the sampling period. In particular, densities of *Lanice conchilega* declined, *Tanaissus lilljeborgi* almost disappeared and the abundance of *Capitella capitata* increased dramatically;

(iv) A large number of "more typical" faunal assemblages were relatively indistinguishable. However, the months within this group of assemblages were separable into a "late summer through to early winter" group and a "late winter to spring" group;

(v) Using the BIO-ENV analysis package, no single environmental variable or combination of variables was sufficiently able to account for the faunal changes that occurred during the sampling period.

(vi) The use of PCA highlighted an important seasonal trend in the faunal community. In addition, faunal changes were related to the degree of sediment sorting. The removal of the weed associated species from the PCA analysis did not eliminate the seasonal characteristics of the fauna, but did reduce their relative importance (i.e. the degree of sorting became the more dominant environmental parameter).

4.5 Discussion

It has been previously suggested in Chapter 2 that the main mid-shore sampling site selected for the two year macrofaunal monitoring programme was physically representative of a large proportion of the intertidal sediment flat at Solent Breezes. Although changes in environmental conditions (primarily sedimentary and hydrodynamic parameters) influenced the fauna both at the top and at the bottom of the shore, the sampling transect further revealed that a relatively consistent assemblage of infaunal species were present across a large part of the mid- to lower-shore region (see Chapter 3). Consequently, the mid-shore infaunal community that was examined in detail during the two year monitoring programme was considered to be representative of a major part of the sediment flat at Solent Breezes. Furthermore, similar expanses of sediment flat existed along much of the adjacent coastline between Hill Head to the south and the mouth of the river Hamble to the north (*pers. obs.*). Therefore, it is suggested that the mid-shore sampling site was also reasonably representative of these similar areas along this coast of Southampton Water.

Holme and Bishop (1980) described the habitat at Solent Breezes as a sheltered, stable sediment flat representative of the sheltered east Solent mainland shores. From a biological perspective, Holme and Bishop's extensive review of the sediment shores of Dorset, Hampshire and the Isle of Wight only included a basic overview of the fauna at Solent Breezes. Three distinct communities were observed in the Solent Breezes area (which included Titchfield Haven and Hill Head). Firstly, a variant of the *Pullastra*-community (as defined by Bishop and Holme, 1980) was observed, in which *Venerupis pullastra* was replaced by the alien species *Mercenaria mercenaria* (Holme and Bishop, 1980; Dixon and Moore, 1987). Some patches of muddy sand contained species characteristic of the *Arenicola*-community (e.g. *Arenicola marina*, *Macoma balthica*, *Cerastoderma edule* and *Nephtys hombergii*), and coarser sands contained high numbers of *Lanice conchilega* (equating to Bishop and Holme's *Lanice*-community). The infaunal survey conducted for the current study clearly confirmed the presence of the *Lanice conchilega* dominated community at the sampling site.

The basic habitat characteristics of the mid-shore area and the dominant species present at the sampling site corresponded to the LGS.Lan biotope description given in the Joint Nature Conservation Committee's MNCR littoral biotope classification guide (Connor *et al.*, 1997). The biotope is described as occurring on moderately exposed, sheltered or very sheltered shores with moderately strong or strong tidal streams. The sediment is characterised as "medium to fine sand which may contain some fines and supports dense populations of *Lanice conchilega*". Eight of the nine characterising species listed by Connor *et al.* (1997) for this biotope occurred at Solent Breezes. The only characterising species of the LGS.Lan biotope that was not recorded at Solent Breezes (i.e. *Macoma balthica*) was also the only one described by Connor *et al.* as being typically "rare" in abundance for this particular biotope.

The biotope itself is recognised as being "uncommon" in Britain, and Solent Breezes can be added to the short list of areas in which the biotope has already been recorded (see Connor *et al.*, 1997). However, it must be noted that an admixture of gravel and shell fragments was present in subsurface layers. The depth of this admixture and the depth of the bedrock clay varied across the region, but both were generally at least 10cm below the sediment surface (see Chapter 2).

The first tentative compilation of a faunal list for the shores of Southampton Water was made by Barnes (1971). A total of 93 species were listed for the entire region, many of which were epifaunal (e.g. sponges, hydrozoans and anthozoans) and a number of which were actually recorded sublittorally (in particular the Decapoda). The list included only 19 polychaete species, 14 crustacean species (including 4 amphipod species) and 24 mollusc species. The fauna of the muddy intertidal regions was dominated by molluscs and polychaetes, but species richness was comparatively low compared to the sandier regions towards the mouth of Southampton Water (Barnes, 1971).

Covey (1998) has recently summarised the biological studies that have been conducted in the Solent region. Within Southampton Water, much of the research has concentrated on individual species such as *Ostrea edulis*, *Mercenaria mercenaria*, *Crepidula fornicata* and wood-boring mollusc species, or has been centred on specific groups of animals (see Covey (1998) for details). The subtidal areas of Southampton Water have been extensively surveyed, but work on the sedimentary shores of Southampton Water since Barnes (1971) has been localised and sporadic (Lauriston, 1977; Bamber and Stockwell, 1988). The scale and intensity of the sampling programme undertaken for the current study generated a comprehensive list of the infaunal species at Solent Breezes, including almost 60 polychaete species and over 20 amphipod species. Although Solent Breezes is situated towards the mouth of Southampton Water, the list is a useful addition to current knowledge.

Intertidal research in other areas of the Solent has included several macrofaunal beach surveys - both on the mainland and on the north coast of the Isle of Wight. Withers and Thorp (1978) investigated the fauna of three sandbanks in Langstone Harbour, and recorded a total of 49 species. The fauna was dominated by psammophilous species (e.g. *Ophelia rathkei*, *Scoloplos armiger*, *Bathyporeia* spp., *Urothoe poseidonis*, *Nephtys hombergii* and *Nephtys cirrosa*), and most of these and many other species were consistent with species found at Solent Breezes.

Similarly, Withers (1979) described the macrofauna of beaches at Ryde and Bembridge, Isle of Wight. Over half of the 62 species recorded at these two sites were also present at Solent Breezes. The fauna at Ryde Sands was most similar to that at Solent Breezes, being dominated by *Lanice conchilega* and containing 13 of the 15 dominant species listed here in Table 4.1. The only two dominant Solent Breezes species that were absent from the fauna recorded at Ryde were *Exogone hebes* and *Streptosyllis websteri*. The absence of these two small syllid polychaetes from the Ryde fauna was likely to have been a consequence of the larger mesh size that was used to sieve the samples (i.e. 1mm).

More recently, Herbert (1991) listed the fauna and flora of the intertidal zone at Osborne Bay, Isle of Wight. Again, many of the polychaete and crustacean species collected from across the sandy shore coincided with those regularly recorded at Solent Breezes (e.g. *Nephtys cirrosa*, *Scoloplos armiger*, *Pygospio elegans*, *Spio martinensis*, *Euclymene oerstedii*, *Lanice conchilega*, *Microprotopus maculatus* and *Urothoe poseidonis*).

Although the data sets referred to above inevitably shared many species both with each other and with the Solent Breezes data set, none of the beaches under investigation corresponded exactly to Solent Breezes either physically or faunistically. The species list compiled for Solent Breezes was considerably longer than those documented for the other beaches. However, it must be remembered that the other studies all produced single point-in-time data sets for their respective localities. The longer-term nature and the shear scale of the Solent Breezes study resulted in a greater number of relatively rare species being detected.

One other long term study of intertidal macrofauna has been conducted within the Solent region. Bamber (1993) analysed the changes that occurred over a four year period in the infaunal community of a clean sandy beach at Stanswood Bay, Hampshire. The psammophilous infaunal community was composed of 54 species, dominated by peracarid crustaceans and polychaetes. All of the dominant infaunal species at Solent Breezes were also present at Stanswood Bay, but patterns of dominance were markedly different at the two sites. Differences in the physical characteristics of the two sites were clearly reflected in the fauna. Several species that were present at Stanswood Bay, but absent from Solent Breezes, are more typical of cleaner sandy substrates (e.g. *Megaluropus agilis* and *Scolelepis foliosa*). Amphipod species were much higher in the dominance rank at Stanswood Bay: *Bathyporeia sarsi* was the top dominant and two of the next three dominant species were amphipods. Notably, the third most dominant species at Stanswood Bay (i.e. the amphipod *Perioculodes longimanus*) was not found at Solent Breezes. Conversely, polychaete species were less dominant at Stanswood Bay: *Lanice conchilega* was the eleventh dominant and the total number of polychaete species (i.e. 22) was much lower (Bamber, 1993).

The assemblage of infaunal species occurring on a particular shore is strongly influenced by the prevailing physico-chemical environment. Species richness and overall faunal abundance tend to increase with decreasing exposure and increasing sediment stability (Allen and Moore, 1987; Raffaelli and Hawkins, 1996). Average particle size usually increases with increasing exposure and a correlation is often found between faunal characteristics and particle size (Allen and Moore, 1987; Brown, 1971; Eleftheriou and Nicholson, 1975). Furthermore, finer sediments are generally associated with higher concentrations of organic detritus (see Chapter 2). Consequently, the fauna on more stable shores is usually dominated by deposit feeding, often sedentary species; while in more exposed areas mobile crustaceans and errant worms predominate (e.g. Allen and Moore, 1987; Withers, 1977).

Within the Solent, a wide range of intertidal habitats occur, with a variety of associated faunal assemblages. Being situated towards the mouth of Southampton Water, the physical characteristics of the shore at Solent Breezes were intermediate between the more sheltered upper reaches of Southampton Water and the more exposed shores of the Solent proper. These intermediate physical characteristics were reflected in the fauna. The 15 most dominant species at Solent Breezes have been described in some detail in a previous section (Section 4.4.2). The majority of the species were either surface or sub-surface deposit feeders, and many were sedentary to some degree. However, the list of dominant species also included three errant polychaetes (*Exogone hebes*, *Nephtys hombergii* and *Streptosyllis websteri*) and the mobile amphipod crustacean *Bathyporeia sarsi*.

The macrofaunal monitoring programme described in this chapter has highlighted a certain level of temporal stability in the infaunal community at Solent Breezes. A large number of monthly data sets were faunistically similar, although these were separable into two seasonal groups. In addition to the seasonal trend, several other important changes occurred in the infaunal community during the sampling period. All these changes have been outlined in Section 4.4.5, and are discussed in more detail below.

Firstly, faunal abundance and diversity were both particularly low in March 1991. These observed minima were likely to have been a result of the relatively harsh environmental conditions that prevailed during the winter of 1990-1991. The low air and seawater temperatures recorded in February 1991 have been discussed previously in Chapter 2. Minimum temperatures were particularly low compared to minima in the subsequent three years and the preceding two years. Furthermore, a re-examination of the raw temperature data revealed that the period of particularly cold weather that occurred before the February 1991 sampling date also continued for ten days after the sampling date before temperatures began to rise. The full impact of the cold temperatures may therefore have only become clear on the March 1991 sampling visit.

Cold winters have previously been observed to affect densities of benthic species in several other coastal regions. In particular, the effects of the extremely severe winter of 1963-1964 have been well documented (Crisp, 1964; Newell, 1964), and the sensitivity of certain species to extremely cold conditions has been frequently noted (e.g. Beukema, 1979; 1985; 1990). Intertidal macrofauna may also move offshore as an active response to low temperatures in winter (Beukema and De Vlas, 1979; Dean, 1978). During periods of emersion, the top layers of intertidal sediments can be exposed to extreme temperature fluctuations. Although the sampling site at Solent Breezes was covered by seawater during a large part of each tidal cycle, the cold air temperatures and the associated cold seawater temperatures are likely to have had an adverse effect on the fauna. Physiological stress imposed on individual species may have resulted in reduced population densities and consequently lowered the overall abundance.

The low diversity recorded in March 1991 was mainly a result of a reduction in species richness rather than a change in equitability. Species richness was lowered as an increased number of relatively rare species were lost, while the evenness component of diversity remained comparatively high. Winter temperatures have previously been shown by Buchanan and Moore (1986) to exert a clear influence on diversity. Long-term biannual sampling of an offshore muddy sand community revealed a strong correlation between winter temperature and Shannon-Weiner's diversity index in March samples. Relatively cold winters favoured survival in the dominant species at the expense of the lesser ranked species (Buchanan and Moore, 1986).

Low winter temperatures have also been observed to enhance subsequent recruitment (Möller, 1986; Beukema, 1982, 1985). A long term study of tidal flats in the Dutch Wadden Sea revealed that high levels of abundance occurred in several dominant polychaete species and four important bivalve species following a severe winter in 1978-1979 (Beukema, 1985). Although the present Solent Breezes study was only conducted over a relatively short two year period, the overall abundance of fauna was markedly higher during the first year following the comparatively cold winter of 1990-1991. In fact, eleven of the fifteen dominant species at Solent Breezes reached their maximum densities during the spring or summer of this first year. The difference between the two annual levels of recruitment was particularly marked in *Lanice conchilega*. Details of the *Lanice conchilega* population are addressed later in Chapter 5, but it is useful to note here that the level of juvenile recruitment in the spring/summer of 1991 was approximately fifteen times greater than the level of recruitment in 1992.

A second mechanism exists that may have resulted in the relatively low faunal abundance and diversity observed in March 1991. Distinct changes occurred in the sedimentary environment at Solent Breezes during the 1990-1991 winter. Whereas the surface sediment at the mid-shore sampling site was generally well sorted with a silt/clay fraction of less than 5%, in February 1991 the sediment was only poorly sorted and in March 1991 it was only moderately sorted (see Chapter 2). Large inputs of refractory organic matter and fine particles were detected in surface sediments during these two months, and it has been previously suggested that the source of this material was the sub-surface clay layer (see Section 2.4.2).

The precise nature of the disturbance events that caused these sedimentary changes remains undetermined. However, the changes would be consistent with a mixing of lower sediment layers into surface layers and a degree of erosion of the underlying clay caused by increased wave action. The available meteorological data provided no direct empirical evidence of any major storm events during the relevant period. To significantly increase the level of wave action at the sampling site, prevailing strong winds would need to have been from the appropriate direction (i.e. onshore) and would need to have occurred during periods of immersion. Unfortunately, the direction and timing of any strong winds could not be established from the available average wind speed data. However, the possibility remains that increased levels of physical disturbance occurred as a result of harsh weather conditions.

The distribution and abundance of fauna in shallow soft sediments are both strongly influenced by wave action, and consequently physical disturbance plays an important part in community dynamics. The effects of storms on benthic populations have previously been inferred simply from observations made before and after a storm or period of storms (Hall, 1994). The impacts of storm events are obviously more intense in intertidal and shallow subtidal regions than in deeper waters. Oliver *et al.* (1980) showed that the fauna living in high energy shallow waters (< 14m) off the coast of California was dominated by small mobile crustaceans and few animals lived in permanent tubes or burrows. In comparison, the deeper water communities were dominated by polychaetes living in permanent or semi-permanent tubes or burrows (Oliver *et al.*, 1980). The authors concluded that increased wave-induced disturbance in shallower areas had resulted in the observed faunal distributions. They also observed that the polychaete populations that did occur at one particular shallow site were heavily depleted by a period of particularly intense wave action during winter. In a similar way, the infaunal community inhabiting the relatively sheltered shore at Solent Breezes could arguably be particularly susceptible to any increase in wave-induced disturbance.

Eagle (1975) recorded dramatic variations in subtidal faunal abundance during periods of severe storms in Liverpool Bay, UK. In particular, populations of the three dominant species, *Abra alba*, *Lagis koreni* and *Lanice conchilega* were markedly depleted, and it was suggested that these species were washed out by increased levels of wave action. Observations made by Rees *et al.* (1977) in the same region have suggested that similar processes occurred in the low intertidal zone.

The passive transport of the adults of various polychaete species by waves and tidal currents has been studied by Tamaki (1987). Distributional changes in one species during winter were attributed to its habit of living in near surface sediments and its inability to attach to larger particles to avoid washout. Species living deeper below the surface were less susceptible to washout and some species could anchor themselves by coiling their abdomen. It seems likely that many species may develop morphological and behavioural adaptations to decrease the probability of storm washout.

The defaunation of the shore at Solent Breezes during the winter of 1990-1991 was by no means complete, and was not necessarily caused by a single disastrous disturbance event. Nevertheless, some principles of post-disturbance recolonisation as applied to heavily or completely defaunated sediments remain relevant. The recolonisation of disturbed sediments and the successional changes that follow have been intensively studies (e.g. McCall, 1977; Dauer and Simon, 1976; Woodin, 1981; Zajac and Whitlatch, 1982a, 1982b). To survive in a particular environment, individual species must be able to resist or recover from disturbances, however infrequently they occur. Recovery of a population can occur through direct recolonisation by adults or through the settlement and development of juveniles.

Rapid recolonisation of a naturally defaunated intertidal site by adult polychaetes has previously been observed by Dauer and Simon (1976). This process of recolonisation was not unexpected as the distributions of many intertidal polychaete species extend well into the subtidal zone. The mechanisms involved in the recovery of faunal abundance at Solent Breezes after March 1991 may also have included some migration of adults from subtidal populations. An entirely separate sampling programme would need to have been conducted alongside the macrofaunal sampling programme to assess the relative importance of adult migration and juvenile recruitment during this period. Such a programme would have been similar to that used to study the temporary meiofauna (i.e. the juveniles of macrofaunal species) at Solent Breezes during 1993 and 1994 (see Chapter 7). However, it was impractical to run these two types of sampling programme concurrently.

It has already been noted that the large increase in abundance of *Lanice conchilega* during the spring and early summer of 1991 was predominantly caused by juvenile recruitment (see also Chapter 5). The maximum densities observed in many of the other dominant species during this period were also likely to have been a result of significant juvenile recruitment.

Barry (1989) described the ability of a tube dwelling sabellid polychaete population to recover from severe disturbance. Individuals responded to disastrous wave-induced disturbance by releasing gametes, thus maximising reproductive effort when their own survival was under threat. Recruitment in this species was related to wave power, with a lag of up to 5 months between the occurrence of storm events and the subsequent peak in recruitment. Although the peak in faunal abundance at Solent Breezes during 1991 can only be compared directly to a single subsequent annual maximum, it is possible that recruitment levels in the spring and summer of 1991 were relatively high as a result of increased levels of disturbance during the preceding winter.

The established view among soft-bottom ecologists is that some species are benefitted by a disturbance while others are not. A rapid increase in the population density of an opportunistic species after a disturbance is considered to be a result of a release from competition or an increase in food availability. However, responses to disturbance vary considerably both within and between species. Zajac and Whitlatch (1982a) showed that responses to disturbance by some estuarine species varied significantly both seasonally and with respect to estuarine position. Some so-called opportunistic species reacted differently to disturbance at different times of the year, exhibiting opportunistic responses in only 1 or 2 months. In addition, groups of species with different life-history characteristics may respond differently depending on their population dynamics at the time of a disturbance (Zajac and Whitlatch, 1991). Therefore, the timing of a disturbance, as well as the nature of a disturbance, will influence the course of subsequent succession.

It is unclear whether the distinct changes that occurred in the fauna at Solent Breezes towards the end of the sampling period were caused directly by a concurrent disturbance. It is possible that a single disturbance event, a series of discrete disturbances, or a more continuous period of disturbance or change exerted an influence on the fauna. However, the standard analytical methods used in this study did not detect any major changes in the sedimentary environment during the final 2-3 months of the sampling period. Physical sedimentary parameters remained relatively stable, apart from the silt/clay content which increased in October 1992. The organic content remained relatively low compared to the significant increases detected during the winter of 1991, and no extraordinary temperature or salinity changes were observed. Clearly a disturbance may have occurred in the physico-chemical environment that was not detected by the standard analytical techniques used. For example, organic matter generally includes a relatively small proportion of bioavailable protein, and the gross measurement of total organic content does not necessarily give a good indication of the amount of potential food items available to deposit feeders (see Chapter 2).

It is therefore conceivable that the levels or types of food resources present within the sediment may have changed prior to or during the last few months of sampling. Any such change would have the potential to affect different species in different ways, thus disrupting the overall composition of the species assemblage.

A disturbance in the form of an organic or inorganic chemical pollutant would also not necessarily have been detected by the standard methods used. The threat of chemical pollution is very real in heavily industrialised estuaries such as Southampton Water. However, the characterisation of such a potential disturbance is beyond the scope of this study, and the hypothetical impacts of an unknown chemical pollutant cannot be speculated upon.

The different roles played by different biological processes in the organisation of soft-sediment infaunal communities are not clearly established (Peterson, 1979; Wilson, 1991b). The effects of epibenthic predators such as birds, fish, gastropods, crabs and other crustaceans have been examined in a multitude of published experiments. The exclusion of epibenthic predators from areas of sediment often results in increases in faunal abundance and biomass. However, a controlling influence is not always exerted by these predators over infaunal densities and there is a significant degree of variation between results, both within and between different habitat types (see Olafsson *et al.*, 1994; Wilson, 1991b for reviews). In addition, predator manipulation experiments are widely distrusted because of the potential hydrodynamic anomalies caused by the cages used to either exclude or enclose predatory species. Nevertheless, the potential impact of large numbers of epibenthic predators cannot be ignored.

Many shorebirds feed on the invertebrate fauna of beaches and tidal flats during low tide and their feeding rates can be remarkable. Some species may seriously deplete population densities of particular prey species (e.g. *Corophium*, Goss-Custard *et al.*, 1977). The impact of shorebirds is also likely to be higher in autumn and winter when shorebird densities are highest and levels of production in prey species are relatively low (Schneider, 1985). During periods of immersion, fish and mobile crustaceans feed extensively on intertidal invertebrates (e.g. Raffaelli *et al.*, 1990). High densities of shrimps, prawns, crabs, flatfish and gobiid fish may use beaches and tidal flats as nursery grounds, consuming large numbers of infaunal animals (Raffaelli and Hawkins, 1996). The diets of plaice and flounder have been found to reflect the composition of the benthic fauna in tidal flat areas, although only parts of individual prey animals may often be cropped, which can subsequently be regenerated (DeVlas, 1979; 1981).

The potential effects of epibenthic predators will vary temporally and spatially, and the level of influence exerted on a prey population will depend on both the type and the intensity of the predation involved. In addition, different prey species will react differently to predation, particularly if the predation only involves the cropping of body parts (e.g. siphons of bivalves, tentacles, tails or heads of polychaetes). For example, experimental removal of portions of polychaetes has been shown to result in decreased defecation (proportional to feeding) and tube-building activity (Woodin, 1984).

Accurate quantification of epibenthic predation at Solent Breezes would have required the use of carefully designed exclusion experiments supported by gut content analyses and laboratory experiments. However, a number of suggestions can be made concerning the possible impacts of epibenthic predation on the infauna. Firstly, the decrease in *Lanice conchilega* abundance towards the end of the sampling period could have been a result of predation. Cropping of the tentacles or the head region of *Lanice conchilega* would severely damage or destroy its ability to feed and rebuild its tube. Such damage to individuals may have lead to an increased level of mortality in a population unless rapid regeneration and recovery could be achieved. Clearly, the potential impact of predation on surface deposit feeders such as *Lanice conchilega* with exposed appendages above the sediment surface would be greater than the impact on head down deposit feeders or species living deeper below the surface. Furthermore, *Lanice conchilega* is a recognised component of the diet of demersal fish (DeVlas, 1979; 1981), and gut content analyses have suggested that *Lanice conchilega* worms may also be extracted whole from their tubes by predatory fish, leaving the tubes behind in the substratum (Eagle, 1975).

Another important characteristic of the faunal changes that occurred during the final three months of the present study was the steady increase in the abundance of *Capitella capitata*. This opportunistic species is a tube building burrower that is positioned with its tail projecting above the sediment surface. The loss of a tail section through cropping would arguably be less detrimental to a polychaete than the loss of a head section, as this would not inhibit its ability to feed during any recovery period. Tail regeneration in *Capitella capitata* is rapid, although the allocation of resources to regeneration may affect fecundity (Hill *et al.*, 1988). In addition, laboratory experiments have illustrated the high regeneration capacity of *Capitella capitata* (Bonsdorff and Pearson, 1997). Predation by the epibenthic decapod *Crangon crangon* was observed to be largely in the form of tail cropping, and although both predation and physical disturbance were shown to significantly affect population density, recovery rates were rapid. If epifaunal predation was an important controlling factor affecting the infauna at Solent Breezes towards the end of the sampling period, the ability of *Capitella capitata* to recover from predation, alongside its tendancy to proliferate in stressful environments, may have resulted in the steady increase observed in its population density during this period.

The effects of predation by infaunal species have been investigated relatively infrequently, but there is evidence to suggest that infaunal predators can greatly influence community structure (Wilson, 1991b). Direct interactions undoubtedly occurred between the infaunal polychaete predators at Solent Breezes and their respective prey species, and the presence of these predatory species (e.g. Nereididae, Nephtyidae and Phyllodocidae) would have inevitably affected the prey populations in some way. However, accurate quantification of these effects would again have required the use of carefully designed exclusion experiments supported by gut content analyses and laboratory experiments.

The most abundant infaunal predators at Solent Breezes were nephtyid polychaetes (mainly *Nephtys cirrosa* and *Nephtys hombergii*). *Nephtys* species are known to feed on small polychaetes (e.g. Clark, 1962), but may also utilise benthic microalgae as an alternative food source (Warwick *et al.*, 1979). Schubert and Reise (1986) have demonstrated *Nephtys hombergii* to be an important infaunal predator in the tidal flat sediments of Königshafen in the northern Wadden Sea. Experimental increases in *Nephtys hombergii* density were shown to cause significant declines in two prey polychaete species (*Scoloplos armiger* and

Heteromastus filiformis). The impact of the predatory behaviour of *Nephtys hombergii* on these prey populations was mainly inferred from enclosure experiments using elevated densities of relatively large specimens of *Nephtys hombergii* (mean lengths between 60 and 120mm). In addition, the natural population of *Nephtys hombergii* at Königshafen contained relatively high numbers of large individuals (mean length 64mm; largest individual 190mm). Although the sampling methods used at Königshafen and Solent Breezes were different, the nephtyid population present at Solent Breezes was made up of much smaller individuals (the majority of worms sampled at Solent Breezes were less than 20mm in length). Nevertheless, these relatively small worms are still likely to have exerted a controlling influence on other fauna.

Bamber (1993) suggested that the appearance and increase in abundance of *Nephtys cirrosa* may have significantly influenced the structure of the infaunal beach community at Stanswood Bay, Hampshire. He argued that the long term development of a dense population of *Nephtys cirrosa* caused a decline in some species through predation. In comparison, there were no significant increases or decreases in the density of nephtyids (or any other predatory species) at Solent Breezes during the sampling period. It is therefore unlikely that any of the major temporal changes that occurred in the Solent Breezes fauna were directly related to infaunal predation.

The ways in which competitive interactions influence species distributions and abundance in infaunal communities are poorly understood. The three dimensional nature of soft sediments reduces the frequency of direct competitive encounters between infaunal animals. Direct interactions are most often found between closely related species that usually live at similar depths in the sediment (Wilson, 1991b). For example, Grant (1981) demonstrated direct interactions between the haustoriid amphipods *Acanthohaustorius millsi* and *Pseudohaustorius caroliniensis*. At high densities, the two species became vertically separated, with *Pseudohaustorius caroliniensis* being forced to occupy deeper, more anoxic layers. Similarly, Croker and Hatfield (1980) examined the relationships between *Acanthohaustorius millsi* and *Haustorius canadensis*, arguing that biological interactions were important in affecting the relative distributions and abundance of these two species. Interference interactions have also been observed in dense aggregations (>100 000m^{-2}) of tube building polychaetes by Levin (1982). The spionid *Pseudopolydora paucibranchiata* was shown to interact aggressively with two co-occurring species (*Streblospio shrubsolii* and *Fabricia limnicola*), resulting in a loss of foraging time for the latter two species. These direct interactions are most likely to occur in extremely dense assemblages occupying a large proportion of the sediment, where feeding areas overlap and appendages of adjacent animals are likely to come into contact with each other.

At Solent Breezes, mean faunal densities were consistently below 8 000m^{-2} and the maximum density in a single core sample was equivalent to 12 400m^{-2} (both of these figures include transient epifaunal species such as *Gammarus locusta*). At such densities, direct intra- or inter-specific interference would have occurred relatively infrequently among small or less abundant species. However, it is possible that *Lanice conchilega* influenced other species through direct interactions because of its relatively large size and its relatively high abundance. In particular, newly settled or emerging juveniles were potentially at risk from predation by *Lanice conchilega.* Chapters 6 and 7 discuss interactions between *Lanice conchilega* and the other fauna at Solent Breezes in more detail.

In benthic communities dominated by deposit feeders in relatively low numbers, competition is more likely to occur through the indirect mechanism of exploitation of food resources. There is a growing body of evidence to suggest that food supply to the benthos is fundamentally important in determining many of the biological characteristics of infaunal communities (Olafsson *et al.*, 1994). In addition, comparisons between natural food levels and artificially enhanced food levels suggest that benthos is food-limited under natural conditions (e.g. Grémare *et al.*, 1989; Levington and Bianchi, 1981). Benthic deposit feeders are adapted to satisfy their nutritional requirements from the organic material present in ingested sediments. However, sedimentary organic material is very heterogeneous and the characterisation of the different food resources used by different deposit feeders is far from complete (Lopez and Levington, 1987; Lopez *et al.*, 1989). Olafsson *et al.* (1994) recently examined the laboratory experiments that have analysed the effects of varying food levels on soft-sediment invertebrates. They concluded that there was a strong indication that both individual growth and reproductive output are sensitive to food levels, but the survival of adult benthic invertebrates is relatively insensitive to food supply.

It has already been suggested that any temporal changes in the food resources present within the sedimentary environment at Solent Breezes may have influenced different infaunal species in different ways. Although there may be a variety of potential food resources in the detrital pool of a sediment, the physiological, morphological and behavioural characteristics of a particular deposit feeding species may restrict what proportion of these resources is utilised. In addition, deposit feeders are totally dependent on their diet for the provision of certain essential nutrients that they cannot synthesise themselves (Phillips, 1984). Consequently, growth and reproduction may be limited by the availability of these essential macro-nutrients (e.g. carbon, nitrogen) or micro-nutrients (e.g. amino acids, fatty acids, vitamins). For example, Marsh *et al.* (1989) demonstrated that micro-nutrients (in particular some amino acids) described growth rates in *Capitella* sp. 1 better than macro-nutrients. Similarly, Grémare (1994) demonstrated that micro-nutrients are probably primarily responsible for the nutritional limitation of reproduction.

Although the physiology of adult invertebrates allows a reduction in growth and fecundity to maximise survival during periods of insufficient food, the higher weight-specific metabolic demands of juvenile animals may increase their vulnerability to starvation (Tenore and Chesney, 1985). A number of studies have indicated that food shortage is responsible for mortality in the juveniles of benthic species (see Olafsson *et al.*, 1994). Issues related to the settlement and survival of juveniles are addressed in more detail in Chapter 7. For the purposes of the current discussion it is sufficient to identify the important role that food limitation soon after settlement may play in regulating infaunal densities.

The gross measurement of total organic content used in the present study did not allow any changes in specific food resources to be monitored. Accurate quantification of these changes and their consequences for the infaunal populations at Solent Breezes would have required detailed identification and biochemical analysis of potential food items, along with bioassays (measurements of growth and reproduction) of individuals species. It is conceivable that different components of the total organic content fluctuated independently on a temporal basis, even when the total organic content remained relatively stable. This hypothesis is supported by the fact that bioavailable protein concentrations varied independently from total organic matter concentrations both temporally (during 1991) and with depth (see Chapter 2 and Mattin, 1992). Such fluctuations in the various components of the total organic content may therefore have affected the different species at Solent Breezes in a variety of ways. Although these potential fluctuations were not quantified, the potential relationships between food resources and faunal patterns require consideration.

Firstly, there may have been periods during which the abundance of food was particularly low. Such low food conditions may have influenced reproduction and growth in adult populations, but the occurrence of adult mortality related to food limitation would probably have been rare. Consequently, low food levels would not necessarily have been accompanied by concurrent population changes, but may have influenced faunal patterns at some future point in time. Similarly, changes in the availability of specific food types or essential nutrients could have affected individual growth and fecundity. Secondly, food limitation either during or soon after juvenile settlement may have influenced subsequent infaunal densities through juvenile mortality. Conversely, enhanced levels of potential food during settlement may have increased survival in newly settled or recently settled individuals. For example, concentrations of bioavailable protein during 1991 peaked in May (Mattin, 1992), which may have enhanced survival in the larvae of some species during this late spring period. Clearly, the potential impact of variable food levels on the survival of juveniles in a particular species will also be influenced by its type of larval development (i.e. planktotrophic, lecithotrophic or direct).

In a discussion focusing on the biological processes that potentially influenced infaunal distributions and abundance, there is a need to consider sediment-mediated biological interactions: i.e. how changes in the sedimentary environment caused by the activity of one species or functional group influences another. Bioturbation and tube building activity can both significantly alter the sedimentary environment (Wilson, 1991b), and each of these is briefly discussed below.

Sedimentary disturbance caused by bioturbators can have a deleterious effect on suspension feeders and tube builders, but the results of such disturbance is related to the size of the bioturbator and the size and frequency of the disturbance. Evidence for the effects of bioturbation is provided by experiments conducted with relatively large bioturbating species (e.g. the bivalves *Macoma balthica* and *Cerastoderma edule* (Reise, 1983); the shrimp *Callianassa californiensis* (Peterson, 1977; Posey, 1986); and the polychaete *Abarenicola pacifica* (Wilson, 1981)). Such large species were rarely recorded at Solent Breezes. Consequently, although the intermittent occurrence of large bioturbators may have contributed to spatial heterogeneity through sediment-mediated interactions, bioturbation was unlikely to have significantly influenced the major faunal patterns observed during the sampling period.

The large tube builder *Lanice conchilega* was the species most likely to have influenced infaunal patterns through sediment-mediated interactions. High densities of tube building species may be associated with diminished numbers of burrowing animals, but have not been observed to totally exclude burrowers (Wilson, 1991b; Woodin, 1974). The limitation of burrowing organisms appears to be a result of a lack of infaunal space. In addition, Brenchley (1982) demonstrated that eel grass root mats and dense tube mats restrict the movement of burrowing deposit feeders. The potential physical and biological effects of different densities of *Lanice conchilega* tubes at Solent Breezes are discussed in detail in Chapter 6, but a few relevant points are included here.

No evidence was found to suggest that high tube densities limited the abundance of other infaunal species. The maximum density of tubes found at Solent Breezes was 2500m^{-2}, potentially giving each individual a minimum of 4cm^{2} of sediment surface (average value if all tubes were occupied). Such densities are unlikely to have significantly adversely affected the abundance of other animals through space limitation or the restriction of movement. In fact patches of sediment containing higher tube densities usually contained higher numbers of other animals. Chapter 6 will argue that an increase in *Lanice conchilega* tube density beneficially influenced the abundance and, to a lesser extent, the diversity of fauna, probably as a result of sediment stabilisation and accumulation in dense patches. It is therefore conceivable that the relatively high numbers of *Lanice conchilega* in the summer of 1991 may have positively influenced the abundance of other species. However, it must be remembered that many of these *Lanice conchilega* were relatively small young individuals whose influence on the sedimentary environment would have been weaker than larger, more established individuals.

An Overview:

It was noted at the end of Chapter 3 that the use of single-point-in-time data to correlate faunal characteristics with environmental parameters does not account for the potentially controlling influence of any variations in the latter prior to the sampling date. The use of a monitoring programme alleviates some of the intrinsic problems associated with single-point-in-time observations, allowing temporal variations in both the fauna and the environment to be followed. However, the data sets produced by a long term study are still time-specific to a degree, with each faunal data set having a suite of respective environmental observations. For correlations made between environmental variables and faunal parameters using univariate or multivariate analyses, coincident data sets are forced to remain time-specific. This restriction does not allow for the different time spans over which potentially controlling parameters may exert an influence; i.e. the impact of an enviromental change on an infaunal population may not be manifested instantly, but may alter the future development of that population.

Time specific correlations are therefore most useful for analysing the direct effects of more catastrophic disturbances that have a relatively rapid impact on the resident infaunal populations; e.g. severe weather (temperatures or storms) or major predation events. However, it must also be recognised that such events may also have a more long term influence on those individuals that are able to survival the period of disturbance. This discussion has already shown that severe weather conditions have the potential to influence populations both on the short term through mortality and on the long term by increasing subsequent reproductive "effort".

The effects of a sub-lethal disturbance or environmental change on the growth and reproduction of an individual, and its consequent expression in the dynamics of a population can only be quantified accurately using supplementary measurements and experimentation. For example, the *Lanice conchilega* population at Solent Breezes has been studied in more detail using simple biometric measurements. Chapter 5 discusses the dynamics of this population in relation to any potentially controlling environmental parameters.

Finally, the interactive nature of controlling mechanisms must be considered. The characteristics of a population or community at a particular time are an expression of its responses to a series of previous interacting disturbances and controlling parameters. Therefore, the level of response to one disturbance or change may be influenced by events prior to that incident. A particular disturbance may be observed more than once during a long term study, but the response of the infauna might be different each time. Clearly, the timing of a disturbance may affect the faunal response simply from a seasonal point of view because of natural seasonal cycles in population densities and reproductive cycles. Equally, the ability of a population to respond to a disturbance may be influenced by other concurrent or historical controlling factors. For example, low background levels of food availability may influence a population's resilience to harsh climatic conditions. In addition, the intensity of any biological interactions may be influenced by previous changes in environmental parameters and/or differences in concurrent controlling mechanisms.

CHAPTER 5

The *Lanice conchilega* Population

5.1 Introduction

Lanice conchilega was the most consistently dominant macrobenthic species at Solent Breezes in terms of abundance and biomass. The *Lanice conchilega* population present at the mid-shore sampling site during the macrofaunal sampling period was studied in detail. In addition, the tubes collected from macrofaunal samples taken between July 1991 and October 1992 were analysed. This chapter presents the results of the population study and examines the relationships between *Lanice conchilega* and the occurrence of its tubes during the sampling period.

5.2 Methods

All *Lanice conchilega* individuals sorted from the monthly macrofaunal samples were measured to examine the changes that occurred in the population over time. Each measurement was made across the thorax at setiger 1-2 below the cephalic lobe. The thorax was chosen as it was the most rigid part of the body of *Lanice conchilega*. The abdominal segments of live *Lanice conchilega* change dramatically in length and width during movement, and the shape of the head region is also variable because of the flexible nature of the mouth area and its associated appendages. Consequently, the relative dimensions of these parts were not consistent in fixed material. In addition, individuals often became fragmented during the collection and processing of samples, and it was necessary to select a measurable parameter from the anterior end to avoid measuring each specimen more than once.

Each *Lanice conchilega* worm was positioned under a low power binocular microscope which was connected to a video camera. The image of each worm was video taped and was subsequently analysed using a suitable video analysis software package. Results were automatically recorded onto a spreadsheet which could be imported into other software packages for further analysis.

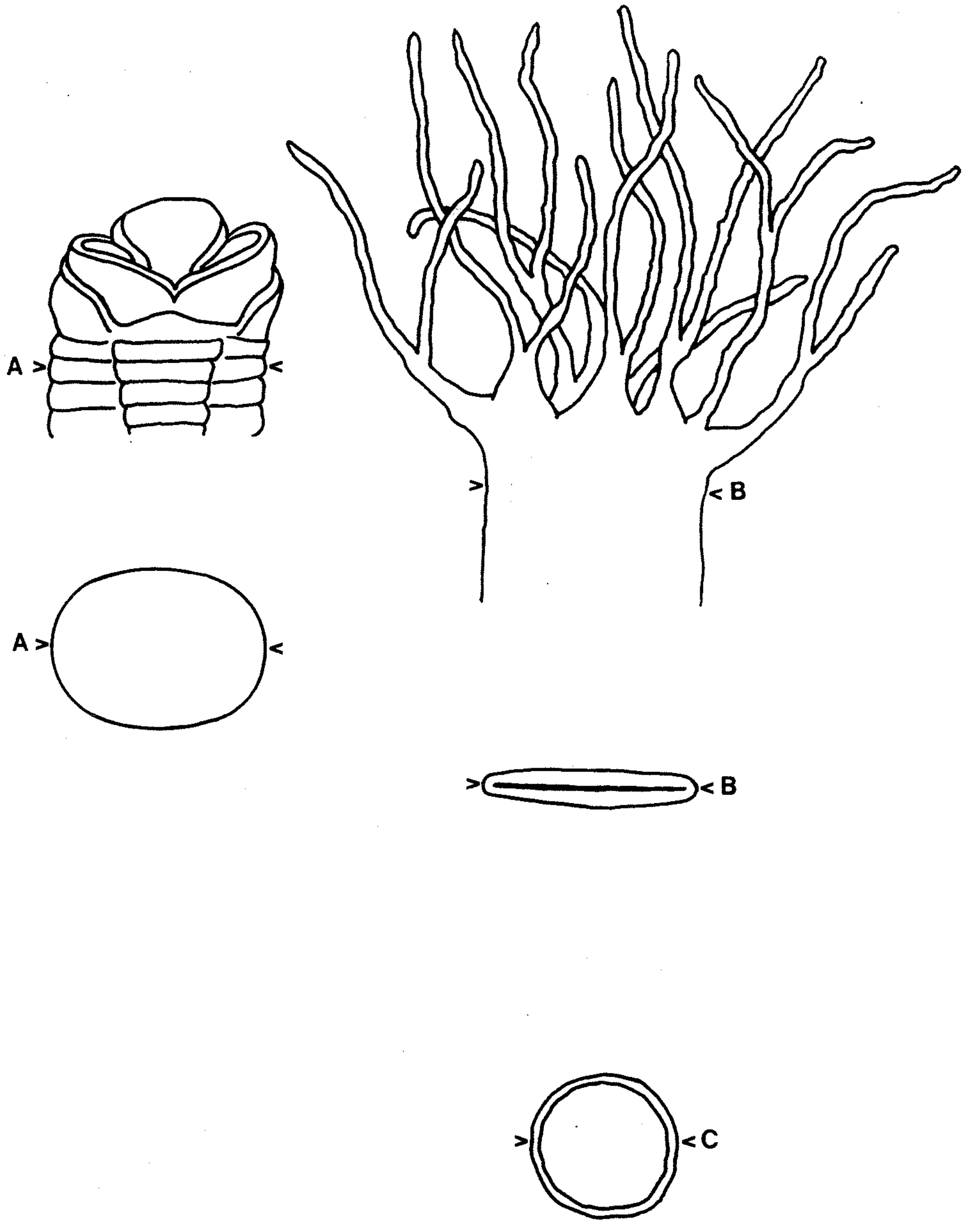


Figure 5.1 The *Lanice conchilega* Population. The dimensions of each *Lanice conchilega* specimen (A) and each tube (B) that were measured for the population study. The tube measurement (B) was converted to tube diameter (C) by multiplying by the conversion factor 2/π.

The widths of *Lanice conchilega* tubes were also measured. The decision to retain all tube material present in individual macrofaunal samples was first made in July 1991. Therefore, such material was only available for the period between July 1991 and October 1992, as previous samples had already been processed.

Tube material was collected from individual samples during the initial sorting stage and was retained in 70% ethanol. Most tubes were in a satisfactory condition, but a degree of fragmentation occurred during sample processing (sieving etc.). Tube width measurements were made at the base of tube crowns to avoid measuring a single tube more than once. Each tube was placed flat on a Petri dish and was measured to the nearest 0.1mm using a travelling microscope. This method was used as a quicker alternative to the video analysis method described above, as the time available for this section of the study was limited.

5.3 Results

The dimensions of each *Lanice conchilega* specimen and each tube that were measured for this section of the study are illustrated in Figure 5.1. The relationships between these dimensions require clarification before the size frequency distributions of the *Lanice conchilega* worms and tubes can be presented. Each tube width measurement was approximately equal to half of the external circumference of the tube (i.e. $\frac{1}{2}(2\pi r) = \pi r$). This could be converted to the external diameter of the tube (i.e. $2r$) using a simple conversion factor ($2/\pi$). The external circumference and the external diameter of each tube were both dependent on the size of the worm and on the size of the particles attached to the mucus layer of the tube.

It would be rather simplistic to state that the external diameter of a tube was always greater than the width of the worm living within it. The calculation of the external diameter from the external circumference is based on the tube being circular in cross-section, and the assumption then would be that the worm itself is also perfectly circular in cross-section. In this case the diameter of the tube would clearly be consistently greater than the width of the worm. However, in reality *Lanice conchilega* worms are not circular in cross-section, but are distinctly dorso-ventrally flattened (Figure 5.1), and consequently the tubes surrounding the worms must also be dorso-ventrally flattened. Therefore, the true external width of a tube in life lies somewhere between the completely flattened shape (i.e. half the external circumference) and the fully inflated shape (i.e. the external diameter).

The exact width of tubes in life could not be calculated with any degree of certainty as the level of dorso-ventral flattening varied between worms. Furthermore, the internal dimensions of individual tubes could not be calculated from the external measurements, as the difference between the external and the internal circumferences must have varied between tubes, depending on the size of particles that were available for tube building. The external diameter and the external circumference were the only two parameters that could be used in the results presented below.

5.3.1 Size-frequency analysis of *Lanice conchilega* and its tubes

The measured *Lanice conchilega* individuals from each monthly set of samples were grouped into 0.2mm size classes and size-frequency histograms were constructed (Figure 5.2). The overwintering population of *Lanice conchilega* (November 1990 - March 1991) consisted of two cohorts, the older of which contained relatively few individuals and subsequently disappeared in April 1991. The mean size of individuals in the main cohort increased in March 1991, but decreased again in April 1991.

Recruitment of a new cohort began in May 1991, but the main influx of young *Lanice conchilega* occurred in June 1991, resulting in a distinctly bimodal distribution. The smallest specimen was found in May 1991 and was approximately 0.38mm in width and 3.0mm in length. This specimen was substantially larger than many of the small polychaetes (e.g. Syllidae) successfully retained on the 0.5mm sieve throughout the sampling period. Therefore, if smaller specimens of *Lanice conchilega* were present in significant numbers in May 1991, they would have been detected. Consequently, the small size of the younger cohort in May 1991 was not simply a result of the mesh size used during the processing of macrofaunal samples.

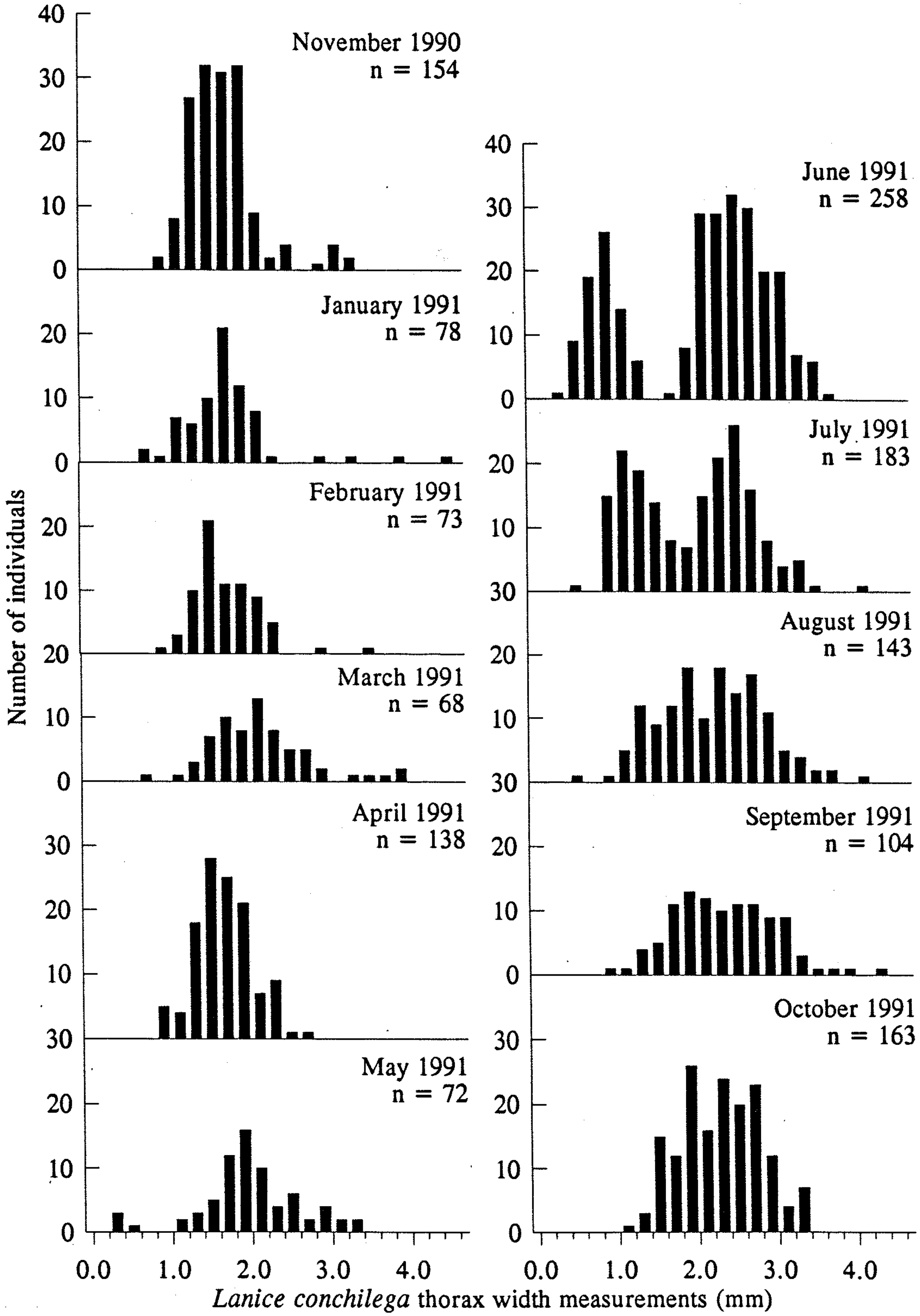


Figure 5.2a The *Lanice conchilega* Population. Size class analysis of the *Lanice conchilega* population at Solent Breezes using thorax width measurements (November 1990 - October 1991). Temporal sequence continues in Figure 5.2b.

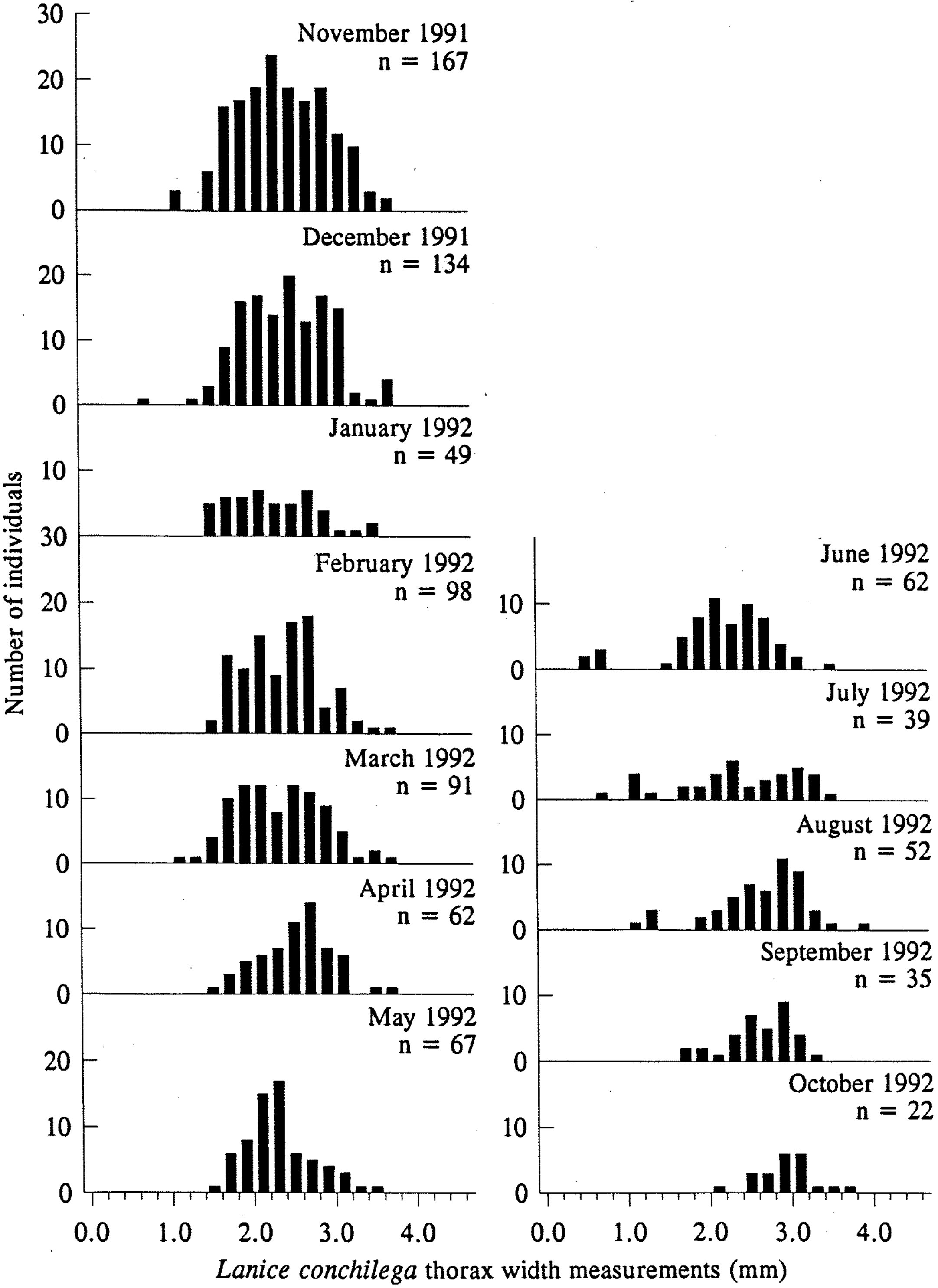


Figure 5.2b The *Lanice conchilega* Population. Size class analysis of the *Lanice conchilega* population at Solent Breezes using thorax width measurements (November 1991 - October 1992). Continued from Figure 5.2a.

The main recruitment pulse in June 1991 was made up of individuals with a mean width of 0.86mm. Again, if smaller specimens were present in significant numbers, they would have been detected.

Morisita's index of dispersion (I_δ) (see Section 4.3.1) was used to calculate the dispersion of individuals from the two cohorts among the ten monthly cores taken in June 1991. The individuals from the younger cohort were randomly distributed (i.e. $I_\delta < 1.0$), whereas individuals from the older cohort were significantly clumped ($p < 0.05$).

The large cohort of younger *Lanice conchilega* remained distinct from the older cohort in July 1991, and the mean size of the younger individuals had increased markedly. Again, the distribution of individuals from the younger cohort was random (i.e. $I_\delta < 1.0$), and individuals from the older cohort were significantly clumped ($p < 0.05$).

In August 1991 the two cohorts became less distinguishable as some younger individuals attained similar body sizes to the smaller members of the older cohort. Similarly, in September 1991 the two cohorts were perhaps only barely distinguishable using two visible modal peaks.

In the subsequent late autumn and winter months, the *Lanice conchilega* population at Solent Breezes was represented by individuals that had a wide range of sizes and that had originated from both the younger and older cohorts. The growth of this mixed group of individuals was minimal during winter and spring.

A relatively low number of *Lanice conchilega* occurred in samples taken between June 1992 and October 1992. There was an extremely small influx of new individuals in June 1992 compared to that of the previous year. However, the growth of this new cohort could still be followed during the subsequent three months. In addition, members the larger group of older individuals increased in size, but decreased in abundance towards the end of the sampling period.

The *Lanice conchilega* tube measurement data from each available monthly set of samples were converted to tube diameter data and were grouped into 0.2mm size classes. Size-frequency histograms were then constructed (Figure 5.3).

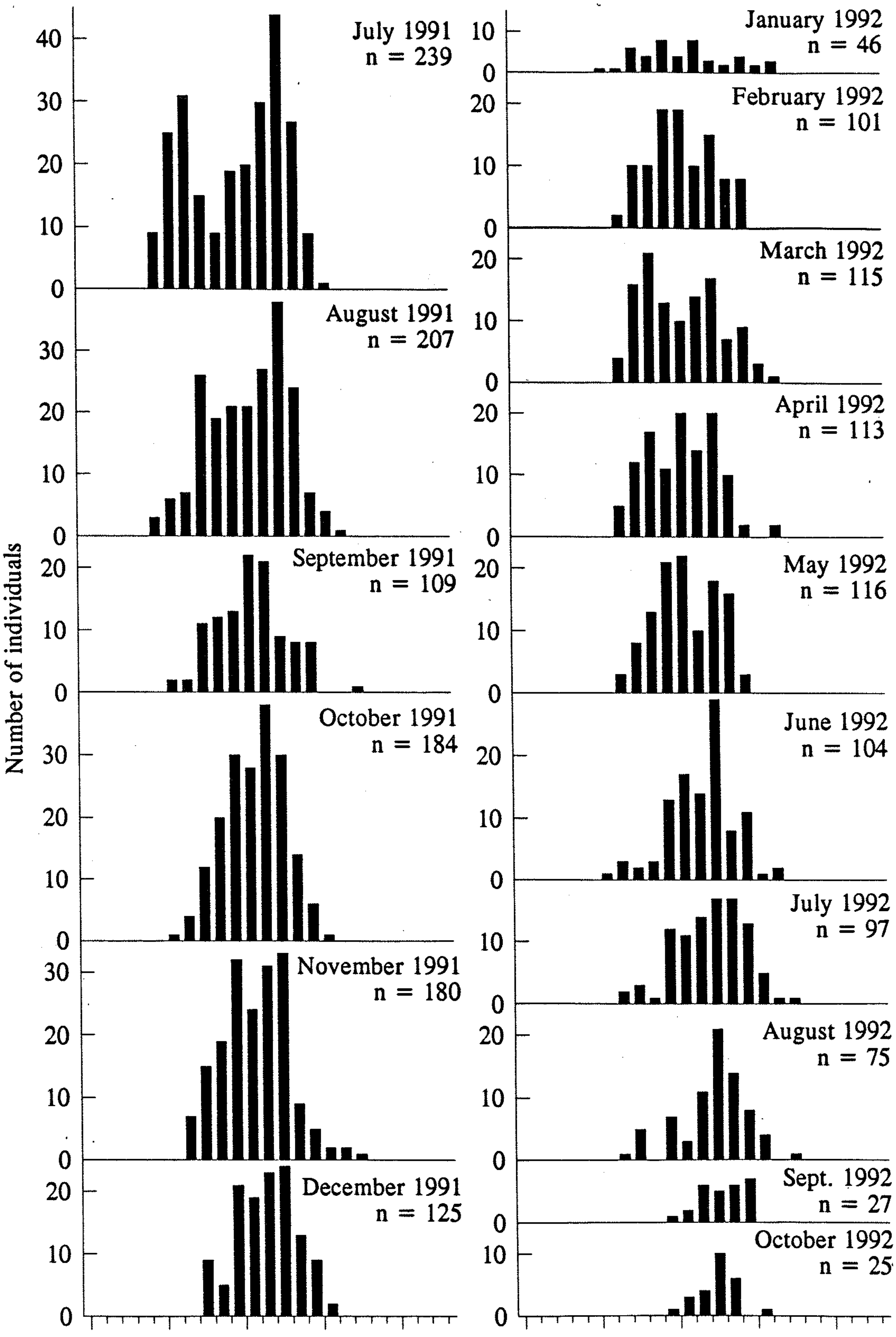


Figure 5.3 The *Lanice conchilega* Population. Size class analysis of the *Lanice conchilega* population at Solent Breezes using tube diameter measurements.

The changes that occurred in the size distribution of tubes between July 1991 and October 1992 were predictably similar to those that occurred in the *Lanice conchilega* population itself. The size distribution was distinctly bimodal in July 1991, and the younger cohort subsequently merged with the older cohort in August 1991. The growth of the resulting group of individuals was again minimal during winter and spring. There was an indication of a degree of bimodality between February 1992 and May 1992, which had been less apparent in the size-frequency distributions of the *Lanice conchilega* population. The small influx of new *Lanice conchilega* individuals that had been observed in June 1992 was matched by a similar number of relatively small tubes.

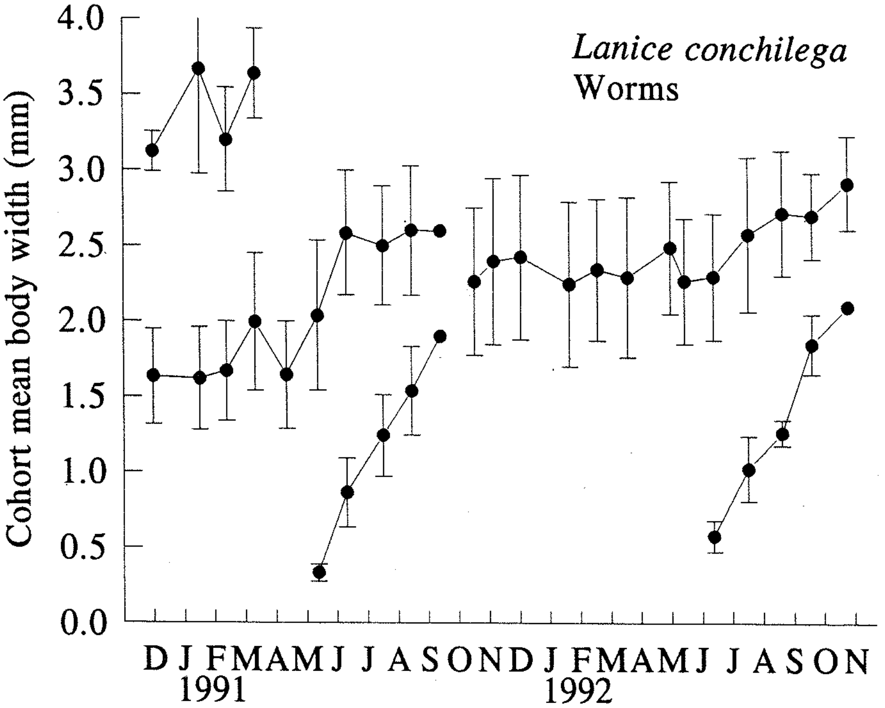
5.3.2 Growth curves

Figure 5.4 shows the changes in mean size in the observed cohorts of both *Lanice conchilega* individuals (upper graph) and *Lanice conchilega* tubes (lower graph). The older *Lanice conchilega* individuals present at the start of the sampling period were much larger than any other individuals. The mean body width of the main cohort was approximately 1.65mm between November 1990 and February 1991. There was a clear increase in mean body width in specimens collected in March 1991, followed by a decrease in April 1991, as previously mentioned.

A distinct period of growth is highlighted in the main cohort between April 1991 and June 1991. The mean body width increased from 1.64mm in April 1991 to 2.59mm in June 1991, after which it remained relatively stable.

The growth of the new cohort between May 1991 and September 1991 is also clearly illustrated. The mean body width of individuals in the new cohort increased from 0.33mm in May 1991 to 1.54mm in August 1991.

Mean values could not be calculated for the two cohorts in September 1991 because the cohorts could not be distinguished clearly. The points shown for both the new cohort and the main cohort in September 1991 are simply modal values taken from Figure 5.2. However, the rate of growth of the new cohort appears to have remained consistent at a rate of approximately 0.35mm (in width) per month.



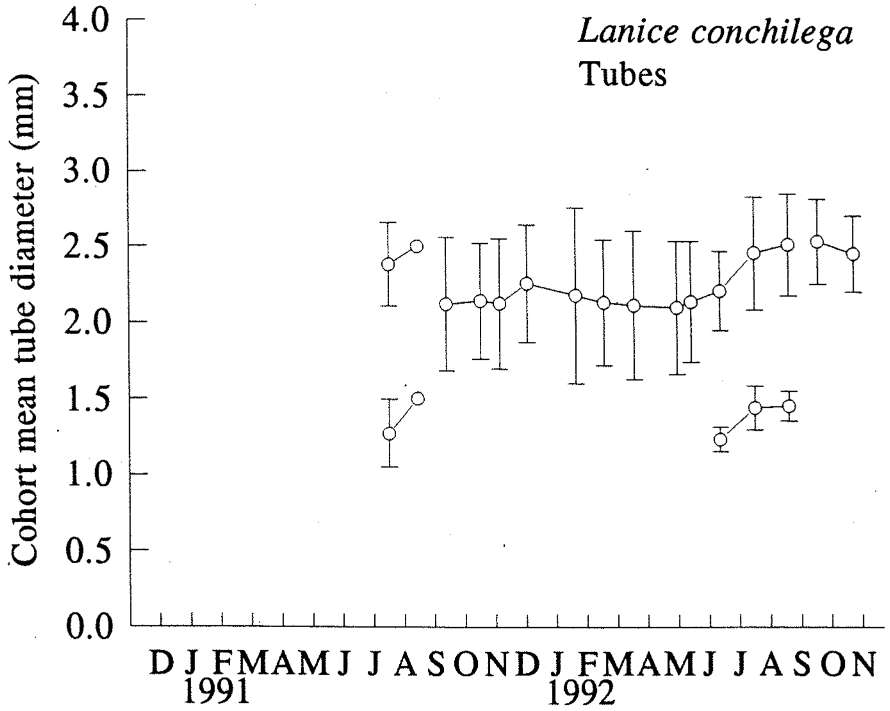


Figure 5.4 The *Lanice conchilega* Population. Changes in the mean thorax width (± S.D.) (upper graph) and the mean tube diameter (± S.D.) (lower graph) in observed cohorts.

A single mean value was calculated in October 1991 as the two cohorts became completely indistinguishable. The mean body width then remained relatively stable throughout the winter and spring, as indicated above from the size-frequency histograms (mean values remained between 2.25mm and 2.50mm from October 1991 to June 1992).

Figure 5.4 also depicts the growth of the second annual cohort of young individuals that was evident between June 1992 and September 1992. The growth rate of this relatively small cohort was similar to that of the previous year's cohort of younger individuals. In addition, the mean body width of the main cohort present in June 1992 increased steadily over the subsequent 4 months from 2.30mm to 2.92mm.

The lower graph in Figure 5.4 shows the changes in mean external tube diameter derived from the size-frequency histograms in Figure 5.3. The points shown for the two cohorts in August 1991 are simply modal values taken from Figure 5.3. In September 1991, the cohorts could not be distinguished clearly and a single mean value was therefore calculated. The mean diameter of tubes in this main mixed cohort was between 2.10mm and 2.25mm during autumn, winter and spring (September 1991 - May 1992). The cohort of smaller tubes present in June, July and August 1992 was separated easily from the main cohort using the raw data, although the two cohorts appear to be somewhat indistinguishable in Figure 5.3. However, the cohorts merged during the two subsequent months.

Finally, it must be noted that the mean external diameter of tubes each month was consistently less than the mean body width of *Lanice conchilega*. As discussed above, this is explained by the shape of a tube in life being dorso-ventrally flattened to accommodate the worm within it.

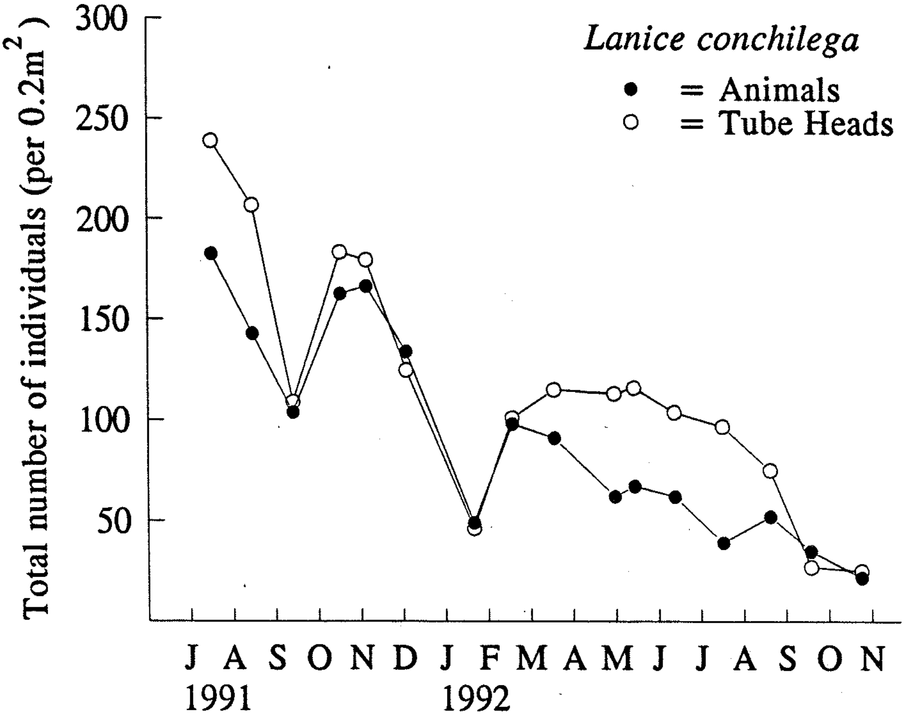
5.3.3 Temporal variability in abundance

Figure 5.5 shows the total number of *Lanice conchilega* and the total number of tube heads enumerated and measured each month (upper graph). The abundance of tube heads was greater than the abundance of worms in the majority of months ("excess" tube heads were present in 13 of the 16 months). In particular, during spring and summer months there was a distinct rise in the proportion of excess tube heads. This trend is emphasised by the lower graph in Figure 5.5, which illustrates the monthly changes that occurred in the ratio between the total number of tube heads and the total number of worms (i.e. T/L).

Between March 1992 and July 1992 the abundance of tube heads remained relatively constant while the abundance of worms decreased. This resulted in the ratio T/L increasing to a maximum of 2.49 in July 1992. In August 1992, the ratio T/L decreased, and in September 1992 the total number of tube heads decreased dramatically and was less than the total number of worms (i.e. T/L < 1).

The distribution of excess tubes present during the spring and summer months was analysed by superimposing the size frequency histograms of tube measurements onto their respective histograms of thorax width measurements (Figure 5.6). The tube measurements presented in Figure 5.6 have not been converted to tube diameters, and therefore each measurement represents approximately half of the external circumference. As it was impossible to relate individual tubes to individual worms, the distributions had to be compared "by eye" to estimate the sizes of the excess tubes.

In March 1992 the distribution of tube widths was similar to the distribution of worm widths, although the distribution of tube widths appears to be extended across a wider range of size classes. In April and May 1992 there was an apparent excess of large tubes. Similarly, in June and July 1992 excess tubes appeared to be present in the upper size classes..



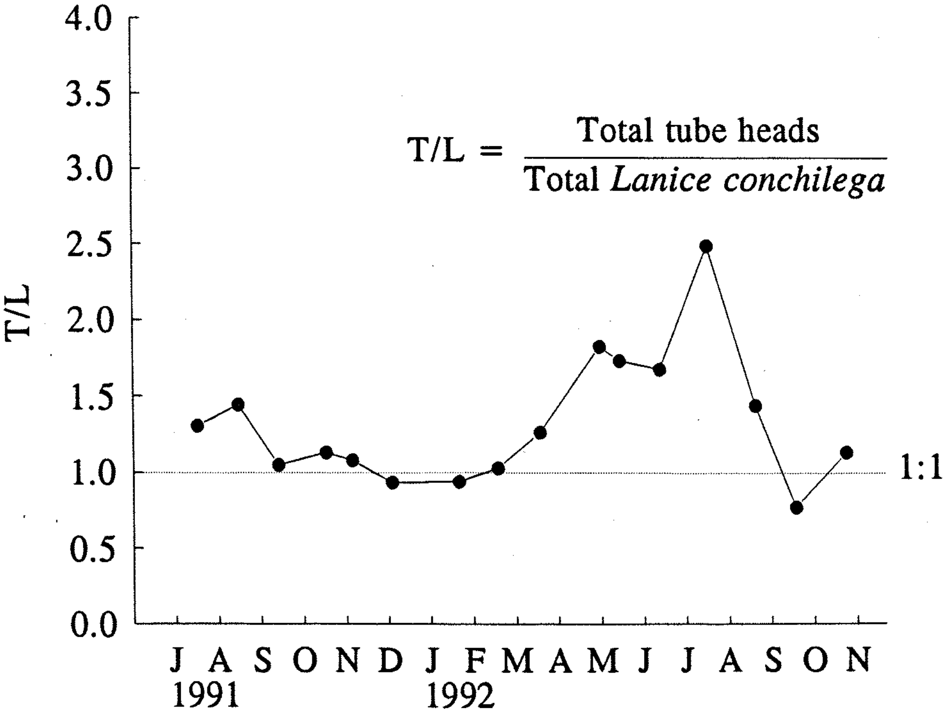


Figure 5.5 The *Lanice conchilega* Population. Changes in the total number of *Lanice conchilega* individuals and the total number of tubes between July 1991 and October 1992 (upper graph), and the ratio between these two parameters (lower graph).

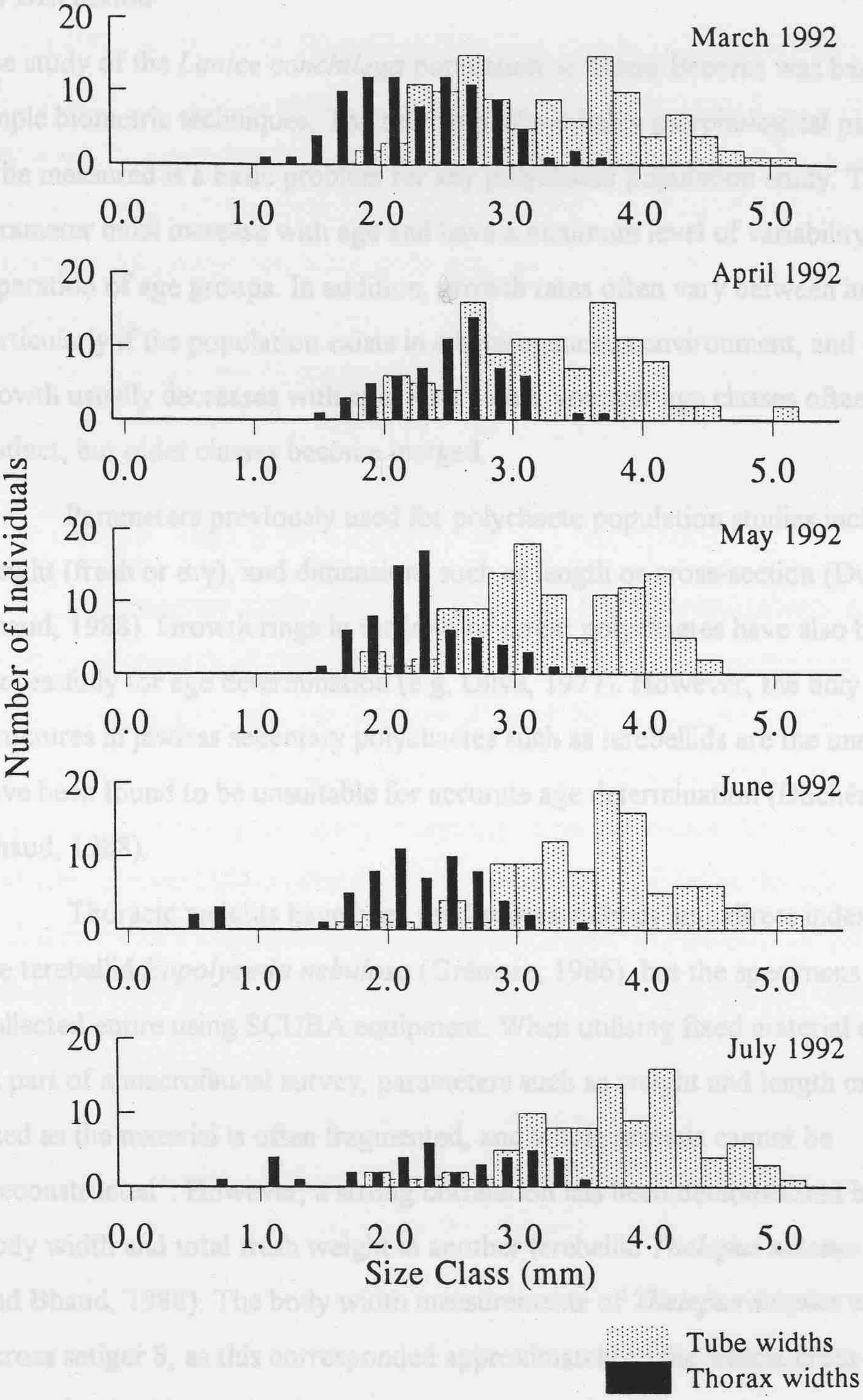


Figure 5.6 The *Lanice conchilega* Population. A comparison of the *Lanice conchilega* thorax width and tube width size class histograms during the period March 1992 to July 1992.

5.4 Discussion

The study of the *Lanice conchilega* population at Solent Breezes was based on simple biometric techniques. The selection of a suitable morphological parameter to be measured is a basic problem for any polychaete population study. The chosen parameter must increase with age and have a minimum level of variability, to allow separation of age groups. In addition, growth rates often vary between individuals, particularly if the population exists in a heterogeneous environment, and the rate of growth usually decreases with age. As a result, younger age classes often remain distinct, but older classes become merged.

Parameters previously used for polychaete population studies include weight (fresh or dry), and dimensions such as length or cross-section (Duchêne and Bhaud, 1988). Growth rings in the jaws of errant polychaetes have also been used successfully for age determination (e.g. Olive, 1977). However, the only hard structures in jawless sedentary polychaetes such as terebellids are the uncini, which have been found to be unsuitable for accurate age determination (Duchêne and Bhaud, 1988).

Thoracic weights have been used successfully as an indirect index of age in the terebellid *Eupolymnia nebulosa* (Grèmare, 1986), but the specimens used were collected entire using SCUBA equipment. When utilising fixed material collected as part of a macrofaunal survey, parameters such as weight and length cannot be used as the material is often fragmented, and whole animals cannot be "reconstructed". However, a strong correlation has been demonstrated between body width and total fresh weight in another terebellid *Thelepus setosus* (Duchêne and Bhaud, 1988). The body width measurements of *Thelepus setosus* were made across setiger 8, as this corresponded approximately to the widest cross-sectional dimension in this species.

For the present study, body width measurements of *Lanice conchilega* were made at setiger 1-2 as this was usually the widest cross-sectional dimension of the thorax. In addition, the use of this dimension at the anterior end of the body optimised the number of measurements per sample whilst minimising the level of variability.

Although many aspects of *Lanice conchilega* have previously been investigated, details of the dynamics of any one population have not been studied using body width measurements. The tubes of *Lanice conchilega* have previously been used for a population study in the Baie de Veys (Ropert, 1996). The internal diameter of each of these tubes was measured with a calibrated conical metal instrument. Measurements were made approximately 5cm below the crown of every tube that contained a *Lanice conchilega* worm (Ropert *pers. comm.*). The use of the internal tube diameter as a biometric dimension eliminates potential error caused by differences in the size of particles incorporated into tubes. However, it also assumes that the internal diameter of a tube is equal to the body width of the worm within it, which is not necessarily the case (see Section 5.3).

In the current study, the use of both body width measurements and tube width measurements allowed comparisons to be drawn between the two distributions each month, and therefore allowed the empty tubes present in samples to be assessed. It is acknowledged that external tube measurements are liable to be relatively inaccurate, particularly in heterogeneous sediments. The size of particles available for tube building and the level of selectivity shown by the tube builder will both directly affect the external dimensions of a tube. In addition, the size of an individual worm may influence the size of particles selected for tube building by that worm.

Comments on the population dynamics of *Lanice conchilega* at Solent Breezes therefore focus on the analysis of body width measurements, although similar basic trends were revealed by the tube width study.

The *Lanice conchilega* population present at the start of the macrofaunal sampling period was dominated by a single cohort of individuals. The overwintering population of adults maintained a maximum density of approximately 700m^{-2} in dense patches, despite relatively extreme winter conditions. Particularly cold air temperatures were recorded before the February 1991 sampling date and these were reflected in the seawater temperature measured during the February 1991 sampling visit (see Chapter 2). Harsh climatic conditions, particularly severe winters, have previously been observed to have a dramatic effect on intertidal *Lanice conchilega* populations in several regions. For example, Newell (1964) listed *Lanice conchilega* as a shore species which had been "completely wiped out" by the hard winter of 1962-63, with all tubes exposed at low tide being empty (Whitstable, U.K.).

Beukema *et al.* (1978) presented direct evidence for the susceptibility of *Lanice conchilega* to low temperatures. They reported that after 4 nights of minimum air temperatures of around -7°C, almost all *Lanice conchilega* were found dead on the tidal flats of the Dutch Wadden Sea. Similarly, in the Weser Estuary, severe ice conditions destroyed a very dense population along with other characteristic species of the *Lanice conchilega* association (Buhr, 1981).

During February 1991 the ground temperature in the Southampton area dropped to a minimum of -10°C and the mean minimum air temperature was 0.0°C. However, the intertidal population of *Lanice conchilega* at Solent Breezes survived the winter. It is important to remember that the sampling site at Solent Breezes is covered by seawater during a large part of each tidal cycle, protecting it from any extended periods of low air temperatures. For the extreme air temperatures to have caused significant mortality, it would have been necessary for them to coincide with long periods of emersion. In comparison, the tidal flats studied by Beukema in the Dutch Wadden Sea are exposed to the air for an average of 5.5 hours in every 12.5 hours, and some higher areas can remain exposed continuously for several days (Beukema, 1985).

An equally important effect of severe winter conditions is the level of reproductive success in subsequent months. The long term study by Beukema suggested that levels of abundance were "unprecedented" in several polychaete species following the severe winter of 1978-79, and particularly heavy spatfalls of four important bivalve species were also observed (Beukema, 1982; 1985).

Although the present study was only conducted over a two year period, the level of recruitment in *Lanice conchilega* was clearly much greater in 1991 than in 1992 (the influx of young *Lanice conchilega* in the second year of the study was extremely small). It is suggested that the relatively severe winter conditions that occurred during January and February 1991 triggered the subsequent high level of reproductive "effort" in *Lanice conchilega* during 1991.

This hypothesis is supported by the relatively large size of the individuals present in samples taken in March 1991. The mean width of specimens in the main cohort increased markedly in this month, perhaps as a result of gamete production. The development of gametes in *Lanice conchilega* occurs in the coelomic fluid of anterior segments, and specialised reproductive nephromixia (through which the gametes are shed) occur from setiger 2 (Smith, 1988, 1989b). Gamete production and the inflation of the paired nephromixia could reasonably be expected to cause anterior segments to become swollen. The subsequent release of gametes would then have resulted in the relative reduction in the size of the anterior segments observed in April 1991.

Such a response to the harsh winter conditions is likely to have occurred throughout the region, resulting in an abundance of larvae in surrounding waters. The larval phase of the *Lanice conchilega* life cycle has been reported to be approximately 8 weeks (Bhaud, 1988; Bhaud and Cazaux, 1990). Therefore, if the synchronised release of gametes occurred some time between the March and April 1991 sampling dates, settlement of larvae would have started approximately 8 weeks later. Recruitment into the *Lanice conchilega* population started in May 1991, but the major influx of new individuals occurred in June 1991. Therefore, the main spawning period must have occurred before the April 1991 sampling date, as predicted.

The size of newly settled *Lanice conchilega* larvae is an important consideration at this point. For the proposed progression of gamete release through to larval settlement to have occurred, the major pulse of new individuals must have been either newly settled or recently settled juveniles. This in turn relies on newly settled juveniles being large enough to be held on the 0.5mm mesh used for the macrofaunal study. The late stage aulophore larvae of *Lanice conchilega* have been documented as being between approximately 3.0mm and 3.5mm in length (Bhaud and Cazaux, 1990; Plate and Husemann, 1994). On settlement, these larvae would therefore be of a sufficient size to be held on a 0.5mm mesh. The width of the late stage aulophore larvae drawn by Bhaud and Cazaux (1990) can be estimated as approximately 0.4mm. The smallest individuals collected in May 1991 were in fact smaller than this (approximately 0.3mm), and members of the new cohort observed in June 1991 were between approximately 0.4mm and 1.4mm. Therefore, these members of the new cohort were either newly settled or recently settled individuals, rather than slightly older individuals that had migrated into the area (e.g. from a subtidal population).

A completely different mechanism of recruitment was described by Ropert (1996) for a *Lanice conchilega* population in the Baie de Veys. There was almost a total absence of juveniles in the local population throughout the study period, but a supply of external individuals resulted in significant increases in the population size. The development and maintenance of the local population relied on a large source of adults at the opening of the Baie de Veys. Strong tidal currents resulted in the physical removal of adults from the source population, and the transportation of these adults towards the study site (Ropert, 1996).

While the possibility of adults being transported both into and out of the population at Solent Breezes exists, the recruitment observed in May and June 1991 was a result of the settlement of large numbers of juveniles. The phenomenon of adult displacement observed by Ropert was reliant on the peculiar topography of the area under investigation. Other authors have suggested that *Lanice conchilega* exhibits little locomotory ability and is not expected to leave its tube or migrate between localities (Smith, 1988; 1989a; Beukema, 1985).

It is interesting to note that the distribution of *Lanice conchilega* individuals belonging to the existing adult population (i.e. the older cohort) in both June and July 1991 was significantly contagious (see Chapter 4). In comparison, the smaller individuals of the new cohort were randomly distributed across the shore in both months.

While established adults are less likely to move, juvenile *Lanice conchilega* are able to relocate during the settlement process if a particular substrate is unsuitable (Bhaud and Cazaux, 1990). The settlement of juveniles at Solent Breezes was random across the mid-shore sampling site. Juveniles therefore showed no significant preference for particular areas of sediment. However, as the young individuals developed and the two cohorts merged, the overall distribution of the population returned to being significantly contagious. A higher level of mortality in those young individuals that had settled between patches of established adults would result in such a return to a significantly contagious distribution. Alternatively, it is possible that young individuals were able to migrate away from unsuitable areas after initial settlement, moving to more suitable areas that also contained higher densities of established adults.

No further input of juveniles was observed during 1991. The age structure of the large group of individuals present between October 1991 and April 1992 was indeterminable. During this period, the population was composed of the younger individuals that had settled early in the summer of 1991, living among older individuals from previous recruitment periods. The age of individual *Lanice conchilega* is not necessarily directly related to size, but it seems fair to suggest that large, older animals were dying during these months, having reached the end of their life cycle. Unfortunately no solid evidence exists that has proved the longevity of *Lanice conchilega*, or the number of times individuals spawn during their lifetime. Beukema *et al.* (1978) described *Lanice conchilega* as a short-lived species that rarely survived a second winter on the tidal flats of the western part of the Dutch Wadden Sea. However, the longevity of *Lanice conchilega* in Britain appears to remain undefined, and it may vary depending on a population's geographical position.

A minimal amount of growth occurred in the Solent Breezes population during winter and early spring. However, during late spring and summer significant growth occurred in both younger and older individuals. The cohort of younger individuals present each year grew rapidly and merged with the older cohort during late summer. The mean body width of the resulting group of individuals increased but remained below 3.0mm. The population studied by Ropert (1996) was almost always unimodal and was centralised on an average tube diameter of 3.5 - 4.0mm. Fundamental differences in the recruitment mechanisms of the two populations may go some way towards explaining the difference between their mean body sizes. The Baie de Veys population was maintained through recruitment of adults supplied from a large subtidal population living in a high energy environment (Ropert, 1996). Individuals living subtidally are clearly not exposed to the same severe seasonal and diurnal changes in environmental conditions. It is therefore conceivable that subtidal *Lanice conchilega* are able to live longer than intertidal

Lanice conchilega. In addition, subtidal individuals are potentially provided with a continual supply of food, particularly in areas of strong currents where suspension-feeding plays a dominant role (Buhr, 1976). Conversely, intertidal individuals are only able to feed during periods of immersion, and harsh winter conditions may affect survival and growth.

The influx of young *Lanice conchilega* in the second year of the current study was extremely small. In addition, the total population was decreasing steadily in size at the end of the sampling period. It is possible that the low level of recruitment caused the overall decrease in abundance, as the maintenance of the population might have relied on a sufficient supply of juveniles to replace older individuals. Alternatively, the environment at Solent Breezes may have become less suitable for *Lanice conchilega*, resulting in a gradual decrease in numbers of established adults and a simultaneous decrease in the likelihood of juvenile settlement in the area.

The distinct changes that occurred in the macrofaunal community at Solent Breezes towards the end of the sampling period are discussed in Chapter 4. However, the decline of *Lanice conchilega* did not continue to a "point of no return", as suitably high densities could be found for both the meiofaunal study (see Chapter 7) and the *Lanice conchilega* density experiments (see Chapter 6).

The size frequency histograms of tube diameters produced similar patterns of population change, but there was an excess of tube heads present in the majority of months. A number of interactive processes might result in the presence of excess tubes. Physical disturbance to the local sedimentary environment may result in tube heads being covered by fresh sediment or tubes being displaced from the vertical. In such circumstances, *Lanice conchilega* is capable of building a new section of tube and a new tube head (e.g. Feral, 1992).

It is possible that tubes with more than one head may have become fragmented during sample processing, and consequently may have been measured more than once. However, old tube heads were usually conspicuous because at least part of a new section of tube remained intact and visible above any old tube head. Indeed, if the fragmentation of tube material during processing was a significant consideration, it would be more likely to result in the loss of tube heads, as the frills of a tube head are more fragile than the tube itself.

Disturbance to a different *Lanice conchilega* population (e.g. in a local subtidal area) may have resulted in the import of empty tubes to the sampling site. However, the relatively buoyant nature of *Lanice conchilega* tubes would have resulted in them being deposited onto the sediment surface or left at the top of the shore at the standline, and it seems unlikely that they would have become incorporated into the mid-shore sediment matrix. If empty tubes had been present on the sediment surface during sampling, their presence would have been observed and noted.

Shorebirds feed on the invertebrate fauna of beaches and tidal flats during low tide and some species may seriously deplete population densities of particular prey species (e.g. *Corophium*, Goss-Custard *et al.*, 1977). The impact of bird predation is also likely to be greater in autumn and winter when shorebird densities are highest (Schneider, 1985). The influence of bird predation on *Lanice conchilega* will depend on both the type and the intensity of the feeding mechanisms involved. Cropping of the tentacles and head region of *Lanice conchilega* would severely damage or destroy the worm, but presumably in this situation the tube head would also be removed. Therefore, this interaction would not result in a relative increase in the number of empty tubes. It is not known whether some species of predatory shorebirds are able to extract tube dwelling infaunal animals such as *Lanice conchilega* from their tubes, leaving the empty tubes in the sediment.

Lanice conchilega is recognised as a component of the diet of demersal fish species such as flounder and plaice (deVlas, 1979; 1981). Again, for such predation to significantly increase the number of excess tube heads present in an area, worms would need to be consumed without their tubes being affected. It is possible that the anterior parts of both the worm and its tube would be cropped together. This would be followed by the regeneration of the worm and the subsequent reconstruction of the tube head. However, gut content observations made by Eagle (1975) have suggested that *Lanice conchilega* worms may be extracted from their tubes which then remain empty in the substratum (worms were present in the guts of flatfish but no accompanying tube remains were found).

Environmental disturbance at the sampling site may have resulted in the presence of excess tubes by causing worms to abandon their tubes or increasing mortality among worms. As already stated, *Lanice conchilega* is not expected to leave its tube to feed or migrate between localities (Smith, 1988; 1989a; Beukema, 1985). It is possible that sediment movements may have forced individuals to abandon their tubes below the surface and build new tubes in the adjacent sediment. However, it seems more likely that existing tubes would simply be extended to re-establish contact with the sediment surface (as above).

It has been established that the abundance of *Lanice conchilega* decreased towards the end of the study period. Conversely, between March and July 1992, the abundance of tubes remained relatively stable. This pattern suggests that individual worms were dying, being removed or emigrating and leaving their tubes behind. Such a hypothesis relies on the extended survival of empty tubes. The longevity of empty *Lanice conchilega* tubes has not been formally quantified, but these relatively durable biogenic structures might arguably survive longer in the sedimentary environment than a dead worm. King (1986) suggested that a dibromophenol present in burrow wall mucous linings inhibits microbial degradation. At least four bromophenols are synthesised by *Lanice conchilega* (Goerke and Weber, 1990; 1991), and these may play a part in restricting the rate of degradation of empty tubes.

The large number of excess tubes present during late spring and summer appeared to be in the larger size classes. However, a separate sampling programme would have been required to quantify the excess tubes accurately. The sampling programme would need to collect worms and tubes with a minimum of disturbance, to ensure worms remained inside their tubes until they could both be measured. For example, it may be possible to use liquid nitrogen to freeze an area of sediment *in situ* before extraction and processing.

CHAPTER 6

Lanice conchilega Tube Density Experiments

6.1 Introduction

The patchiness of *Lanice conchilega* at Solent Breezes has been highlighted by the results presented in Chapter 4. However, these results only include the *Lanice conchilega* individuals found in cores taken as part of the regular macrofaunal sampling programme. As previously indicated, a large number of *Lanice conchilega* tube heads were visible on the sediment surface at Solent Breezes throughout this study. The tube heads were a parameter that could be quantified simply, and this allowed additional investigations to be conducted into the fauna occurring within areas of sediment containing different tube densities. This chapter describes a sampling regime that was specifically designed to compare such areas.

The investigations aimed to test the hypothesis that the presence of *Lanice conchilega* individuals and their tubes exerted a significant influence on the other macrofaunal species present either individually or collectively.

6.2 Field Work and Laboratory Methods

6.2.1 *Lanice conchilega* and its tubes

An initial investigation was conducted into the relationship between the abundance of *Lanice conchilega* tube heads and the abundance of *Lanice conchilega* animals in samples previously collected and processed as part of the macrofaunal study. The decision to retain all tube material present in individual macrofaunal samples was first made in July 1991. Therefore, such material was only available for the period between July 1991 and October 1992, as previous samples had already been processed.

Tube material was collected from individual samples during the initial sorting stage and was retained in 70% ethanol. Most tubes were in a satisfactory condition, but a degree of fragmentation occurred during sample processing (sieving etc.). Tube heads usually remained intact and were simply enumerated. In addition, width measurements of individual tubes were made, but these results have been presented in Chapter 5 alongside the thorax width measurements conducted for the *Lanice conchilega* population study.

Finally, the total dry weight of tube material was calculated for each sample. Material was dried in an oven at 60°C, allowed to cool in a dessicator, and weighed at room temperature on a table top balance. The weight of tube material per sample was measured after all other measurements had been completed as the drying process essentially destroyed the structure of the tubes.

6.2.2 *Lanice conchilega* tubes and the other infauna

To examine any possible direct or indirect effects that the presence of *Lanice conchilega* tubes may have had on the other infauna, four additional sets of samples were taken from areas containing different tube head densities. A set of samples (of size *n*) were taken in each of the following months:

(i) June 1992, $n = 11$;

(ii) March 1993, $n = 10$;

(iii) August 1993, $n = 9$;

(iv) March 1994, $n = 10$.

For each sample, a circular "quadrat" (surface area = 0.071m^2) was placed over a selected area of sediment and the number of tube heads visible on the sediment surface within the quadrat was counted. A small core (6cm internal diameter) was then taken from the centre of each quadrat to a depth of 25cm. Core samples were transferred individually to separate labelled containers and were processed in the laboratory as described in Section 3.2. Data analyses were conducted using univariate and multivariate methods described in Section 3.3. Margalef's index (*d*), Shannon-Wiener's diversity index (*H'*), Pielou's evenness index (*J*) and Caswell's *V*-statistic were calculated for all individual core data sets; Principal Component Analysis was performed using the PRIMER analysis package.

6.3 Results

6.3.1 *Lanice conchilega* and its tubes

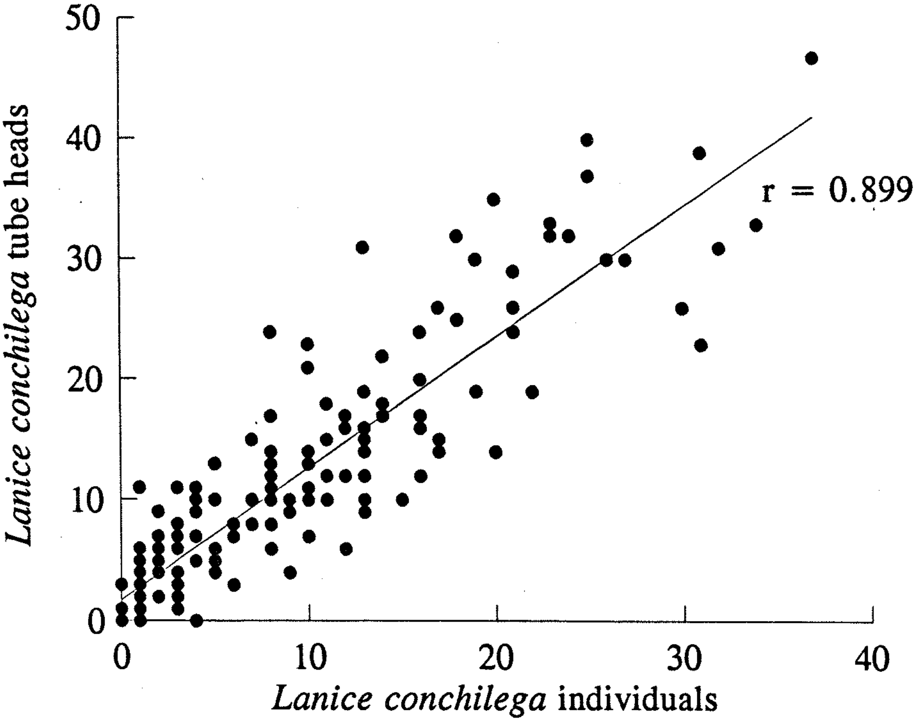
The upper graph in Figure 6.1 shows the relationship between the number of *Lanice conchilega* animals per sample and the number of *Lanice conchilega* tube heads per sample for all the macrofaunal samples taken between July 1991 and October 1992 (inclusive). A strong positive correlation existed between these two variables ($r = 0.899$; $p < 0.001$), but there were often more tube heads than *Lanice conchilega* individuals, and sometimes more *Lanice conchilega* individuals than tube heads. The equation of the regression line highlights the "excess" of tube heads that was often present in the samples:

$$T = 1.08L + 1.70$$

(T = the number of tubes; and *L* = the number of *Lanice conchilega* individuals.)

The relationship between the number of *Lanice conchilega* individuals per sample and the weight of tube material per sample is also illustrated in Figure 6.1 (lower graph). There was a similarly strong positive correlation between these two variables ($r = 0.855$; $p < 0.001$); i.e. samples containing greater numbers of *Lanice conchilega* individuals predictably contained more tube material.

Although the relationships established here between *Lanice conchilega* individuals, tube head densities and weights of tube material were all reasonably predictable, they still required confirmation and quantification. Clearly, the abundance of tube heads on the sediment surface and the amount of tube material in an area are both a reflection of the abundance of *Lanice conchilega* individuals living within that area. The tube head counts used below can therefore also be used as an approximation of the amount of tube material and the abundance of *Lanice conchilega* individuals within the different areas of sediment.



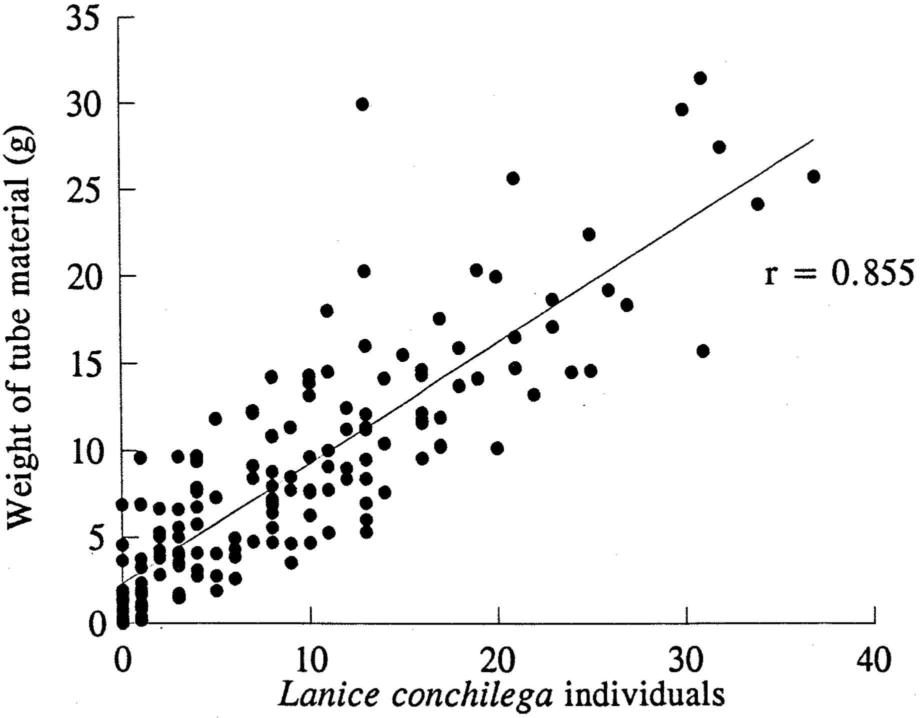


Figure 6.1 *Lanice conchilega* Density Experiments. The relationship between *Lanice conchilega* abundance and tube head density (upper graph); and the relationship between *Lanice conchilega* abundance and the weight of tube material (lower graph).

6.3.2 *Lanice conchilega* tubes and the other infauna

Complete faunal lists for the four sets of samples taken from areas containing different densities of *Lanice conchilega* tube heads are presented in Appendix 2. The total number of tube heads counted per quadrat ranged between zero and 77. The number of *Lanice conchilega* individuals present in each sample was recorded separately and these values were excluded from all calculations. The number of species, the abundance of individuals, the diversity and the evenness were therefore all calculated for the "other fauna" in each sample.

The abundance of individuals and the number of species in individual core samples were both low compared to the monthly macrofaunal samples described in Chapter 4 because of the relatively small diameter of the sampling core. However, mean abundance values in the four sets of samples were similar to the mean values previously calculated for the monthly macrofaunal samples when both are expressed as numbers per m^2. The fauna in each set of samples was dominated by relatively small polychaete species, particularly *Exogone hebes*, *Streptosyllis websteri*, *Aricidea minuta* and *Pygospio elegans*. Additional fauna occurring in samples included a number of other polychaete species, oligochaetes, and various small peracaridan crustaceans. The number of species varied between 1 and 13 per sample, the abundance of individuals varied between 1 and 39 per sample and the diversity varied between 0 and 3.52.

From an early stage in the analysis, it was evident that samples taken from the centre of quadrats containing higher densities of tube heads often contained greater numbers of species and individuals. Therefore, the changes in faunal abundance (*N*), species richness (*d*), evenness (*J*) and diversity (*H'*) that occurred with increasing tube head density were examined using linear regression (see Table 6.1). In the two "summer" months (June 1992 and August 1993) a strong positive relationship existed between tube head density (T) and the three faunal parameters: abundance (*N*), species richness (*d*) and diversity (*H'*). However, in the two "winter" months (March 1993 and March 1994) tube head density was only significantly correlated with the abundance of individuals (*N*).

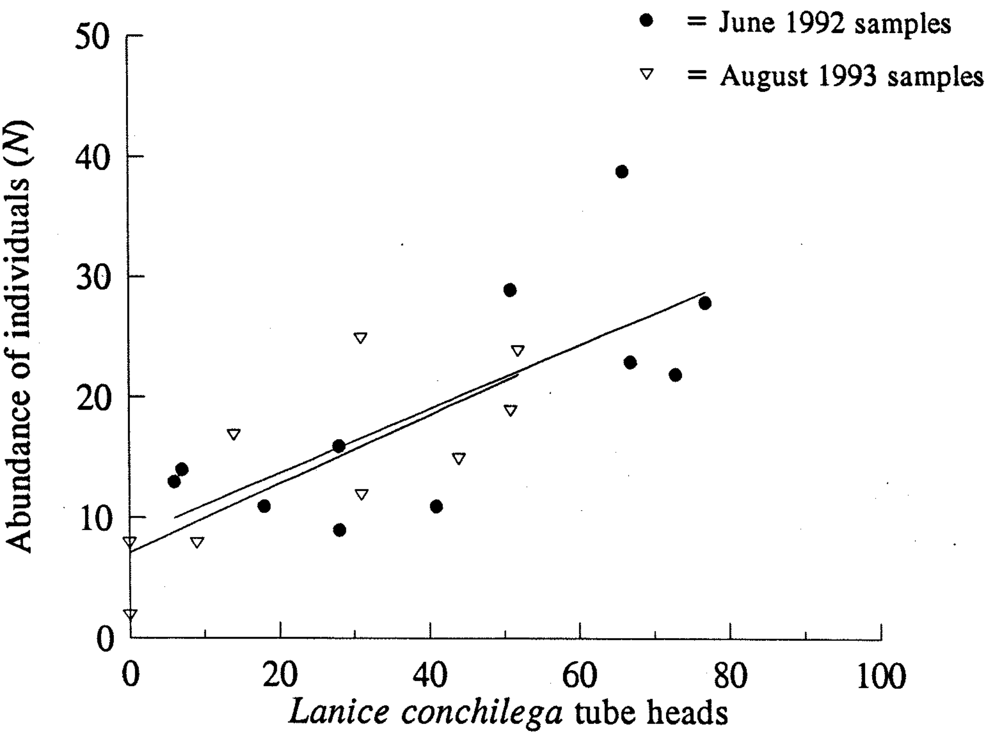
June 1992	r	p	**March 1993**	r	p
T vs N	0.739	0.009*	T vs N	0.910	<0.001*
T vs d	0.661	0.027*	T vs d	0.476	0.164
T vs J	0.032	0.926	T vs J	0.165	0.648
T vs H'	0.780	0.005*	T vs H'	0.523	0.121
August 1993	r	p	**March 1994**	r	p
T vs N	0.767	0.016*	T vs N	0.799	0.006*
T vs d	0.824	0.006*	T vs d	0.597	0.068
T vs J	0.084	0.830	T vs J	0.468	0.173
T vs H'	0.785	0.012*	T vs H'	0.398	0.254

*Values of p less than 0.05 indicate significant positive correlations.

Table 6.1. Correlation coefficients (r) and p values calculated using linear regression analysis for the number of tube heads per sample (T) against faunal abundance (N), species richness (d), evenness (J) and diversity (H').

Figures 6.2 and 6.3 present graphically the relationships between tube head density and abundance, and between tube head density and diversity for the "summer" and "winter" data sets respectively. The lower graphs highlight the difference between "summer" and "winter" with respect to changes in diversity with increasing tube head density. The diversity was relatively constant in samples taken in March 1993 (apart from 1 sample that contained just 1 individual), and actually appeared to decrease slightly with increasing tube head density in the March 1994 samples (Figure 6.3), although neither of these relationships were significant.

The evenness component of diversity (J) was not correlated with tube head density in any of the four sets of samples. The results of the V-statistic calculations conducted for the "summer" and "winter" data sets are presented in Figure 6.4.



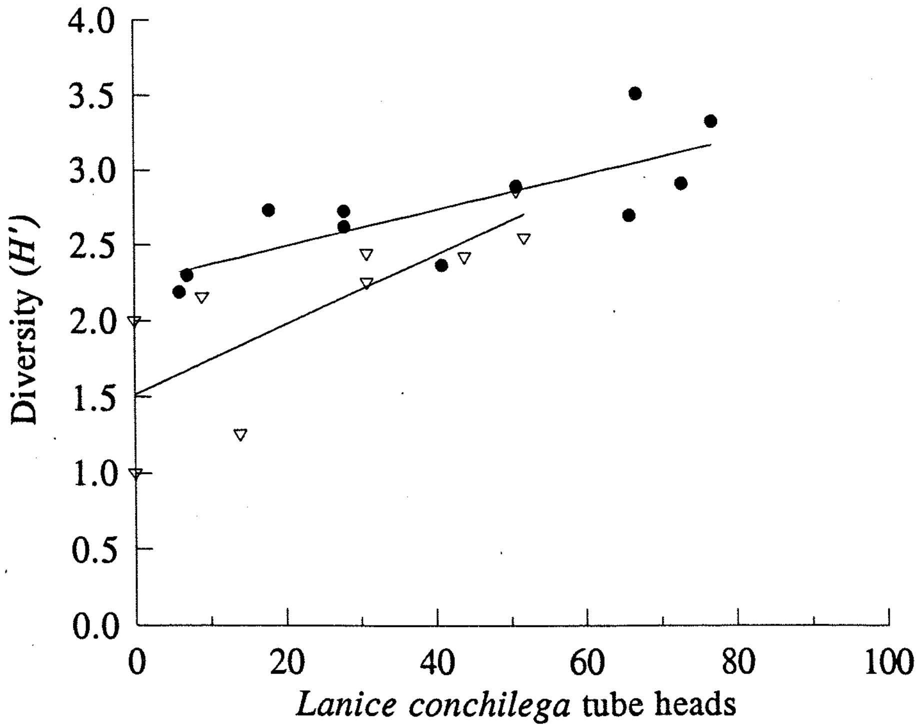
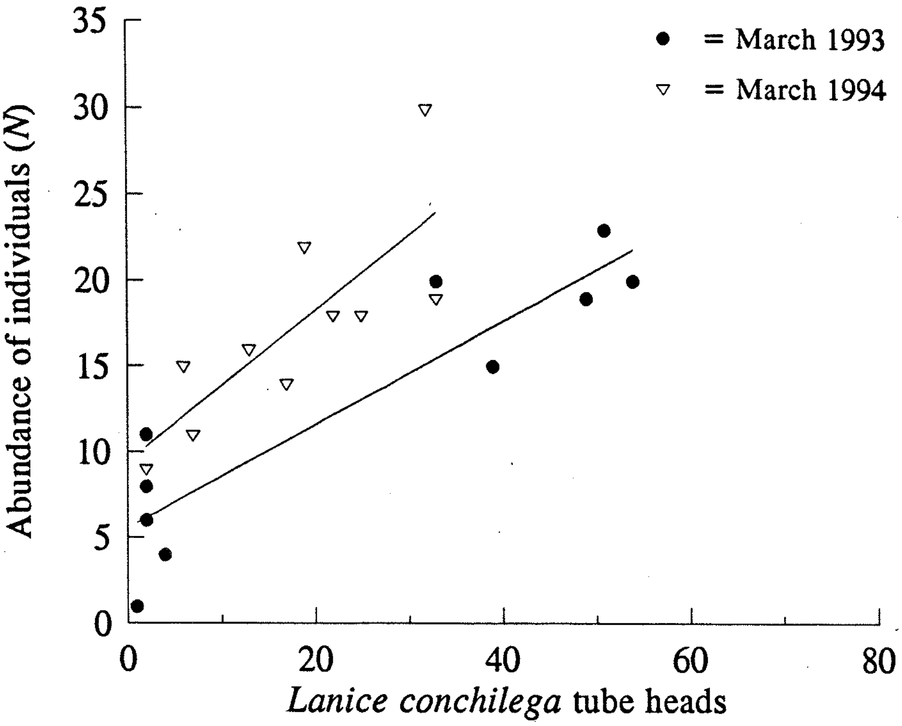


Figure 6.2 ***Lanice conchilega*** **Density Experiments.** Changes in the abundance of individuals (*N*) and diversity (*H'*) with increasing tube head density in the "summer" months June 1992 and August 1993.



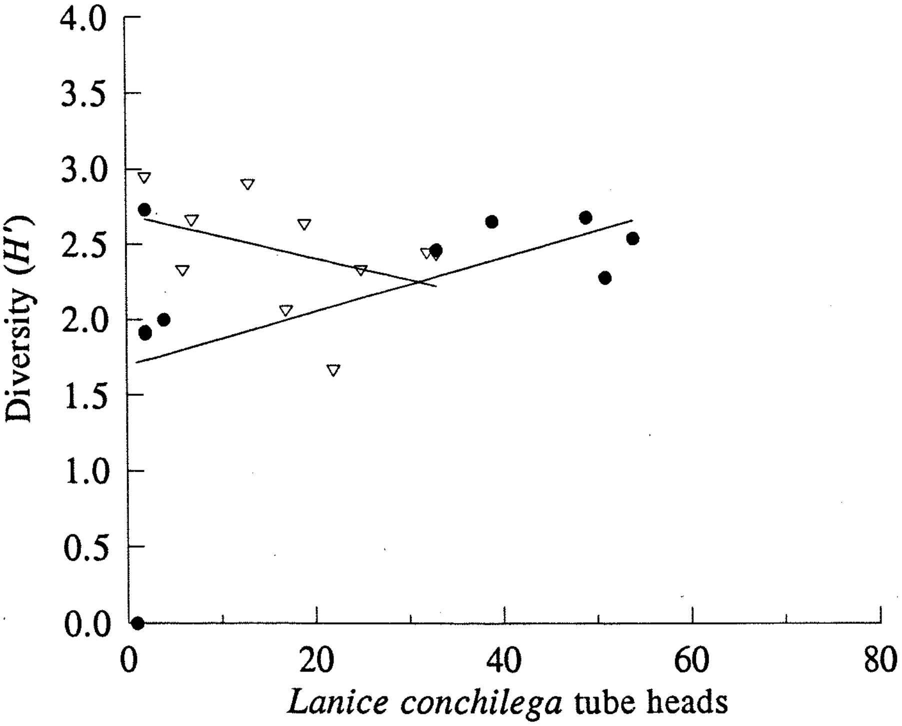
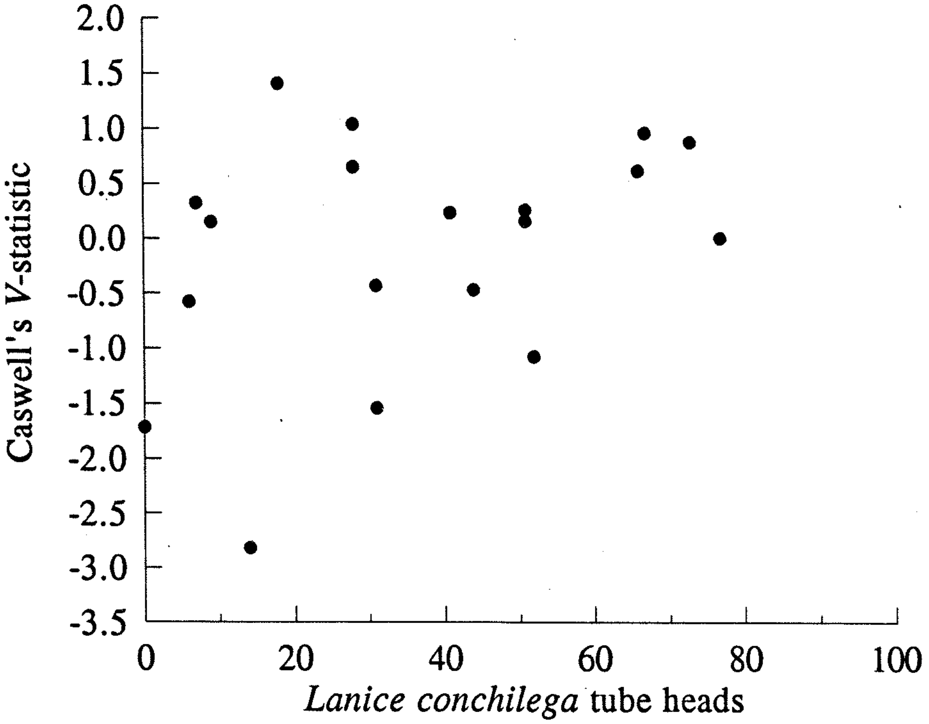


Figure 6.3 ***Lanice conchilega*** **Density Experiments.** Changes in the abundance of individuals (*N*) and diversity (*H'*) with increasing tube head density in the "winter" months March 1993 and March 1994.



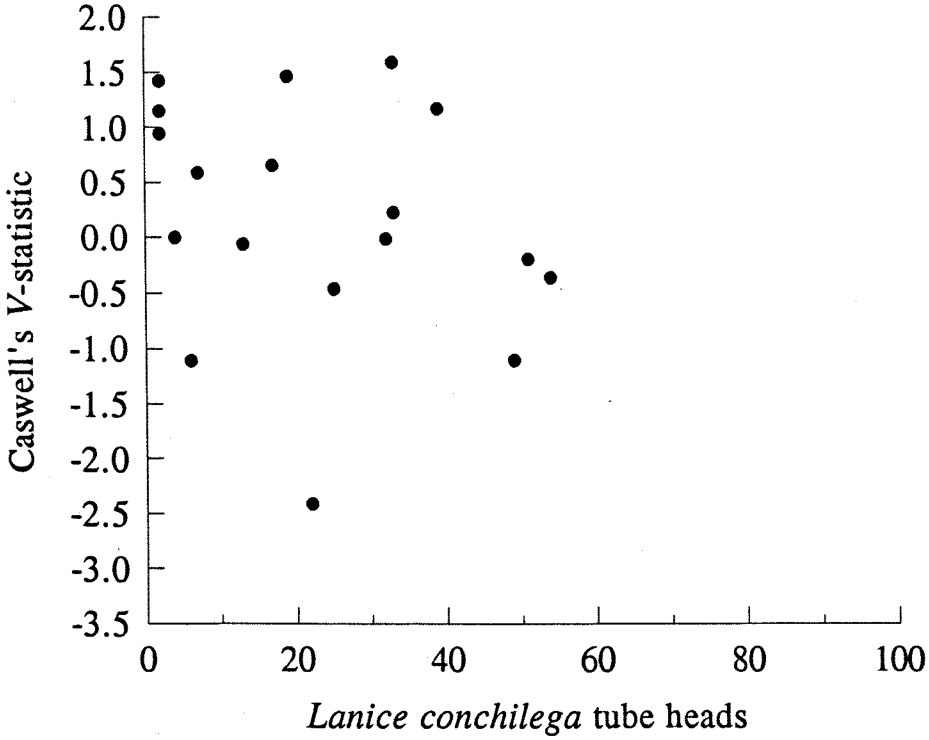


Figure 6.4 *Lanice conchilega* Density Experiments. Changes in Caswell's *V*-statistic with increasing tube head density in "summer" months (upper graph) and "winter" months (lower graph).

Values of *V* fluctuated between approximately -2.8 and 1.5, but there was no significant relationship between *V* and *Lanice conchilega* tube head density.

Principal Component Analysis

Principal Component Analysis was used to further examine any correlations that may have existed between faunal patterns and *Lanice conchilega* tube head density. The species matrices constructed for the analysis of the four data sets did not require reduction by the exclusion of rare species. Spearman rank order correlation was used to examine any relationships that existed between tube head density and either of the first two principal components (i.e. PC1 and PC2) produced by each analysis. Table 6.2 presents the correlation coefficients calculated for each of the four data sets along with their respective values of p.

	PC1	PC2
June 1992 Tube Head Density	0.793 ($p = 0.005$)*	0.688 ($p = 0.021$)*
March 1993 Tube Head Density	0.877 ($p = 0.001$)*	0.117 ($p = 0.733$)
August 1993 Tube Head Density	0.504 ($p = 0.161$)	0.563 ($p = 0.107$)
March 1994 Tube Head Density	0.576 ($p = 0.080$)	0.018 ($p = 0.\ 946$)

*Values of p less than 0.05 indicate significant correlations.

Table 6.2. Correlation coefficients and p values calculated using Spearman rank order correlation for tube head density against the first two principal components.

Tube head density was significantly correlated with the first principal component (PC1) in June 1992 and March 1993 ($p < 0.05$). It was also significantly correlated with PC2 in June 1992. In addition, there was a reasonable correlation between tube head density and PC1 in March 1994, although this correlation was not significant at the 5% level. The possible implications of these correlations are discussed later in Section 6.4.

6.3.3 *Lanice conchilega* tubes and *Exogone hebes*

This section briefly describes the analysis of the distributional patterns of individual species in the samples taken from areas containing different densities of *Lanice conchilega* tube heads. As a precursor to this analysis, the larger samples taken during the main macrofaunal study described in Chapter 4 were re-examined to establish which species (if any) were correlated with *Lanice conchilega* and its tubes. The dominant species at Solent Breezes (listed in Table 4.1) were examined individually and any significant positive correlations between a species and either *Lanice conchilega* animals or *Lanice conchilega* tubes in monthly macrofaunal samples were noted.

Linear regression analyses were conducted for each of the 23 monthly macrofaunal data sets to produce a correlation coefficient (r) and a value of p for the abundance of each species per sample against the abundance of *Lanice conchilega* individuals per sample. Similarly, monthly correlation coefficients and p values were calculated for each species against both the abundance of tube heads per sample and the weight of tube material per sample for the period between July 1991 and October 1992. A total of 770 values of r and p were calculated, but few significant positive (or negative) correlations existed. However, the abundance of *Exogone hebes* per sample was often significantly positively correlated with the abundance of *Lanice conchilega* per sample, the number of tube heads per sample and the weight of tube material per sample. All of the other dominant species were not significantly correlated with either *Lanice conchilega* individuals or tubes in more than three cases.

In the samples taken for the *Lanice conchilega* tube density experiments described in the current chapter, *Exogone hebes* was the only species to be significantly correlated with tube head density. The sampling regime was specifically designed to compare areas of sediment within patches of *Lanice conchilega* against areas outside patches, and therefore eliminated complications such as "edge effects" that may have occurred in the randomly positioned monthly macrofauna samples. Linear regression analysis was conducted for each of the 4 data sets and Table 6.3 presents the correlation coefficients (r) and the p values calculated for each regression.

	r	p
June 1992	0.747	0.008*
March 1993	0.797	0.006*
August 1993	0.346	0.362
March 1994	0.833	0.003*

*Values of p less than 0.05 indicate significant correlations.

Table 6.3. The correlation coefficients (r) and p values calculated for the relationship between *Lanice conchilega* tube heads and *Exogone hebes*.

A significant positive correlation existed between the abundance of *Exogone hebes* per sample and the number of tube heads per quadrat in June 1992, March 1993 and March 1994. However, no such relationship existed between *Exogone hebes* and tube head density in August 1993. Possible reasons for these relationships between *Exogone hebes* abundance and tube head density are explored at the end of the following discussion.

6.4 Discussion

Simple regression analysis has been used to confirm and quantify the predictable positive correlations between the density of *Lanice conchilega* and the density of tube heads, as well as the density of *Lanice conchilega* and the weight of tube material. An excess of tube heads was often present in the monthly macrofaunal samples, and there were occasionally more animals than tube heads. The relationships between *Lanice conchilega* and its tubes in these monthly samples have been examined in greater detail in Chapter 5. However, for the current chapter, it was necessary to establish that the tube head counts used were an acceptable approximation of both the abundance of *Lanice conchilega* and the amount of tube material within different areas of sediment. The following discussion legitimately assumes that areas containing relatively high densities of tube heads also contained relatively high densities of *Lanice conchilega* individuals.

Tube building species potentially influence other benthic organisms in a variety of ways, either through direct interactions or through indirect sediment-mediated interactions. The following discussion outlines the influences that *Lanice conchilega* tubes potentially exerted on the physical environment at Solent Breezes and explores the direct and indirect interactions that would then have occurred between *Lanice conchilega* (both animals and tubes) and the other fauna. The potential consequences of these interactions for the other macrofaunal animals are first examined to shed light on the consistently significant positive correlation that existed between *Lanice conchilega* tube density and the abundance of other macrofauna.

Tubes that extend above the sediment surface may either stabilise or destabilise the sediment. From a purely hydrodynamic perspective, individual animal tubes are destabilising because of the local scour that occurs around each one (Eckman *et al.*, 1981). Flume experiments have suggested that extremely dense aggregations of tubes may stabilise sediments by collectively influencing the near-bed hydrodynamics and producing a "skimming flow" effect. However, this effect has yet to be demonstrated using real tube beds (Hall, 1994). It appears that hydrodynamic stabilisation is only likely to occur in exceptional circumstances and correlations between animal tubes and stabilised sediments are more often a result of sediment binding by mucus (Eckman *et al.*, 1981).

Structures such as *Lanice conchilega* tubes that extend above the sediment surface create localised areas of both increased and decreased flow velocity, with a net loss of flow energy through friction (Carey, 1983). Carey (1983) observed that individual *Lanice conchilega* tubes clearly produced an area of reduced flow velocity, but he was unable to detect direct sedimentation of particulates from suspension. However, the net loss of flow energy produced by groups of tubes has been predicted to result in an increased net sedimentation (Buhr, 1979). Results presented in Chapter 2 suggest that a degree of sediment accumulation occurred within dense patches of *Lanice conchilega* tubes at Solent Breezes. This accumulation would have required both the sedimentation of particles from suspension and a degree of particle stabilisation.

Eckman *et al.* (1981) presents a diagram estimating the minimum tube density required to stabilise sediments as a function of tube diameter. The maximum *Lanice conchilega* tube diameter measured at Solent Breezes was less than 4mm and the maximum density of tubes observed during the present study was equivalent to 2500m^{-2}. Even a combination of these two maxima produces a point on Eckman *et al.*'s diagram that falls well below the critical line above which tubes are considered to become hydrodynamically stabilising. It is possible that the crowns present on individual tubes may have effectively increased the "tube diameter" component, resulting in a potentially stabilising influence at high tube densities. For example, tubes of 1cm diameter at densities of approximately 2000m^{-2} can be predicted to have a stabilising influence using Eckman *et al.*'s diagram. However, it is unlikely that a group of tube crowns each consisting of flexible fine filaments would influence local hydrodynamics in exactly the same way as a similar group of solid tubes. Therefore, stabilisation of sedimentary particles at Solent Breezes was perhaps more likely to have been a result of mucus binding rather than through any "skimming flow" effect.

Sediment binding by mucus is one of the most important biological mechanisms influencing sediment stability (Dyer, 1986). Potential sources of mucus in sediments dominated by a tubiculous macrofaunal species include microbes such as bacteria and benthic diatoms, meiofaunal organisms and the macrofaunal tube builder itself. Large tubes enhance diffusional fluxes (Aller, 1980; Aller and Yingst, 1978) and may therefore encourage microbial growth, thus promoting mucus binding (Eckman *et al.*, 1981). Furthermore, meiofaunal abundance at Solent Breezes was generally greater in areas of sediment containing high *Lanice conchilega* tube densities (see Chapter 7). The mucus produced by *Lanice conchilega* during tube building and feeding was also a likely contributor to the relatively high concentrations of sedimentary bioavailable protein present in areas of high tube densities (see Chapter 2). Sediment stabilisation and net accumulation have been suggested as the controlling mechanisms that resulted in the significant increase observed in the depth of sediment above the underlying clay layer at higher tube densities (see Chapter 2).

The enhanced stability and accumulation of sediment within dense patches of *Lanice conchilega* clearly had the potential to significantly influence the other resident macrofauna. In each set of samples taken for this section of the study, the total abundance of other macrofaunal individuals was positively correlated with tube head density. Firstly, abundance was arguably influenced by the increase in available vertical space that occurred with increasing tube density. As the depth of sediment above the clay layer increased at higher tube densities, the volume of overlying sediment per unit area must also have increased. Samples were taken to a depth that was consistently below the start of the clay layer, and therefore always included all of the overlying muddy-sand sediment. As macrofaunal distributions did not extend into the relatively hard clay, an increase in the depth of the overlying sediment would have essentially constituted an increase in sample volume.

High densities of tube building species can be associated with diminished numbers of burrowing animals, but have not been observed to totally exclude burrowers (Wilson, 1991b; Woodin, 1974). Previously observed limitation of burrowing organisms appears to have been principally a result of a physical reduction in infaunal space. In addition, Brenchley (1982) demonstrated that dense tube mats may restrict the movement of burrowing deposit feeders. However, there is no evidence to suggest that high *Lanice conchilega* tube densities limited the abundance of other infaunal species at Solent Breezes. In fact, it has been illustrated that the opposite was true because of a relative increase in vertical space in high density areas. The maximum observed density of tubes was $2500m^{-2}$, potentially giving each individual a minimum of $4cm^2$ of sediment surface surrounding it (average value if all tubes were occupied). Such densities are unlikely to have significantly adversely affected the abundance of other animals through space limitation or the restriction of movement, particularly as the fauna in each set of samples was dominated by relatively small species (e.g. *Exogone hebes*, *Streptosyllis websteri*, *Aricidea minuta*, *Pygospio elegans* and *Tanaissus lilljeborgi*).

Species living at or near the sediment-water interface may have been positively influenced by the stabilising influence of mucus binding in high tube density areas. These species are potentially susceptible to passive re-suspension, and sediment stabilisation could have reduced the impact of any wave-induced disturbance. The passive transport of the adults of various polychaete species by waves and tidal currents has been observed by Tamaki (1987). Distributional changes in one species during winter were attributed to its habit of living in near surface sediments, whereas species living deeper below the surface were less susceptible to washout. Chapter 7 considers passive re-suspension and transport as a mechanism potentially influencing meiofaunal distributions in high and low tube density areas. In the relatively low-energy environment at Solent Breezes, this mechanism may have been important in determining the spatial distributions of juvenile macrofauna (i.e. the temporary meiofauna), but may have played a less dominant role in the determination of adult distributions. To accurately establish the relative importance of this mechanism in controlling macrobenthic distributions, the mobility and resistivity to wave action of each developmental stage of each species would need to be investigated. However, the possibility remains that the small scale spatial distributions of at least some of the species present at Solent Breezes were affected by the stabilising influence of mucus binding in high tube density areas.

Lanice conchilega tube density also could have significantly influenced the overall abundance of macrofauna from a food resource perspective. The sediment accumulating within dense patches of tubes would include both inorganic and organic particles. In Chapter 2 it was established that no significant change in total organic content occurred in the surface sediment with increasing tube density. However, the simultaneous accumulation of both inorganic and organic particles would not necessarily increase the concentration of organic material in surface layers. Nevertheless, the significant increase in sediment volume above the underlying clay layer that occurred with increasing tube density would have constituted an increase in both inorganic and organic particles. Therefore, the increase in sediment volume would not only provide more space for infaunal animals, but more importantly would also provide organic material within that space as potential food for deposit feeding species.

Food supply to the benthos is fundamentally important in determining many of the biological characteristics of infaunal assemblages (Olafsson *et al.*, 1994). However, sedimentary organic material is very heterogeneous and the characterisation of the different food resources used by different deposit feeders is far from complete (Lopez and Levington, 1987; Lopez *et al.*, 1989). The gross measurement of total organic content used in the present study did not allow any changes in specific food resources to be monitored. It is conceivable that different organic components fluctuated independently with increasing tube density, even when the total organic content of surface sediments remained relatively stable. Mattin (1992) detected significantly higher concentrations of bioavailable protein in areas containing dense aggregations of *Lanice conchilega* tubes. It has previously been suggested that one potential source of this labile protein was the mucus produced by *Lanice conchilega*. This mucus and its associated microbial populations may have provided an important additional source of nutrition for both juvenile and adult deposit feeders.

Olafsson *et al.* (1994) recently reviewed the laboratory experiments that have analysed the effects of varying food levels on soft-sediment invertebrates. He concluded that there was a strong indication that both individual growth and reproductive output are sensitive to food levels, but the survival of adult benthic invertebrates is relatively insensitive to food supply. Although the physiology of adult invertebrates allows a reduction in growth and fecundity to maximise survival in conditions of insufficient food, the higher weight-specific metabolic demands of juvenile animals may increase their vulnerability to starvation (Tenore and Chesney, 1985). A number of studies have indicated that food shortage is responsible for mortality in the juveniles of benthic species (see Olafsson *et al.*, 1994). Therefore, if *Lanice conchilega* tube density significantly influenced the availability of suitable food resources, this would potentially lead to an enhanced level of survival in infaunal juveniles in high tube density areas.

There are numerous ways in which *Lanice conchilega* and its tubes potentially influenced the larval and juvenile stages of other infaunal species at Solent Breezes. The relative importance of pre- and post-settlement processes in structuring soft-sediment communities is by no means well established, and it seems that the different adult-juvenile interactions that have been previously inferred from field and laboratory experiments are rarely universally applicable. In addition, some of the proposed mechanisms are at least in part antagonistic with respect to their ultimate expression, i.e. the influence of one mechanism may be facilitatory and the influence of another co-occurring mechanism may be inhibitory. Nevertheless, it is necessary to outline the important direct and indirect interactions that could have occurred between *Lanice conchilega* and the non-adult stages of the other infauna, and therefore attempt to determine if any were likely to have influenced faunal characteristics in areas of high tube density.

Local hydrodynamics are expected to influence larval settlement on at least some spatial scale (Snelgrove and Butman, 1994). Therefore, as animal tubes exert important effects on flow above the sediment surface, they are likely to influence larval settlement and consequently adult abundances. Eckman (1979) examined recruitment in various polychaetes and tanaid crustaceans near simulated tubes and concluded that larval distributions in the benthos were influenced by fine-scale hydrodynamics. Tube spacing and density have also been shown to affect recruitment (Eckman, 1983), but it has not been established whether or not passive deposition was entirely responsible for the larval patterns observed (Snelgrove and Butman, 1994). Although passive deposition of larvae operates on several spatial scales, inferences may be complicated by the ability of some larvae to actively respond to some aspect of the flow environment or to some resultant sedimentary variable (e.g. organic matter). For example, larvae passively entrained into small experimental depressions in different types of sediment have been observed to escape if the substratum is unsuitable (Snelgrove *et al.*, 1993).

At Solent Breezes, a net accumulation of sediment occurred in areas containing higher densities of *Lanice conchilega* tubes. Therefore, if passive deposition was a dominant factor controlling the settlement of planktonic larvae, settlement may have been enhanced in areas of high tube density as a result of small-scale hydrodynamics at the sediment-water interface. In addition, the presence of increased concentrations of muco-proteins on the sediment surface had the potential to influence the settlement of some larvae through active habitat selection mechanisms (see later). However, the existence of either enhanced passive settlement or active habitat selection remains unconfirmed.

Juveniles may be redistributed after settlement during the early stages of benthic life. Such redistribution may be a significant dispersal mechanism both for recently settled larvae and, perhaps more importantly, for the early developmental stages of species with entirely benthic lifecycles (i.e. direct developers) (Sigurdsson *et al.*, 1976). Juveniles living at or near the sediment-water interface at Solent Breezes were therefore particularly susceptible to disturbance and passive re-suspension caused by increased wave action. The stabilising influence of mucus binding in high tube density areas potentially reduced the impact of any wave-induced disturbances.

Chapter 7 will show that there was no evidence to suggest that total juvenile densities were significantly greater in high tube density areas. Superficially this seems to imply that no significant interactions occurred between *Lanice conchilega* and the juvenile stages of other infaunal species. However, the physical adult-juvenile interactions described above potentially facilitate larval recruitment or juvenile resettlement following re-suspension. In contrast, direct interactions between large tube building animals (rather than their tubes) and juvenile infauna are predominantly inhibitory (see below), and therefore act in opposition to any facilitatory interactions.

Woodin (1976) hypothesised that tube builders occupying a large proportion of the available space should effectively inhibit larvae through their feeding and defecation on the sediment surface. More specifically, Wilson (1980) demonstrated that the feeding activities of the terebellid polychaete *Eupolymnia heterobranchia* significantly lowered the survivorship of the larvae of *Nereis vexillosa* in the laboratory. Field experiments have often been unable to satisfactorily distinguish between avoidance of high adult densities by larvae and increased mortality in settling larvae caused by ingestion by the resident adults (Wilson, 1991). In an attempt to assess the relative importance of pre- and post-settlement processes, Olafsson *et al.* (1994) examined all previously documented experiments that investigated the influence of adults on recruitment in soft sediments. They concluded that adult-juvenile interactions generally reduce rather than enhance recruitment, and the controlling influence of adults on juvenile density appears to operate mainly after settlement rather than while larvae are in the water column. Some studies have indicated that changes in sediment chemistry caused by the activities of adult invertebrates may alter the behaviour of settling larvae (e.g. Woodin, 1991). However, the most consistently influential adult-juvenile interactive mechanism is that between predatory infaunal species and recently settled juveniles.

The overall implication is that the activities of *Lanice conchilega* worms in high density areas are likely to have negatively affected the juveniles of other species, despite the fact that the majority of these juveniles remained in the benthos throughout their development. It is conceivable that changes in sediment chemistry (including an increase in muco-protein concentration) in high density areas altered the behaviour of potentially settling planktonic larvae, resulting in either a negative or positive effect depending on the behavioural response induced. In addition, if *Lanice conchilega* actively ingested small juvenile stages (as observed by Wilson (1980) for *Eupolymnia heterobranchia*), it would essentially have been acting as a predator and this would have had a significant adverse influence on juvenile survivorship, even if the majority of juveniles were direct developers.

It has been shown that the various potential influences of *Lanice conchilega* animals and their tubes on juvenile recruitment and survivorship include both facilitatory and inhibitory interactions. The effects of such antagonistic controlling mechanisms would conceivably counteract each other. This appears to have resulted in a lack of any consistently significant difference between areas of high and low tube density with respect to total juvenile abundance (as described in Chapter 7).

The consistently significant correlation between *Lanice conchilega* tube density and the abundance of other macrofauna therefore seems more likely to have been a result of direct or indirect adult-adult interactions. In particular, the increased sedimentation and stabilisation of particles that resulted in a net accumulation of sediment at high tube densities was predicted to have resulted in an increase in infaunal space. In addition, the mucus derived labile organic matter and its associated microbes could have enhanced levels of potential food resources for deposit feeders in denser *Lanice conchilega* patches.

Lanice conchilega tubes may also have provided a certain level of localised refuge from some forms of epibenthic predation pressure. Experiments involving the exclusion of epibenthic predators from areas of sediment have often resulted in increases in faunal abundance and biomass. However, a controlling influence is not always exerted by these predators over infaunal densities and there is a significant degree of variation between results, both within and between different habitat types (Olafsson *et al.*, 1994; Wilson, 1991b). Shorebirds can feed at remarkable rates on the invertebrate fauna of tidal flats during low tide. Some species may seriously deplete population densities of particular prey species (e.g. *Corophium*, Goss-Custard *et al.*, 1977). During periods of immersion, fish and mobile crustaceans may feed extensively on intertidal invertebrates (e.g. Raffaelli *et al.*, 1990). High densities of shrimps, prawns, crabs, flatfish and gobiid fish may use beaches and tidal flats as nursery grounds, consuming large numbers of infaunal animals (Raffaelli and Hawkins, 1996). However, it must be noted that *Lanice conchilega* may itself be susceptible to predation from some types of epibenthic predators (e.g. flatfish) (DeVlas, 1979; 1981). In addition, if tubes were acting as refuge areas, their influence may only have been significant on a relatively small scale, with the risk of predation increasing with distance from the nearest tube.

This discussion has concentrated on the consistently significant positive correlation between *Lanice conchilega* tube density and the total abundance of other fauna. However, the univariate and multivariate analyses described in the results section of this chapter highlighted several other aspects that require consideration. A positive correlation between tube density and the diversity of other fauna was evident in summer, but this relationship did not exist in winter. In summer, species richness was the dominant component controlling diversity, with a greater number of species generally occurring in areas with higher tube densities. However, in winter relatively rare species were lost from both high and low density areas. The increased abundance that was observed with increasing tube density was not predominantly caused by the addition of more species, but was a result of higher abundance in a few species. This lead to an increase in dominance (or a decrease in evenness) which negatively influenced diversity and consequently there was no significant increase in diversity with increasing tube density during winter. Temperatures during winter have previously been shown by Buchanan and Moore (1986) to exert a clear influence on diversity. Relatively cold temperatures favoured survival in the dominant species at the expense of the lesser ranked species (Buchanan and Moore, 1986). An additional explanation for the loss of rare species from both high and low density areas could have involved the migration of these species to subtidal sediments during winter. Intertidal macrofauna may move offshore as an active response to low temperatures in winter (Beukema and De Vlas, 1979; Dean, 1978). It is conceivable that relatively rare species occurring on the shore at Solent Breezes were less resilient to winter temperatures or were essentially subtidal species on the edge of their respective distributions. Consequently individuals belonging to these species may have migrated to subtidal areas during winter, irrespective of whether they were originally living in high or low tube density areas.

The principal component analysis conducted for the current chapter was used to further investigate the relationships between faunal patterns and *Lanice conchilega* tube density in each set of samples. In June 1992 and March 1993 tube density was significantly correlated with the first principal component. Therefore, *Lanice conchilega* and its tubes arguably exerted an important influence on faunal characteristics during these months. Unfortunately, there were no complementary sediment data directly related to the faunal samples taken for this section of the study to use in the correlation analysis alongside tube density. However, it has already been established in Chapter 2 that no significant changes occurred in the granulometric characteristics or the total organic content of sediment with increasing tube density (two entirely unrelated sets of sediment samples were taken in June 1992 and September 1993). In addition, it has been argued that the significant changes observed in bioavailable protein and sediment depth (above the clay layer) were caused by the presence and activities of *Lanice conchilega*. The mechanisms through which *Lanice conchilega* potentially influenced the other fauna have already been discussed with particular reference to these last two sedimentary variables.

In March 1994 the relationship between *Lanice conchilega* tube density and the first principal component still existed ($p = 0.08$), but the correlation was not significant at the 5% level. This reduction in significance was probably a result of the relatively low tube densities present in this month. The maximum density was only 33 per quadrat (equivalent to approximately $465m^{-2}$), compared to at least 52 per quadrat (equivalent to approximately $732m^{-2}$) in the three other months.

In August 1993 the relationship between *Lanice conchilega* tube density and the first principal component did not exist, suggesting that there was one or more environmental variables that exerted a stronger influence on the fauna. It is postulated that the influence of tube density was overridden by the presence of large amounts of macroalgae that covered the sediment surface in this month. During the August 1993 sampling visit, the percentage macroalgal cover was routinely estimated to be 70-80%. In comparison, macroalgal cover on the two winter sampling visits was negligible (less than 5%), and in June 1992 it was only 30%. The macroalgae could have influenced the fauna in several ways. Firstly, macrophytes produce mucus. This second source of mucus would have been present in both high and low tube density areas, and therefore may have "interfered" with the influence of *Lanice conchilega*-derived mucus. The macrophytic mucus may have enhanced stabilisation across the shore and was a potential source of food for deposit feeders. Secondly, the macroalgae itself was a potential food source, particularly if fragments became incorporated into the pool of sedimentary organic matter, which may have had a localised influence on the spatial distributions of deposit feeding species. Thirdly, the macroalgae provided another potential source of refuge for surface or near-surface dwelling species. This again had the potential to override any similar influence originating from the presence of tubes in relatively high densities. The influence of macroalgae may also provide an explanation for the breakdown of the relationship between tube density and the abundance of *Exogone hebes* in August 1993 (see below).

A significant positive correlation was found to exist between tube density and *Exogone hebes* in June 1992, March 1993 and March 1994. Chapter 7 will also show that both juvenile and adult *Exogone hebes* were consistently found in greater abundance in high tube density samples. Many of the interactions between *Lanice conchilega* and the other fauna discussed above were particularly applicable to species inhabiting the uppermost layers of the substratum. *Exogone hebes* is a free-living, active polychaete that lives on or near the sediment surface. Both adult and juvenile *Exogone hebes* would therefore have been positively influenced by any stabilising influence of mucus binding in high tube density areas, and their susceptibility to passive re-suspension would consequently have been reduced. In addition, *Lanice conchilega* tubes may also have provided a certain level of localised refuge from predation pressure. However, if this mechanism significantly influenced *Exogone hebes*, it should also have influenced other species of a similar size living in the uppermost sediment layers, particularly the other dominant syllid polychaete *Streptosyllis websteri*. There was no significant relationship between *Streptosyllis websteri* and tube density.

One fundamental difference between *Streptosyllis websteri* and *Exogone hebes* rests in their feeding habits. *Streptosyllis websteri* is known to feed on benthic diatoms (Garwood, 1982; Hartmann-Schröder, 1971), whereas all members of the subfamily Exogoninae are selective surface deposit feeders that may also feed opportunistically on carrion and live prey (Fauchald and Jumars, 1979). The mucus produced by *Lanice conchilega* may have represented a potential food source for *Exogone hebes*. This potential interaction may provide a simple explanation for their association in June 1992, March 1993 and March 1994, and the absence of a relationship in August 1993.

Although *Lanice conchilega* and *Exogone hebes* are radically different with respect to body size and feeding apparatus, their documented food sources appear to be similar. Both are able to act as selective deposit feeders with the capacity to take small (i.e. meiofaunal) invertebrates, and may therefore both occur in greater densities where potential food items are more abundant. Furthermore, the crowns of *Lanice conchilega* tubes passively contribute to the collection of food particles. Therefore, *Exogone hebes* may have been "attracted" to high tube density areas where the net loss of flow energy could have resulted in an increased sedimentation of suitable food particles. Clearly, these food related mechanisms rely on the absence of any significant competitive interaction between *Lanice conchilega* and *Exogone hebes*.

Exogone hebes was the only dominant species at Solent Breezes that has previously been observed to have a viviparous mode of development (Pocklington and Hutcheson, 1983). This viviparity may have been occurring in the *Exogone hebes* population at Solent Breezes (see Chapter 7), and may therefore have resulted in the production of relatively large "first stage" benthic juveniles. It has been suggested that *Lanice conchilega* actively ingested small juvenile stages and therefore had a significant influence on juvenile survivorship. The fully differentiated juveniles produced by *Exogone hebes* may have been too large to be at risk from predation by *Lanice conchilega*. The elimination of this inhibitory mechanism would have allowed any facilitatory influences of *Lanice conchilega* and its tubes to become more dominant.

CHAPTER 7

The Meiofauna

7.1 Introduction

The meiofaunal section of this study explores the possibility that *Lanice conchilega* and its tubes potentially influenced the meiofaunal animals present at Solent Breezes. The sampling programme was designed to examine temporal changes in the meiofauna over one annual cycle, and to compare the meiofauna present within patches of *Lanice conchilega* tubes with the meiofauna occurring between patches throughout this period. Investigations were simplified by restricting the sampling to areas of high tube densities and areas of low (usually zero) tube densities, and therefore not including any intermediate densities. The study investigated both the permanent members of the meiofauna (i.e. those animals that remain within the meiofaunal size range) and the temporary members of the meiofauna - in particular the juveniles of macrofaunal polychaete species.

7.2 Field Work and Laboratory Methods

The fieldwork for the meiofaunal study was conducted between February 1993 and March 1994. Regular monthly sampling visits were made to the mid-shore site at Solent Breezes, and on each visit sampling was completed within one hour of low tide. Sets of samples were taken from two areas of high *Lanice conchilega* tube density (i.e. High Density A and B), and two areas of low *Lanice conchilega* tube density (i.e. Low Density A and B). For each set of samples, a circular "quadrat" (surface area = $0.071m^2$) was placed over a selected area of sediment and the number of *Lanice conchilega* tube heads visible on the sediment surface within the quadrat was counted. High density areas consistently contained at least 50 tube heads and low density areas usually contained no tube heads. A single set of samples consisted of a total of 10 samples taken from within a quadrat - i.e. 5 samples for the "permanent meiofauna" study, and 5 samples for the "temporary meiofauna" study.

7.2.1 The permanent meiofauna

Sampling of the permanent meiofauna was restricted to the surface layers of sediment. The majority of animals live in the top 6-8 cm in muddy sediments (Holme and McIntyre, 1984), but it is acknowledged that meiofaunal animals can occur to greater depths in sandy sediments. The sampling regime was designed to examine the main meiofaunal taxa in surface layers to a consistent depth, and the volume of samples taken each month had to be restricted to allow processing of all samples to be completed successfully. Cores of approximately 1cm diameter have been found to be suitable for estuarine sediments where meiofaunal densities are usually high (Holme and McIntyre, 1984).

Five samples were taken from evenly spaced positions within each quadrat using a small corer (internal diameter = 1.4cm). Each core sample was taken to a depth of 6.5cm, resulting in a total sample volume of 10cm^3. The samples were ejected into individual glass vials using a small, well fitting plunger, and were fixed and stained in the laboratory using a solution of 4% formalin containing Phloxine B (C.I. No. 45410) at a concentration of 0.1gl^{-1}. This preservation method was considered to be acceptable for the main meiofaunal taxa that were to be identified and enumerated.

The meiofauna was extracted from samples using a simple decantation method. Each sample was washed into a 1 litre capacity measuring cylinder with tap water and the volume of water was made up to approximately 900ml. The cylinder was stoppered and then inverted five times to suspend the sediment and fauna. After allowing the cylinder to stand for 10 seconds, the liquid was carefully decanted into a 63μm sieve. The complete process was then repeated four times, and the material remaining on the sieve was carefully washed into a Petri dish for analysis.

A grid pattern on the base of the Petri dish allowed the whole of the dish to be scanned accurately under a low power binocular microscope. The squares of the grid were analysed in turn and the fauna in each grid was identified, enumerated and recorded. Finally, the fraction of each sample remaining in the measuring cylinder was washed into a separate Petri dish and was analysed to check the efficiency of the decantation method. In addition, larger specimens of macrofaunal species occasionally occurred in this fraction and these could therefore be recorded. The meiofaunal animals were identified into the following basic taxa:

(i) Foraminiferida;

(ii) Nematoda;

(iii) Acarina;

(iv) Harpacticoida;

(v) Nauplii;

(vi) Ostracoda;

(vii) Tardigrada.

In addition, occasional juvenile and adult specimens of macrofaunal groups (i.e. polychaetes, oligochaetes and crustaceans) were identified to the lowest possible taxonomic level.

7.2.2 The temporary meiofauna (juvenile macrofauna)

The five "temporary meiofauna" samples were also taken from evenly spaced positions within each quadrat, but were taken using a larger corer (internal diameter = 3.40cm) to a depth of 10cm. This larger core was used to increase the sample densities of the various polychaete juveniles and other components of the temporary meiofauna, as these were significantly lower in abundance than the major meiofaunal taxa listed above. The sampling regime was designed to maximise the number of juvenile specimens that could be identified and enumerated accurately in the time available for this section of the study.

Core samples were ejected individually into small re-sealable plastic bags and were fixed and stained in the laboratory using a solution of 4% formalin containing Phloxine B (C.I. No. 45410) at a concentration of $0.1gl^{-1}$. The fauna was extracted from each sample using the decantation method described above for the permanent meiofauna samples. Because of the relatively large size of each sample, the material remaining on the 63µm sieve was divided into four or more portions which were analysed individually. Each portion was washed into the Petri dish and the grid pattern on the base again allowed the whole dish to be scanned accurately under a low power binocular microscope.

The temporary meiofauna in each sample (i.e. juvenile and small adult specimens of macrofaunal species) was extracted using a glass pipette and retained in 70% ethanol. The permanent meiofaunal taxa were ignored. The fraction of each sample remaining in the measuring cylinder was washed into a separate Petri dish and the larger specimens of macrofaunal species that occasionally occurred in this fraction were also extracted and retained in 70% ethanol.

Animals were identified and enumerated using a low power binocular microscope and a high power compound microscope. The identified fauna from each sample was then stored in 70% ethanol. The identification of some early juvenile stages was initially hampered by a lack of distinguishing features, and these stages were given temporary descriptive names. However, as species specific characteristics developed over time during the sampling period, their true identities were revealed.

7.3 Results

7.3.1 The permanent meiofauna

The meiofauna in samples taken from both high and low density areas of *Lanice conchilega* tubes during the sampling period are presented in Appendix 2. Two sets of samples (A and B) were taken from low tube density areas and two sets (A and B) were taken from high density areas each month. In each table mean values are given for each individual set of samples (i.e. either A or B) and for the two sets combined (i.e. A and B = Total).

The lowest abundance of meiofaunal animals in a single core sample was 36 in March 1993, and the highest abundance was 1115 in August 1993. Similarly, the minimum mean abundance of meiofaunal animals in a single set of five samples was 65.8 in March 1993 (Low Density B) and the maximum was 616.0 in August 1993 (High Density B). Figure 7.1 presents the mean number of individuals in each set of meiofaunal samples taken during the sampling period. The overall abundance of meiofauna was consistently greater in samples from high tube densities than in samples from low tube densities, but variation between samples was generally high.

Representatives from the Foraminiferida, Nematoda, Harpacticoida, Ostracoda and Tardigrada were consistently present in all sets of samples and these groups are addressed individually below. Other groups occurring occasionally in samples included the Acarina, small pericarid crustaceans (Cumacea and Tanaidacea) and small polychaetes in various stages of development.

The following sections outline the patterns of change in abundance of the dominant meiofaunal taxa at Solent Breezes over the 13 month sampling period. Figures 7.2 to 7.4 show the mean number of individuals of these taxa found each month in areas of both high and low *Lanice conchilega* tube densities. The mean abundance values used for these plots are total means (i.e. A and B combined) for either high or low tube density samples. However, the comparisons drawn below between the two areas of high tube density and the two areas of low tube density use the individual sets of samples (i.e. High Density A and B; and Low Density A and B). Differences in the mean values were analysed using a standard one way analysis of variance (ANOVA) followed by the Student-Newman-Keuls Test for pairwise multiple comparisons.

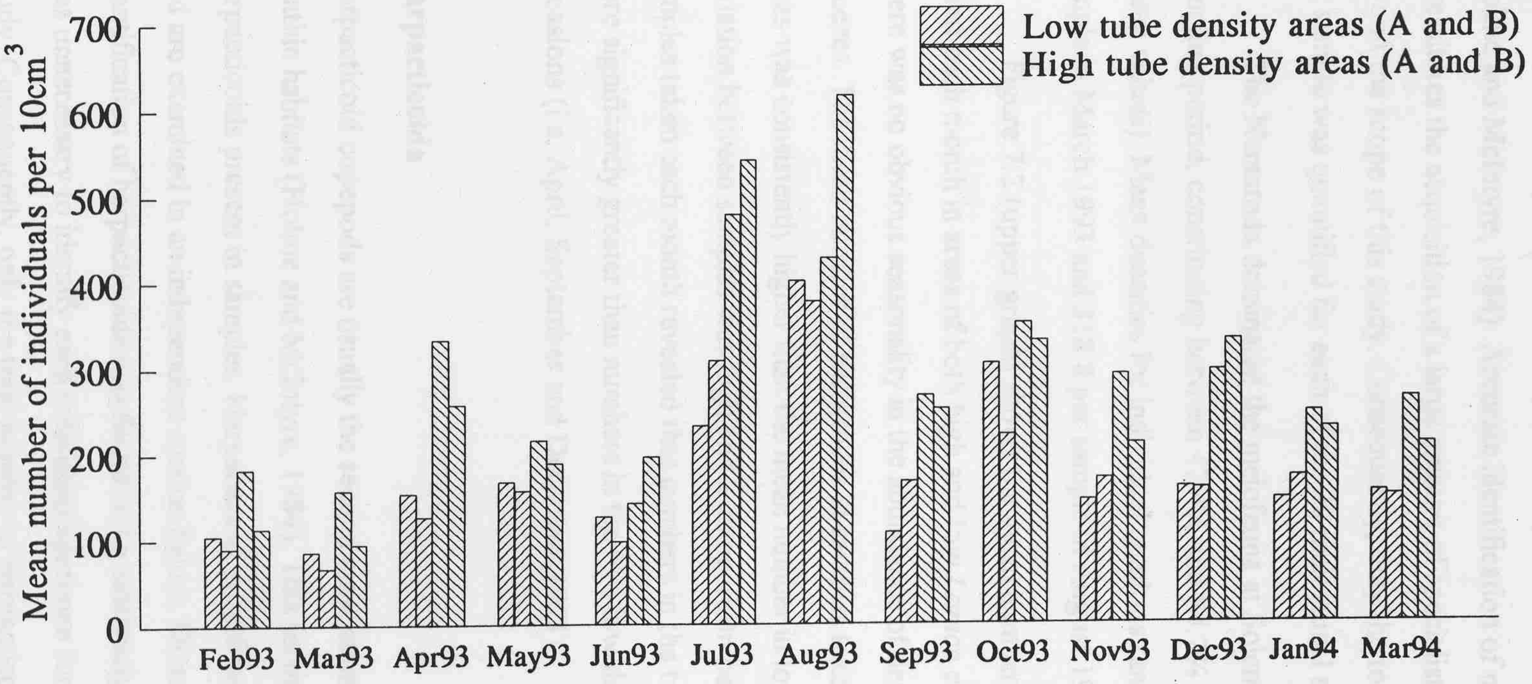


Figure 7.1 The Permanent Meiofauna. The average abundance of meiofaunal animals in the four sets of samples taken each month (i.e. two sets from high *Lanice conchilega* tube density areas (A and B) and two sets from low tube density areas (A and B)).

Nematoda

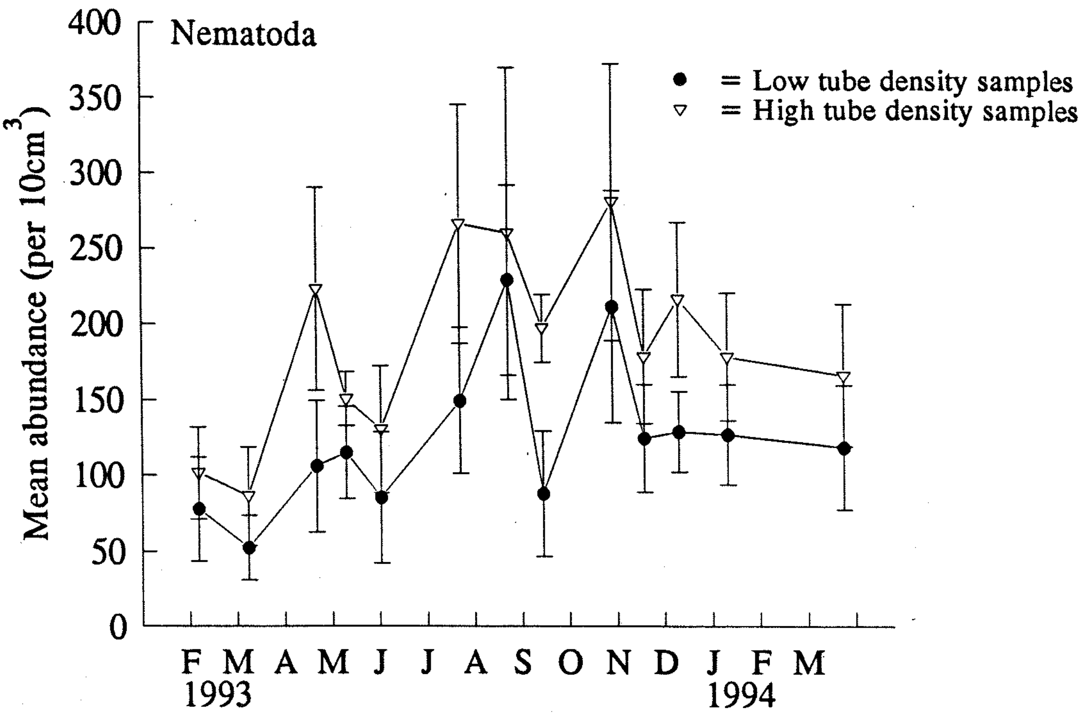
The Nematoda is the dominant meiofaunal group in most benthic habitats, and freeliving marine species are often particularly abundant in intertidal sediments (Holme and McIntyre, 1984). Accurate identification of nematode species necessitates the acquisition of a large amount of specialist knowledge that extends beyond the scope of this study. Consequently, only the total number of nematodes per sample was quantified for each of the 20 meiofaunal samples taken each month.

The Nematoda dominated the meiofauna at Solent Breezes throughout the sampling period, constituting between 47.4% and 84.7% of the fauna in samples (mean values). Mean densities for individual quadrats ranged between 40.3 per sample in March 1993 and 318.8 per sample in August 1993.

Figure 7.2 (upper graph) shows the mean number of nematodes (± S.D.) found each month in areas of both high and low *Lanice conchilega* tube densities. There was no obvious seasonality in the abundance of nematodes at Solent Breezes. The mean number of nematodes in samples taken from high tube density areas was consistently higher than the mean number in low density areas. However, variation between samples was high and a comparison between the four sets of samples taken each month revealed that numbers in the two high density areas were significantly greater than numbers in the two low density areas on only three occasions (i.e. April, September and December 1993).

Harpacticoida

Harpacticoid copepods are usually the second most abundant meiofaunal group in benthic habitats (Holme and McIntyre, 1984). This section only considers the adult harpacticoids present in samples. Harpacticoid nauplii were enumerated separately and are examined in an independent section below. Dissection and accurate identification of harpacticoids was found to be extremely labour intensive and it was unnecessary to identify each individual specimen for the purposes of this study. Consequently, only the total number of harpacticoids per sample was quantified for each of the 20 meiofaunal samples taken each month.



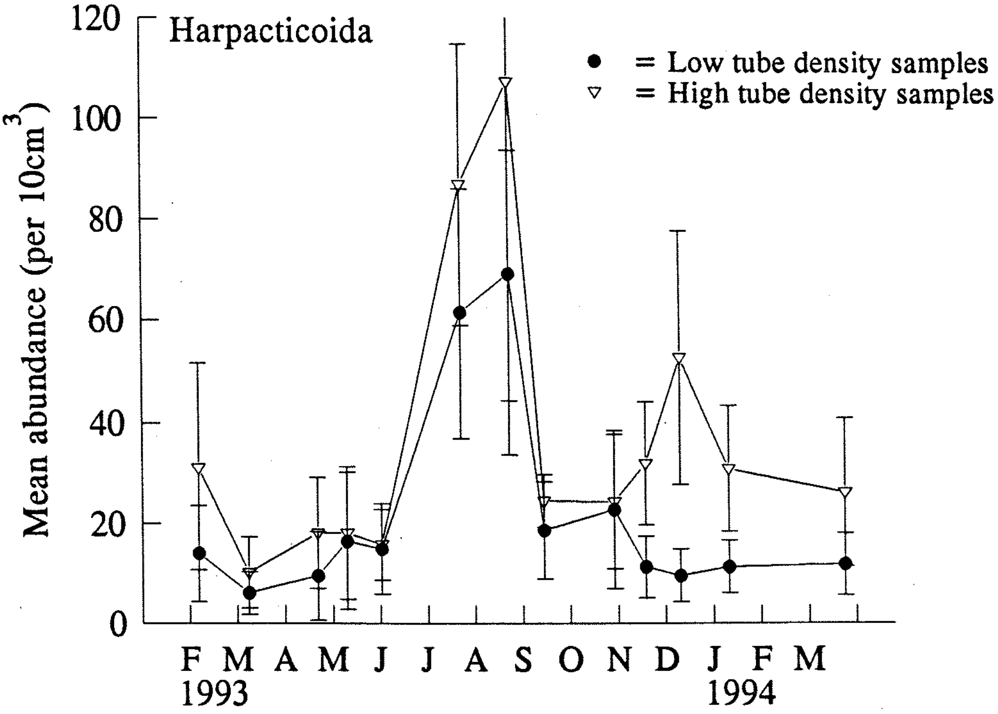


Figure 7.2 The Permanent Meiofauna. Temporal changes in the abundance of Nematoda (upper graph) and Harpacticoida (lower graph) in high and low *Lanice conchilega* tube density areas.

The following species from four separate families were identified simply to give examples of the harpacticoids occurring at Solent Breezes:

(i) *Asellopsis intermedia* (Family: Laophontidae);

(ii) *Canuella perplexa* (Family: Canuellidae);

(iii) *Halectinosoma* sp. (Family: Ectinosomatidae);

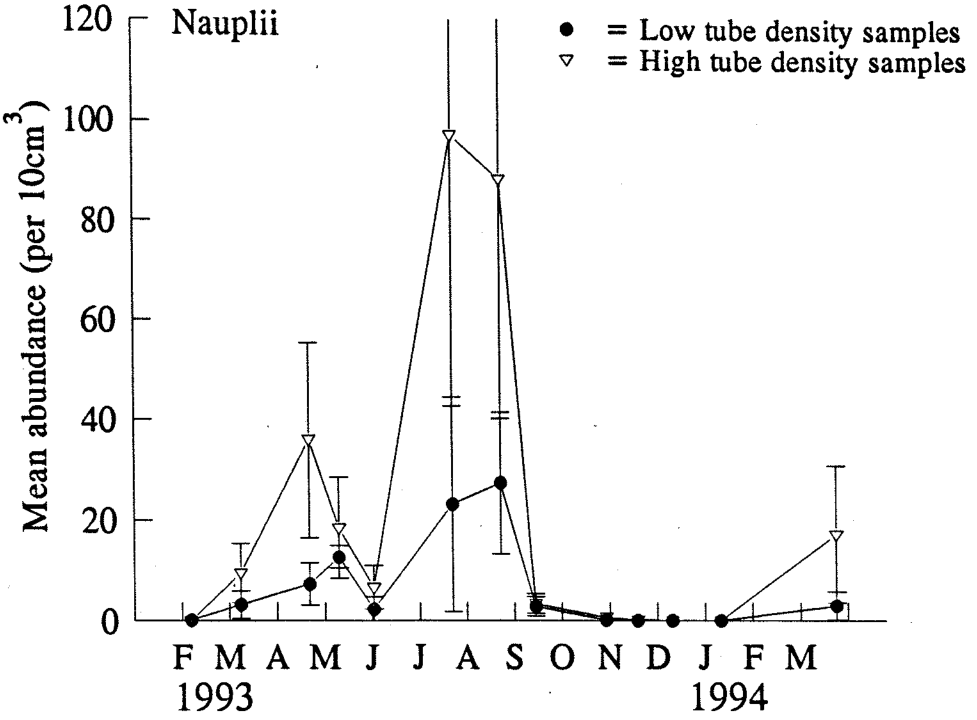
(iv) *Rhizothrix* sp. (Family: Rhizothricidae).

The Harpacticoida was usually the second most dominant group in meiofaunal samples taken from Solent Breezes, constituting between 4.6% and 22.3% of the fauna (mean values). Mean densities ranged between 3.0 per sample in March 1993 and 121.8 per sample in August 1993.

Figure 7.2 (lower graph) shows the mean number of harpacticoids (± S.D.) found each month in areas of both high and low *Lanice conchilega* tube densities. There was a significant pulse of recruitment in both high tube density areas and low tube density areas during July and August 1993. In addition, the mean number of harpacticoids in samples taken from high tube density areas was consistently higher than the mean number in low density areas. However, variation between samples was high and a comparison between the four sets of samples taken each month revealed that harpacticoid abundance in the two high density areas were significantly greater than abundance in the two low density areas on only three occasions (i.e. November and December 1993, and January 1994).

Harpacticoid nauplii

The harpacticoid nauplii present in meiofaunal samples were not formally identified but densities varied immensely. Figure 7.3 (upper graph) shows the mean number of nauplii (± S.D.) found each month in areas of both high and low *Lanice conchilega* tube densities. In several winter months nauplii were completely absent from samples. In other months (April, July and August) the mean number of nauplii in samples taken from high tube density areas was consistently higher than the



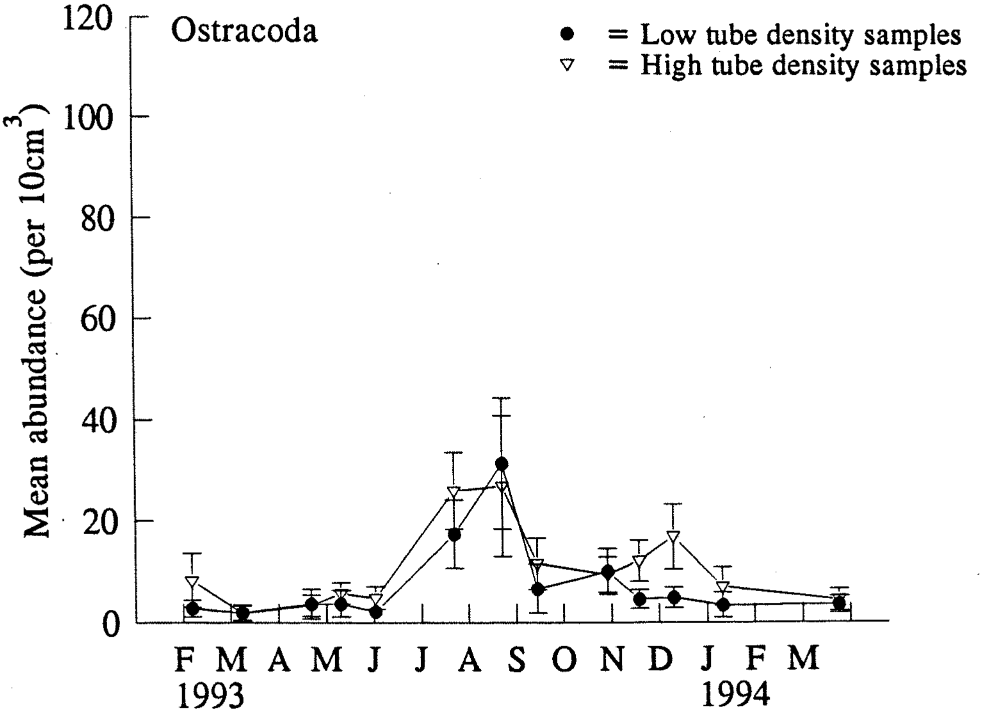


Figure 7.3 The Permanent Meiofauna. Temporal changes in the abundance of harpacticoid nauplii (upper graph) and Ostracoda (lower graph) in high and low *Lanice conchilega* tube density areas.

mean number in low tube density areas. Maximum mean densities of 97.0 per sample and 88.1 per sample occurred in high tube density areas in July and August 1993 (equivalent to 19.1% and 16.9% of the total fauna respectively).

Variation between samples was high but a comparison between the four sets of samples taken each month revealed that numbers in the two high tube density areas were significantly greater than numbers in the two low tube density areas in April, July and August 1993 ($p < 0.05$).

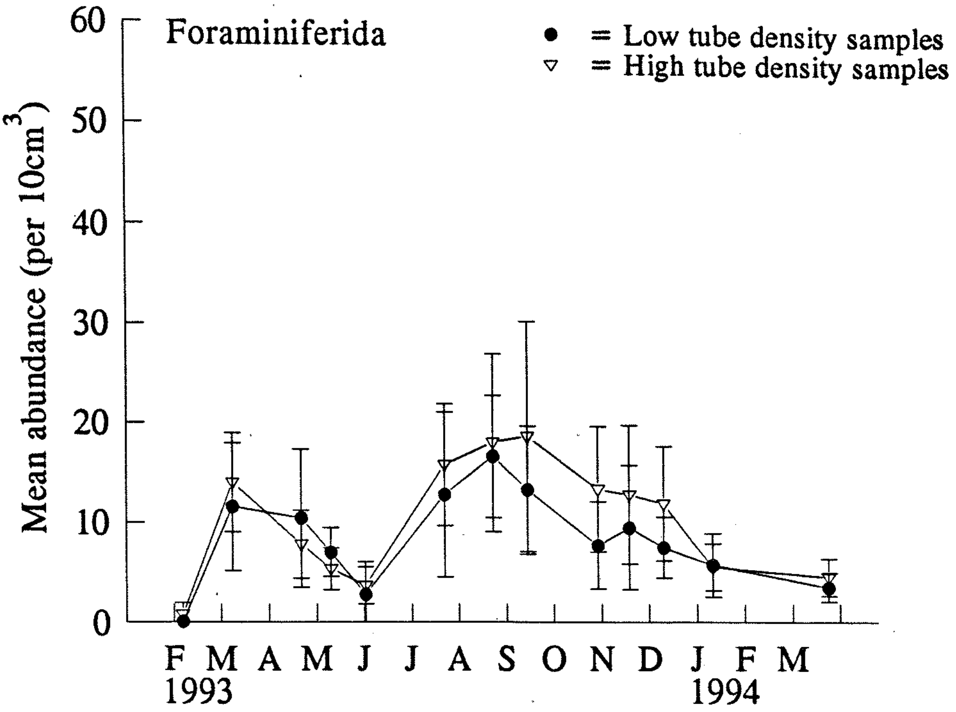
Ostracoda

Species of the Class Ostracoda occur in many marine and freshwater habitats and are often common in intertidal areas (Hayward and Ryland, 1990a). Ostracods were present in more than 98% of the meiofaunal samples taken from Solent Breezes, constituting between 0.9% and 8.0% of the fauna (mean values).

Figure 7.3 (lower graph) shows the mean number of ostracods (± S.D.) found each month in areas of both high and low *Lanice conchilega* tube densities. Relatively low numbers were present in samples taken during winter months, and maximum ostracod densities occurred in August 1993 for both high tube density samples and low tube density samples. A significant difference occurred between high and low tube density samples in November and December 1993 ($p < 0.05$).

Foraminiferida

The order Foraminiferida is represented in all marine and estuarine habitats, and numerous species occurred in the meiofauna at Solent Breezes. Again, the identification of individual specimens to species level was impractical within the time-span of the study. Forams constituted between zero and 23.2% of the fauna in samples (mean values), and there was a large degree of variation between samples. Consequently, no significant difference occurred between mean numbers found in samples taken from areas of high tube densities and mean numbers in low tube density areas (Figure 7.4 upper graph). In addition, there was no obvious seasonality in the abundance of forams.



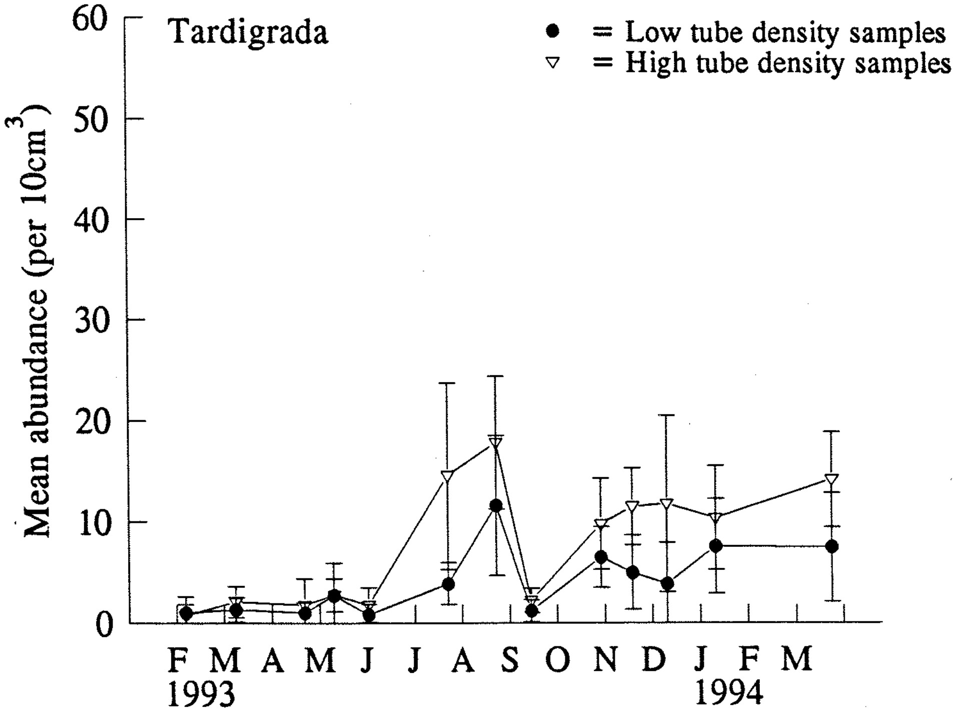


Figure 7.4 The Permanent Meiofauna. Temporal changes in the abundance of Foraminiferida (upper graph) and Tardigrada (lower graph) in high and low *Lanice conchilega* tube density areas.

Tardigrada

Marine tardigrades occur intertidally in mid-shore sediments or below, and a number of species have been recorded from various locations around the British Isles (Hayward and Ryland, 1990a). Individuals live in the interstitial waters between sand grains to a depth of approximately 10cm. The tardigrades found at Solent Breezes were identified to genus (i.e. *Batillipes* sp.), and were present in 84.2% of the meiofaunal samples. Mean densities ranged between 0.8 per sample in February 1993 and 17.8 per sample in August 1993.

Figure 7.4 (lower graph) shows the mean number of tardigrades (± S.D.) found each month in areas of both high and low *Lanice conchilega* tube densities. The mean number of tardigrades in samples taken from high tube density areas was usually higher than the mean number in low density areas. However, variation between samples was high and no significant differences existed between high and low density areas. In addition, there was no obvious seasonality in the abundance of tardigrades.

7.3.2 The temporary meiofauna (juvenile macrofauna)

The temporary meiofauna present in samples taken from both high and low density areas of *Lanice conchilega* tubes are listed in Appendix 2. Low density samples and high density samples are shown in separate tables, and in each table mean values are given for each set of samples (i.e. either A or B) and for the two sets combined (i.e. A and B combined = Total). The total abundance of temporary meiofaunal animals in individual core samples ranged between 1 and 37 (equivalent to between 1101 and 40 752m^{-2}). The minimum mean abundance of animals in a single set of five samples was 3.2 in November 1993 and the maximum was 25.8 in July 1993 (equivalent to 3525 and 28 417m^{-2} respectively).

Figure 7.5 presents the mean number of individuals in each set of samples. The abundance of temporary meiofauna was often greater in samples taken from high tube density areas. However, variation between samples was high and the mean abundance in **both** sets of high density samples was only significantly greater than in **both** sets of low density samples on one occasion (April 1993).

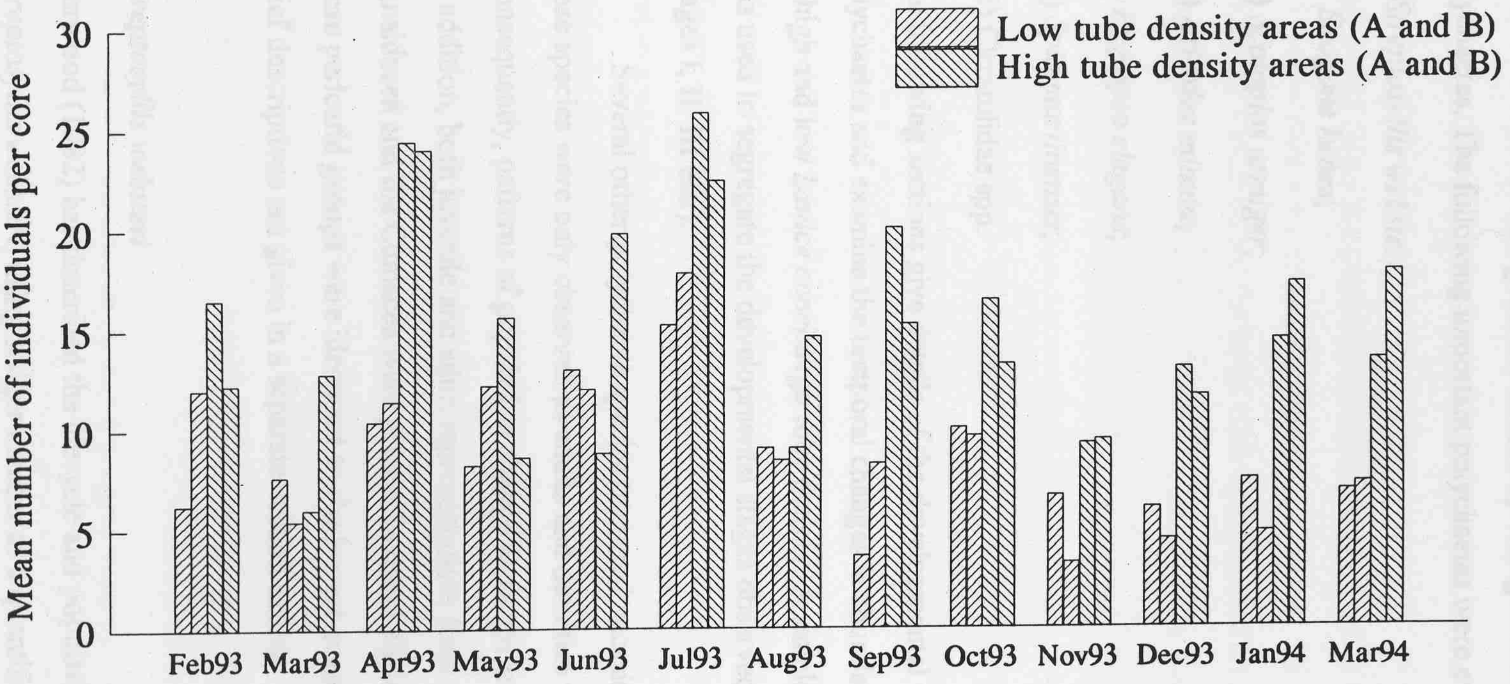


Figure 7.5 The Temporary Meiofauna. The average abundance of temporary meiofauna in the four sets of samples taken each month (i.e. two sets from high *Lanice conchilega* tube density areas (A and B) and two sets from low tube density areas (A and B)). Core sample size = 9.08cm^2 (surface area).

During the early stages of the analysis it became clear that only polychaetes were present in sufficient numbers to be considered individually. Major changes in overall abundance were generally caused by changes in the abundance of polychaetes. The following important polychaetes were examined in detail:

(i) *Streptosyllis websteri*;

(ii) *Exogone hebes*;

(iii) *Scoloplos armiger*;

(iv) *Aricidea minuta*;

(v) *Pygospio elegans*;

(vi) *Spio martinensis*;

(vii) Cirratulidae spp.

The following sections give details of the developmental stages observed for these polychaetes and examine the temporal changes in abundance that occurred in areas of high and low *Lanice conchilega* tube density. A simple sequential classification was used to segregate the developmental stages observed for each species (i.e. Stages I, II, III etc.).

Several other polychaete species occurred occasionally in samples, but these species were only observed as adults and densities were relatively low. Consequently, patterns of population change were not analysed for these species. In addition, both juvenile and adult representatives from the Amphipoda, the Tanaidacea and the Cumacea were present in relatively low densities. Specimens of these pericarid groups were identified to the lowest possible taxonomic level and brief descriptions are given in a separate section below.

Streptosyllis websteri

Garwood (1982) has described the lifecycle and population dynamics of *Streptosyllis websteri*, using setiger number as a quantifiable parameter that could be related directly to body length. However, the morphological characteristics of the developing juveniles of *Streptosyllis websteri* have not been previously described.

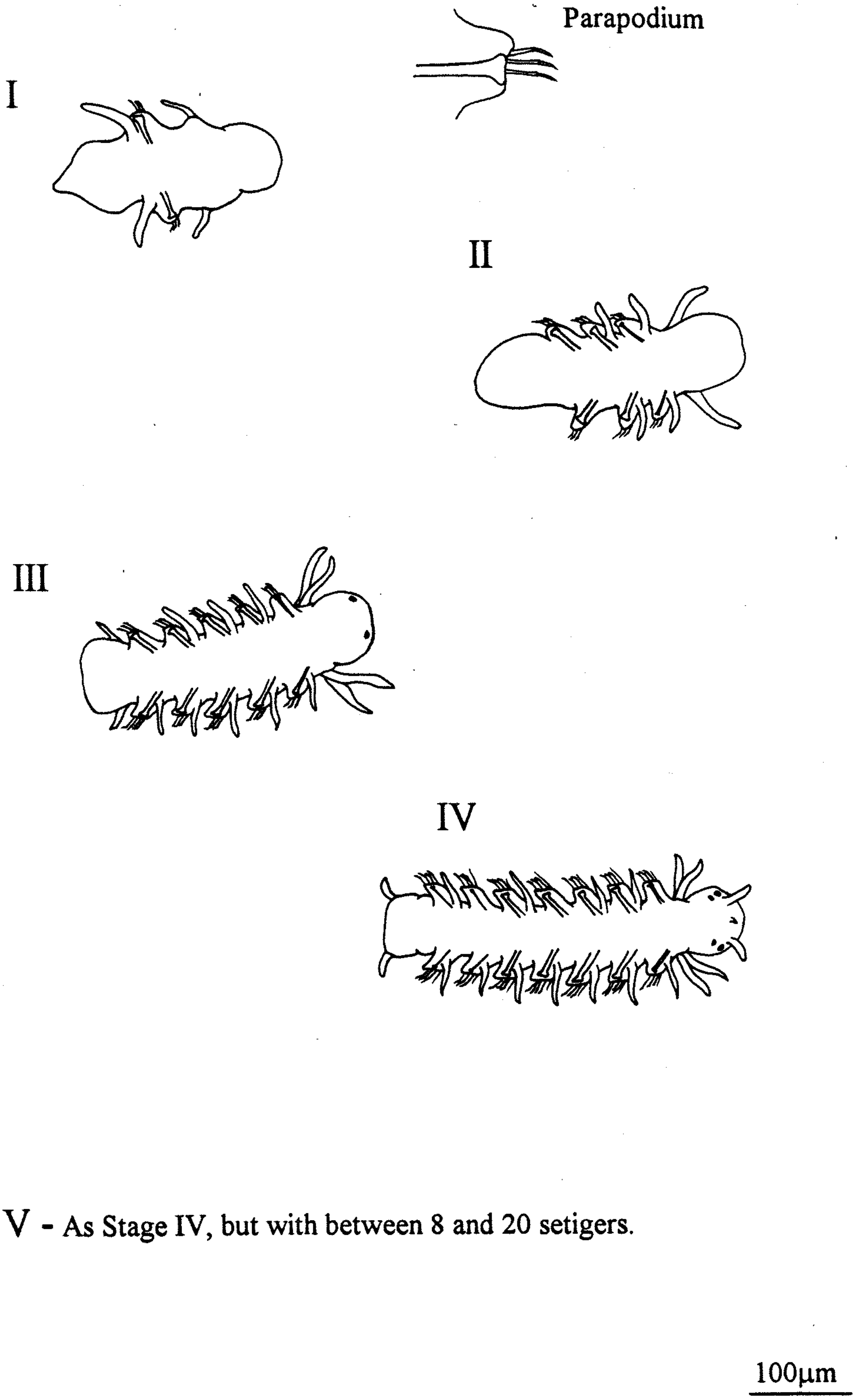
The 5 stages of development observed for *Streptosyllis websteri* are shown in Figure 7.6. The presence of characteristic large knobbed acicula allowed juvenile specimens of *Streptosyllis websteri* to be recognised from the earliest stage of development. Stage I juveniles had a single pair of parapodia, each with a slightly emergent knobbed aciculum and 3-4 long-bladed jointed (compound) chaetae. A small dorsal cirrus accompanied each parapodium, and a single pair of tentacular cirri was evident behind the head region. In addition, the developing proventriculus was faintly visible within the body. Live specimens of an earlier achaetous larval stage have been previously observed and described by Garwood (1982), but this stage was not observed in the samples from Solent Breezes.

Stage II juveniles were defined as having 2 or 3 setigers. The knobbed acicula were distinctly larger in the second and third pairs of parapodia. A dorsal cirrus was usually present on each setiger and a single pair of tentacular cirri was again evident behind the head region.

The 5-setiger stage of development (Stage III) usually had a small pair of eyes towards the front of the head region. Enlarged acicula were visible in all setigers, and a single unjointed (simple) chaeta accompanied the compound chaetae in each parapodium. In addition, a small pair of anal cirri and a second pair of tentacular cirri had developed on the majority of Stage III specimens.

Stage IV juveniles were defined as having 7 or 8 setigers, the first 5 having enlarged knobbed acicula and the remaining having relatively small knobbed acicula. This configuration of acicula distinguishes *Streptosyllis websteri* from other *Streptosyllis* species. Dorsal cirri were usually present on most setigers and both compound and simple chaetae were present as described for Stage III specimens. In addition, 3 developing antennae were visible on the heads of a few Stage IV juveniles.

Individuals with more than 8 setigers were defined as Stage V juveniles. The distinction between juveniles and adults was unclear, but an arbitrary separation was made at 20 setigers. Specimens with between 8 and approximately 20 setigers had dorsal and tentacular cirri, along with antennae at increasing but variable stages of development. Small eyes were generally visible and the developing proventriculus was distinct.



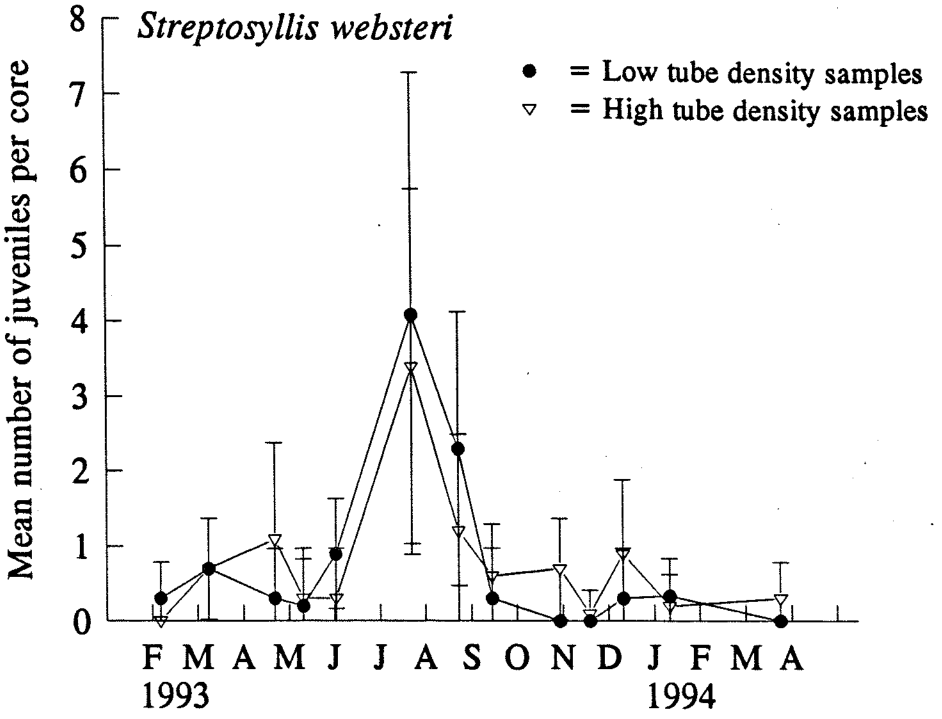
V - As Stage IV, but with between 8 and 20 setigers.

Figure 7.6 The Temporary Meiofauna. The five stages of development observed for *Streptosyllis websteri* at Solent Breezes.

Adult specimens of *Streptosyllis websteri* have previously been described as having between 32 and 42 setigers (Fauvel, 1923; Hartmann-Schröder, 1971). However, standard macrofaunal methods using 0.5mm or 1.0mm mesh sizes only collect relatively large specimens of *Streptosyllis websteri*. Specimens collected in the present study that had more than approximately 20 setigers appeared to be morphologically complete (i.e. as adults). Therefore, for the purposes of this study adults were defined as simply having more than 20 setigers.

Figure 7.7 presents the mean number of juveniles (± S.D.) and the mean number of adults (± S.D.) in monthly samples from both high and low tube densities. There was no significant difference between the mean values each month, and a clear pulse of recruitment was observed in July 1993 (upper graph). The number of juveniles declined during August and September as their development into adulthood progressed. Maximum numbers of adults occurred in September (High Density samples) and October (Low Density samples), after which mean values decreased gradually during winter.

Figure 7.8 also presents the mean numbers of *Streptosyllis websteri* in monthly samples, but highlights the different juvenile stages present each month in either high tube density or low tube density samples. Individuals at the earliest stage of development (i.e. Stage I) were observed in March 1993, and Stage II juveniles were also present between February and April 1993, then reoccurring in March 1994. The major pulse in recruitment observed in July 1993 was caused by Stage III and IV juveniles in both high tube density and low tube density samples. The extended period between the sampling dates in June and July (i.e. 7 weeks) probably allowed a large input of new individuals to be missed during June which subsequently developed to Stages III and IV by the July sampling date. Garwood (1982) has previously observed the development of juvenile *Streptosyllis websteri* from the 1-setiger stage to the 5-setiger stage which occurred in approximately one month. Therefore, more frequent sampling in the present study would presumably have detected Stage I and Stage II juveniles during June.



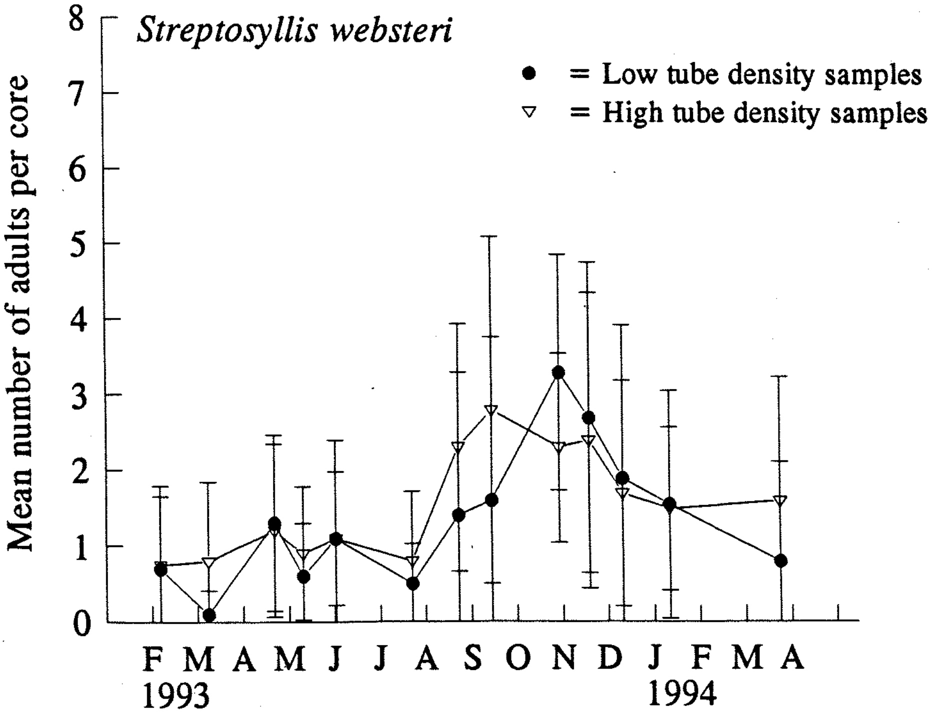


Figure 7.7 The Temporary Meiofauna. Temporal changes in the abundance of juvenile (upper graph) and adult (lower graph) *Streptosyllis websteri* in high and low *Lanice conchilega* tube density areas. Core size = 9.08cm^2 (surface area).

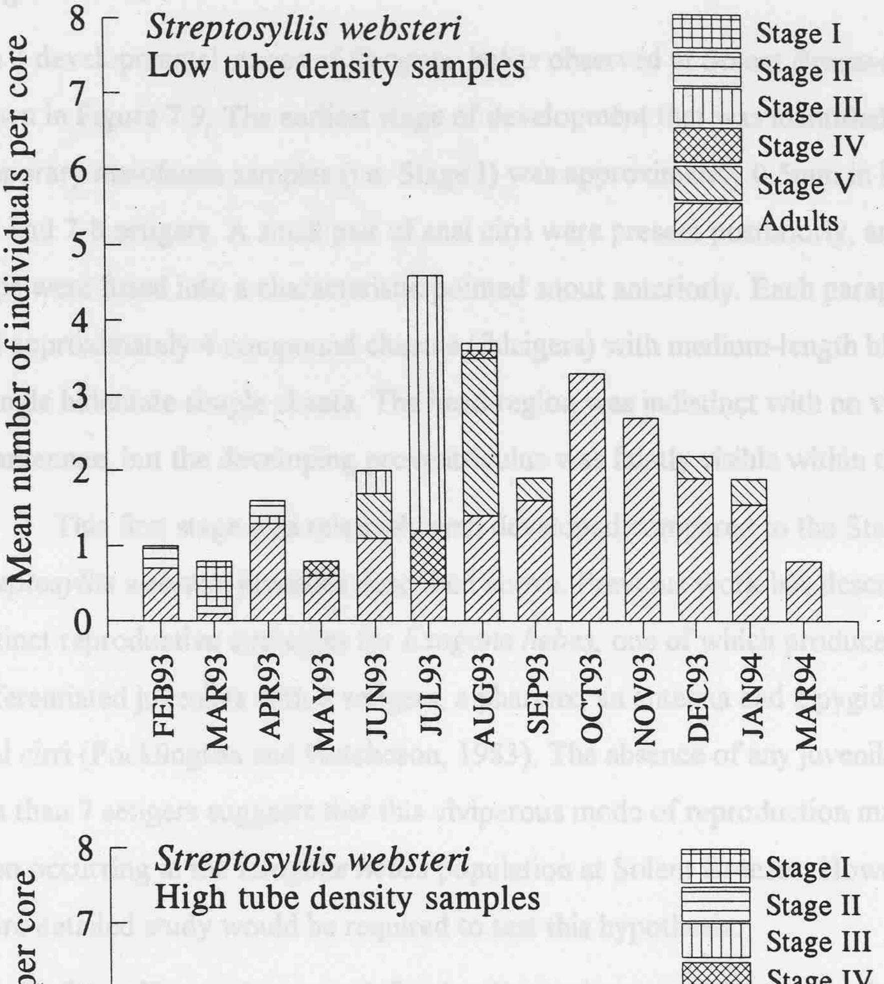


Figure 7.8 The Temporary Meiofauna. Temporal changes in the abundance of *Streptosyllis websteri* juvenile stages and adults in high and low *Lanice conchilega* tube density areas. Core size = 9.08cm^2 (surface area).

Exogone hebes

The 3 developmental stages of *Exogone hebes* observed at Solent Breezes are shown in Figure 7.9. The earliest stage of development that was identified in the temporary meiofauna samples (i.e. Stage I) was approximately 0.5mm in length and had 7-8 setigers. A small pair of anal cirri were present posteriorly, and the palps were fused into a characteristic pointed snout anteriorly. Each parapodium had approximately 4 compound chaetae (falcigers) with medium-length blades and a single bidentate simple chaeta. The head region was indistinct with no visible eyes or antennae, but the developing proventriculus was faintly visible within the body.

This first stage was relatively well developed compared to the Stage I *Streptosyllis websteri* juveniles described above. Previous work has described two distinct reproductive strategies for *Exogone hebes*, one of which produces fully differentiated juveniles with 5 setigers, a pharynx, an antenna and a pygidium with anal cirri (Pocklington and Hutcheson, 1983). The absence of any juveniles with less than 7 setigers suggests that this viviparous mode of reproduction may have been occurring in the *Exogone hebes* population at Solent Breezes. However, a more detailed study would be required to test this hypothesis.

Stage II juveniles were defined as having between 10 and 12 setigers. The chaetal characteristics described for Stage I juveniles remained constant, but there was a slight elongation of the anal cirri and the addition of a small median antenna. Dorsal cirri were not visible in either Stage I or Stage II juveniles, but these can often be difficult to observe in fully grown adult *Exogone* specimens.

Stage III juveniles typically had 15-16 setigers and were approximately 1mm in length. Two small accompanying antennae were often visible either side of the developing median antenna. In addition, dorsal cirri were occasionally observed above the parapodia on a number of setigers.

Adult specimens of *Exogone hebes* have previously been described as having between 30 and 44 setigers (Fauvel, 1923; Hayward and Ryland, 1990a). However, for the purposes of the present study, adults were defined as simply having more than approximately 20 setigers, as these individuals appeared to be morphologically complete (at least externally).

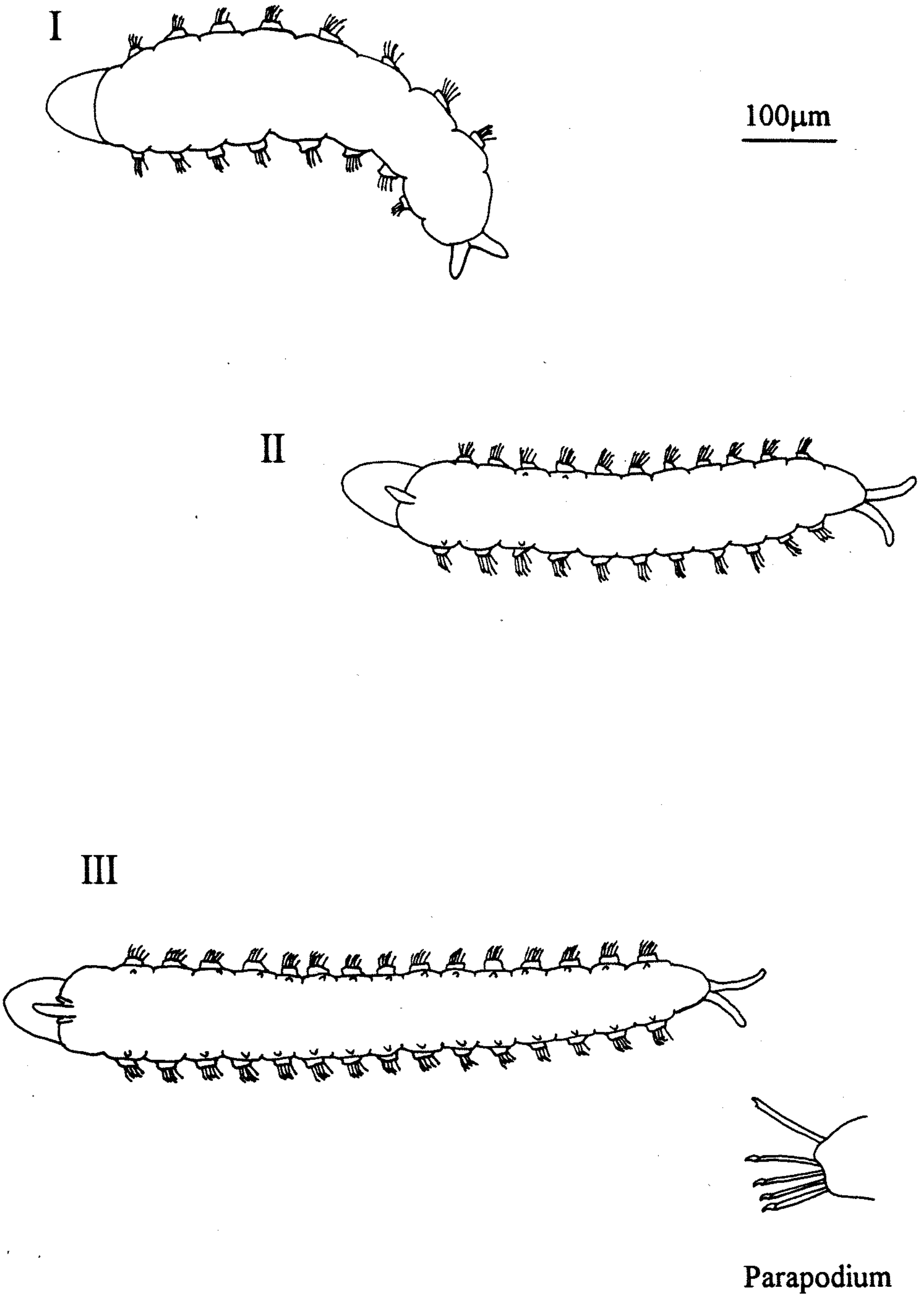
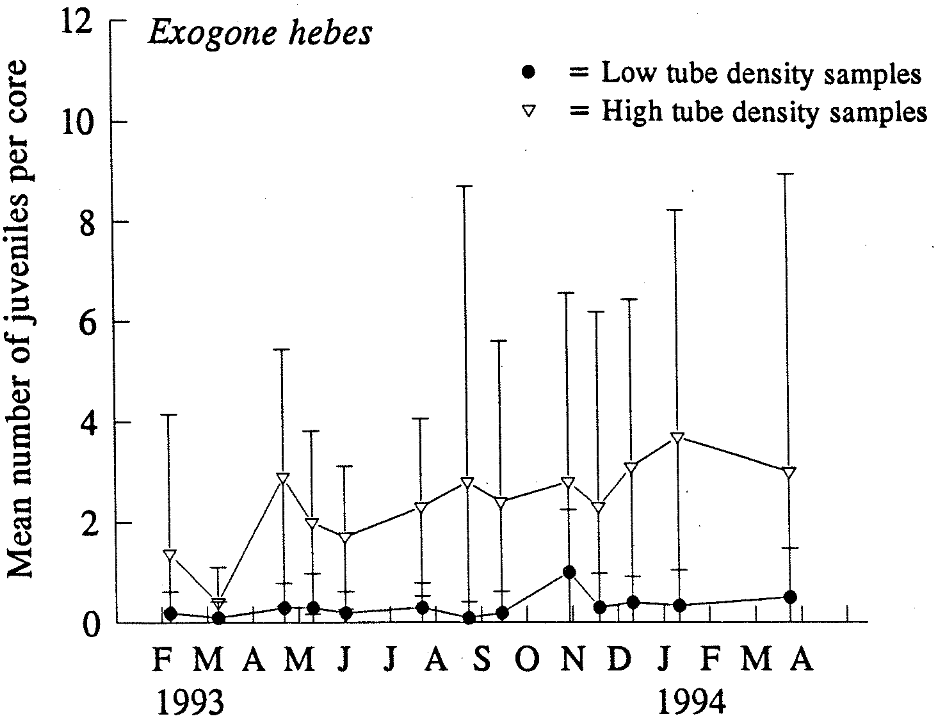


Figure 7.9 The Temporary Meiofauna. The three stages of development observed for *Exogone hebes* at Solent Breezes.



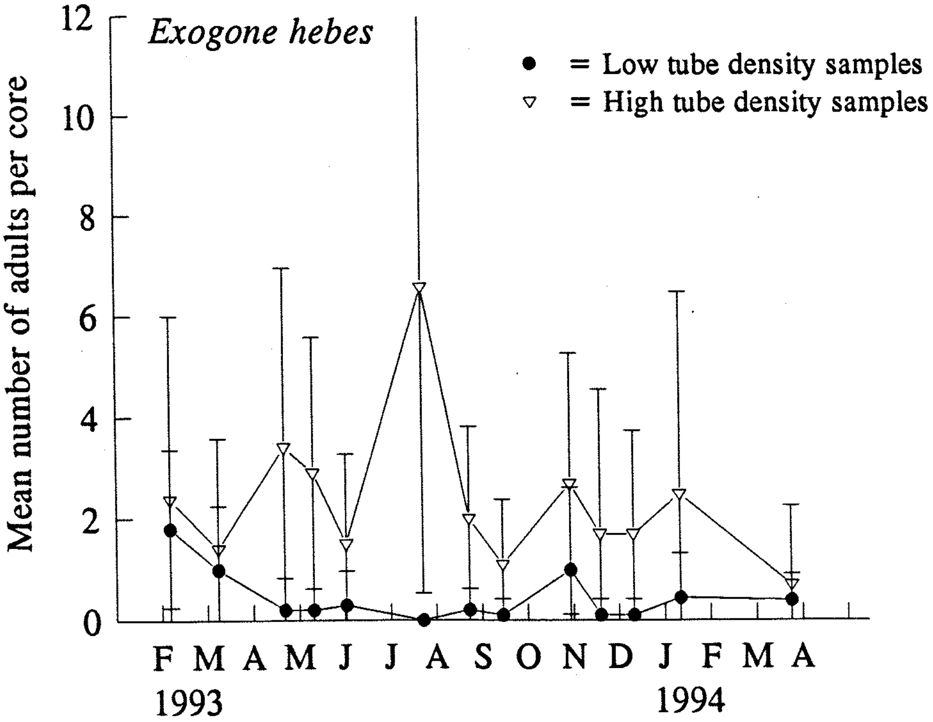


Figure 7.10 The Temporary Meiofauna. Temporal changes in the abundance of juvenile (upper graph) and adult (lower graph) *Exogone hebes* in high and low *Lanice conchilega* tube density areas. Core size = 9.08cm^2 (surface area).

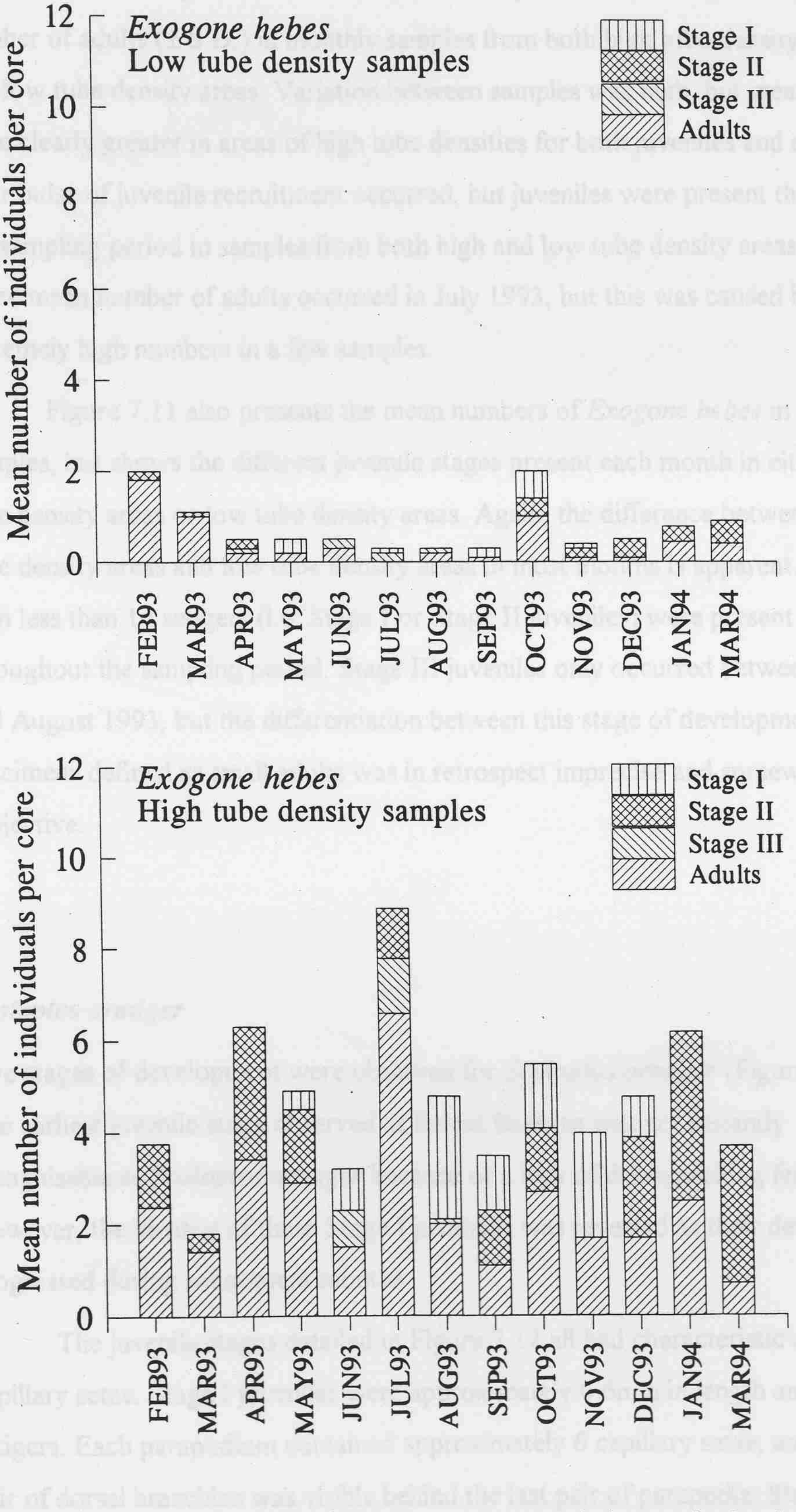


Figure 7.11 The Temporary Meiofauna. Temporal changes in the abundance of *Exogone hebes* juvenile stages and adults in high and low *Lanice conchilega* tube density areas. Core size = 9.08cm^2 (surface area).

Figure 7.10 presents the mean number of juveniles (± S.D.) and the mean number of adults (± S.D.) in monthly samples from both high tube density areas and low tube density areas. Variation between samples was high, but mean values were clearly greater in areas of high tube densities for both juveniles and adults. No clear pulse of juvenile recruitment occurred, but juveniles were present throughout the sampling period in samples from both high and low tube density areas. A peak in the mean number of adults occurred in July 1993, but this was caused by extremely high numbers in a few samples.

Figure 7.11 also presents the mean numbers of *Exogone hebes* in monthly samples, but shows the different juvenile stages present each month in either high tube density areas or low tube density areas. Again, the difference between high tube density areas and low tube density areas in most months is apparent. Juveniles with less than 14 setigers (i.e. Stage I or Stage II juveniles) were present throughout the sampling period. Stage III juveniles only occurred between June and August 1993, but the differentiation between this stage of development and specimens defined as small adults was in retrospect imprecise and somewhat subjective.

Scoloplos armiger

Five stages of development were observed for *Scoloplos armiger* (Figure 7.12). The earliest juvenile stage observed at Solent Breezes was not instantly recognisable as *Scoloplos armiger* because of a lack of distinguishing features. However, the identity of these Stage I juveniles was revealed as their development progressed during subsequent months.

The juvenile stages detailed in Figure 7.12 all had characteristic crenulated capillary setae. Stage I juveniles were approximately 0.6mm in length and had 9-10 setigers. Each parapodium contained approximately 6 capillary setae, and a single pair of dorsal branchiae was visible behind the last pair of parapodia. Stage II juveniles were defined as having 12-14 setigers and 3-4 pairs of branchiae.

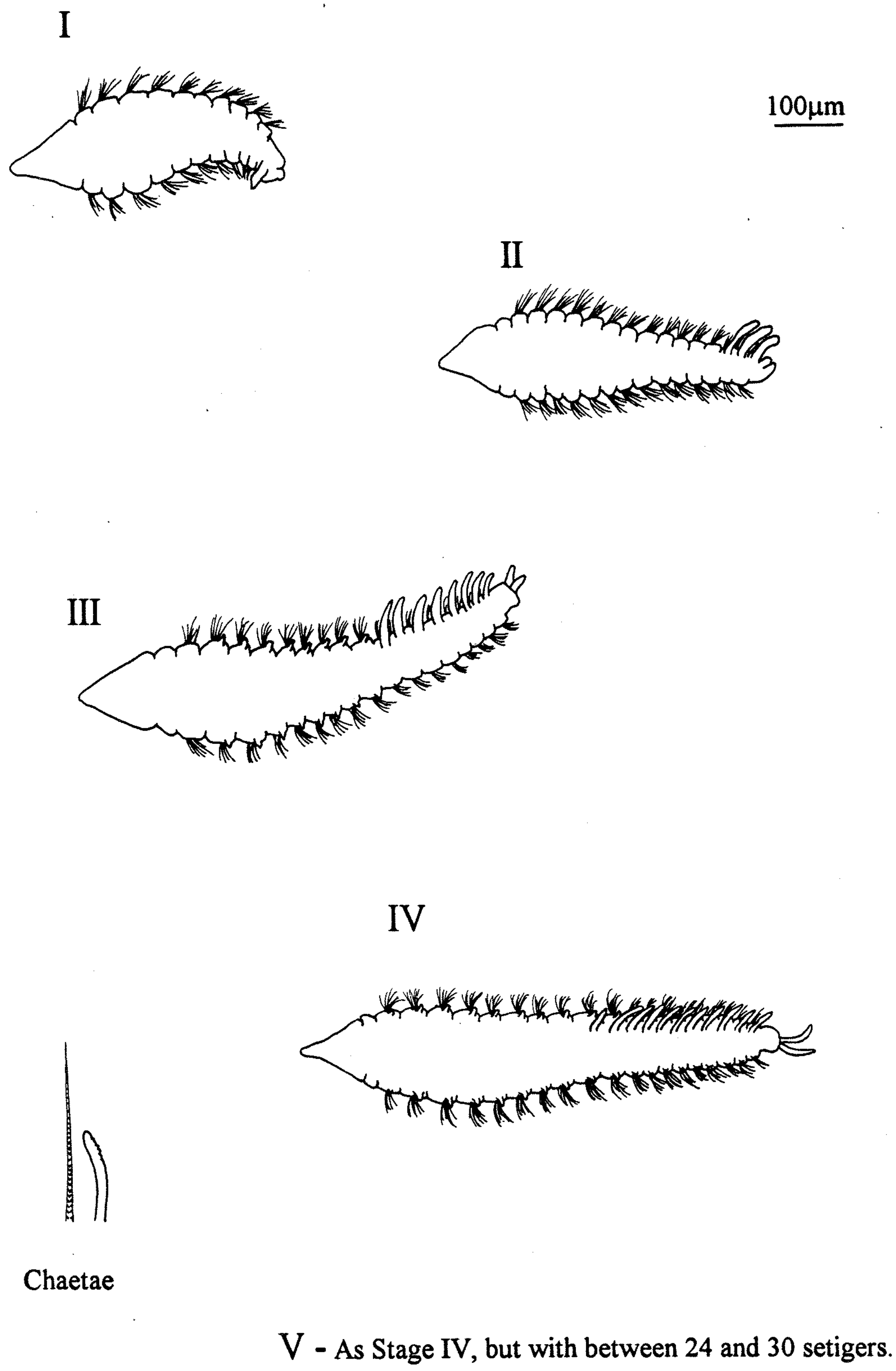
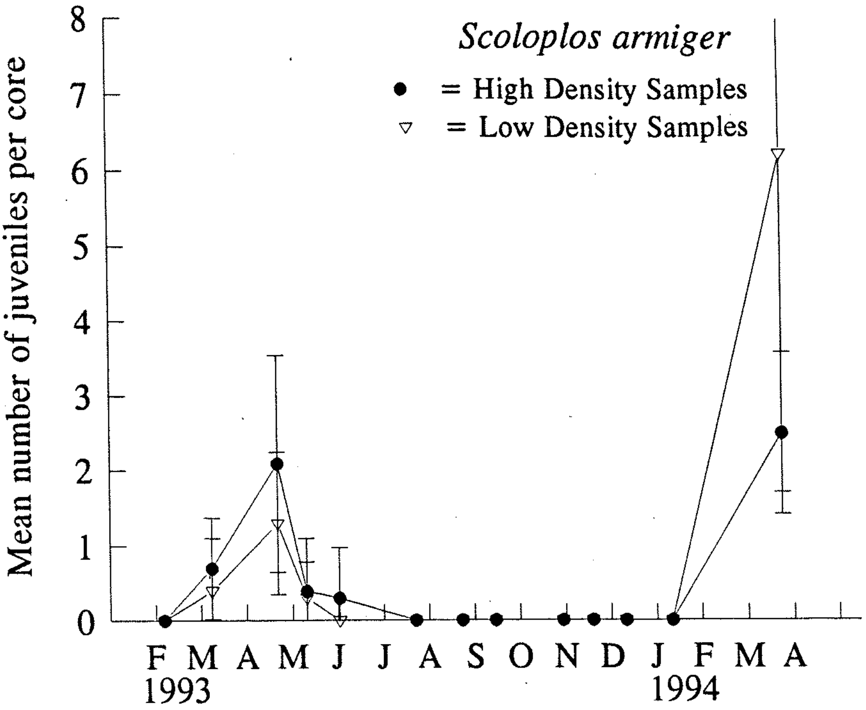


Figure 7.12 The Temporary Meiofauna. The five stages of development observed for *Scoloplos armiger* at Solent Breezes. N.B. Only one of each pair of branchiae is shown.



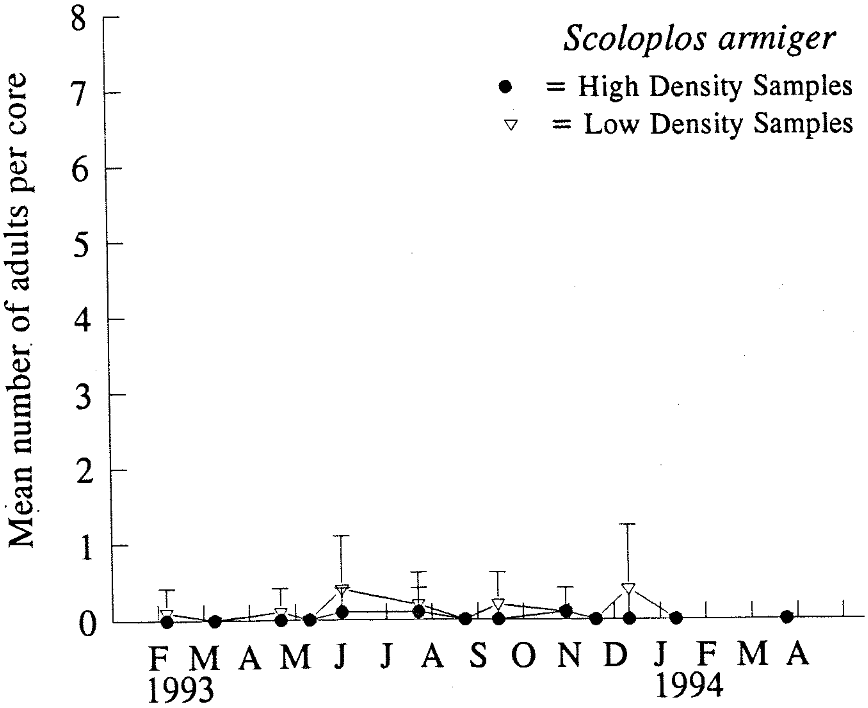


Figure 7.13 The Temporary Meiofauna. Temporal changes in the abundance of juvenile (upper graph) and adult (lower graph) *Scoloplos armiger* in high and low *Lanice conchilega* tube density areas. Core size = 9.08cm^2 (surface area).

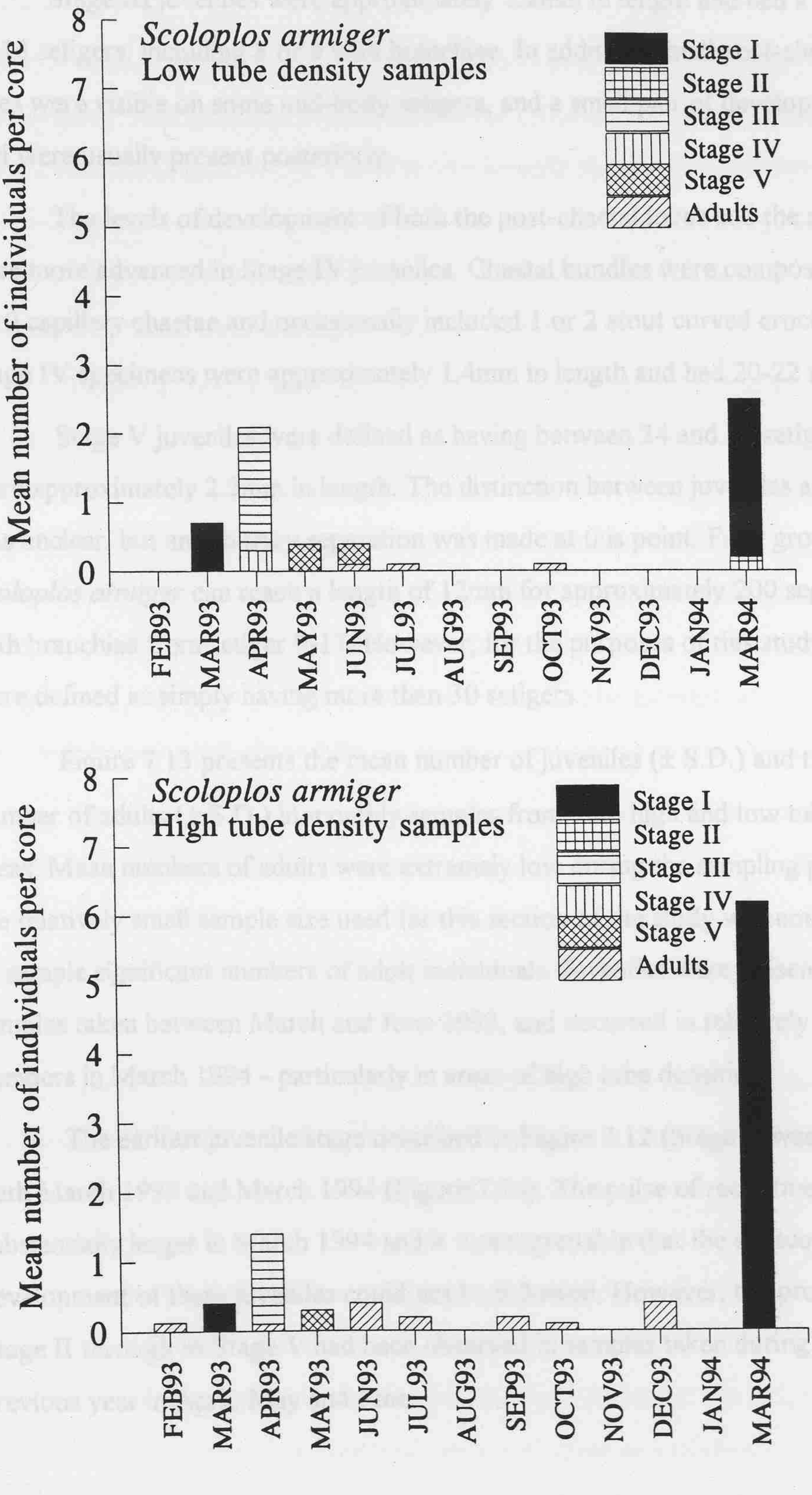


Figure 7.14 The Temporary Meiofauna. Temporal changes in the abundance of *Scoloplos armiger* juvenile stages and adults in high and low *Lanice conchilega* tube density areas. Core size = 9.08cm^2 (surface area).

Stage III juveniles were approximately 1.2mm in length and had a total of 16-18 setigers, including 8 or 9 with branchiae. In addition, small post-chaetal lobes were visible on some mid-body setigers, and a small pair of developing anal cirri were usually present posteriorly.

The levels of development of both the post-chaetal lobes and the anal cirri were more advanced in Stage IV juveniles. Chaetal bundles were composed of 6-10 capillary chaetae and occasionally included 1 or 2 stout curved crochets. Stage IV specimens were approximately 1.4mm in length and had 20-22 setigers.

Stage V juveniles were defined as having between 24 and 30 setigers and were approximately 2.2mm in length. The distinction between juveniles and adults was unclear, but an arbitrary separation was made at this point. Fully grown *Scoloplos armiger* can reach a length of 12mm for approximately 200 segments with branchiae from setiger 9-17. However, for the purposes of this study adults were defined as simply having more than 30 setigers.

Figure 7.13 presents the mean number of juveniles (± S.D.) and the mean number of adults (± S.D.) in monthly samples from both high and low tube density areas. Mean numbers of adults were extremely low during the sampling period, but the relatively small sample size used for this section of the study was not expected to sample significant numbers of adult individuals. Juveniles were present in samples taken between March and June 1993, and occurred in relatively high numbers in March 1994 - particularly in areas of high tube densities.

The earliest juvenile stage described in Figure 7.12 (Stage I) was present in both March 1993 and March 1994 (Figure 7.14). The pulse of recruitment was substantially larger in March 1994 and it was regrettable that the subsequent development of these juveniles could not be followed. However, the progression of Stage II through to Stage V had been observed in samples taken during the previous year in April, May and June.

Aricidea minuta

Details of the development of *Aricidea minuta* have not been previously documented. Five stages of development were observed for *Aricidea minuta* at Solent Breezes (Figure 7.15). The first two juvenile stages observed were not instantly recognisable as *Aricidea minuta* because of a lack of distinguishing features. However, the identity of these juveniles was revealed as their development progressed during subsequent months.

Stage I juveniles were between 0.2 and 0.3mm in length and were defined as having 5 setigers. Specimens had a large achaetous frontal region and a distinct pair of anal cirri posteriorly. Each parapodium had 5 or 6 curved capillary chaetae that varied considerably in length. Stage II juveniles were similar to Stage I juveniles but had 7 or 8 setigers. In addition, the level of differentiation of the anterior head region was more advanced. Stage III juveniles had between 9 and 12 setigers and were approximately 0.45mm in length. The anterior achaetous region was differentiated into three faint segments behind the developing head.

Small paired branchiae were first observed on Stage IV juveniles. In addition, segmentation of the developing anterior region was clear, with short chaetae being visible on at least two of the three new segments. These Stage IV specimens had approximately 16 setigers and several modified pseudocompound chaetae were often visible in posterior setigers.

Stage V juveniles were between 1.0 and 1.2mm in length and had approximately 20 setigers. Segmentation of the anterior region behind the head was complete and chaetal bundles were present on the three anterior segments. Consequently, the first pair of branchiae occurred on setiger 4, as they do in adult specimens. Stage V juveniles appeared to be morphologically similar to adult specimens, apart from the absence of a median antenna. Therefore, this characteristic was used to distinguish adults and juveniles for the purposes of this study. *Aricidea minuta* has previously been described as a relatively small species with approximately 45 segments (Hartmann- Schröder, 1971). However, most specimens at Solent Breezes with more than 25 setigers appeared to be morphologically complete with a median antenna on the head. The distinction between juveniles and adults was therefore made using this characteristic.

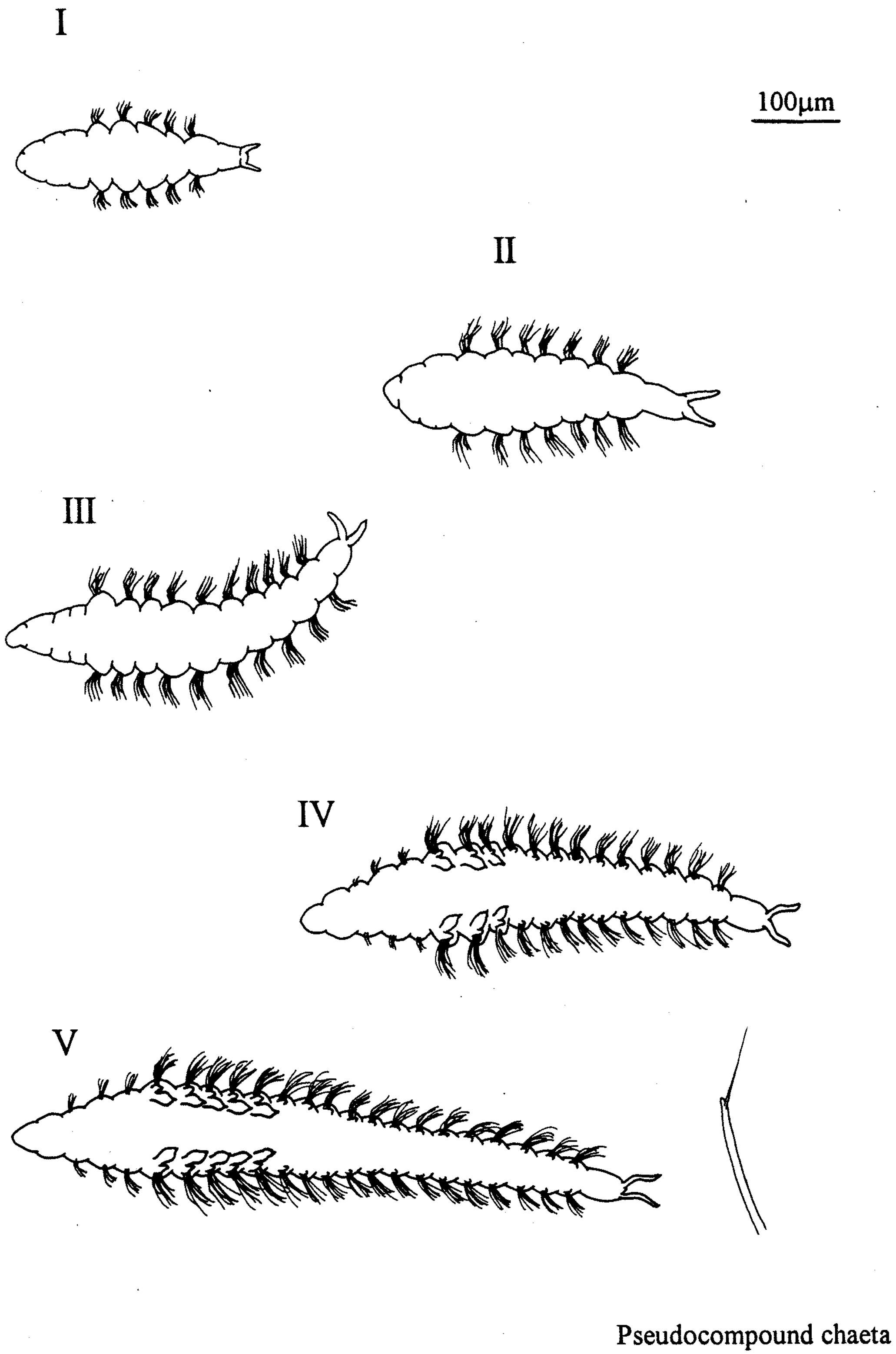
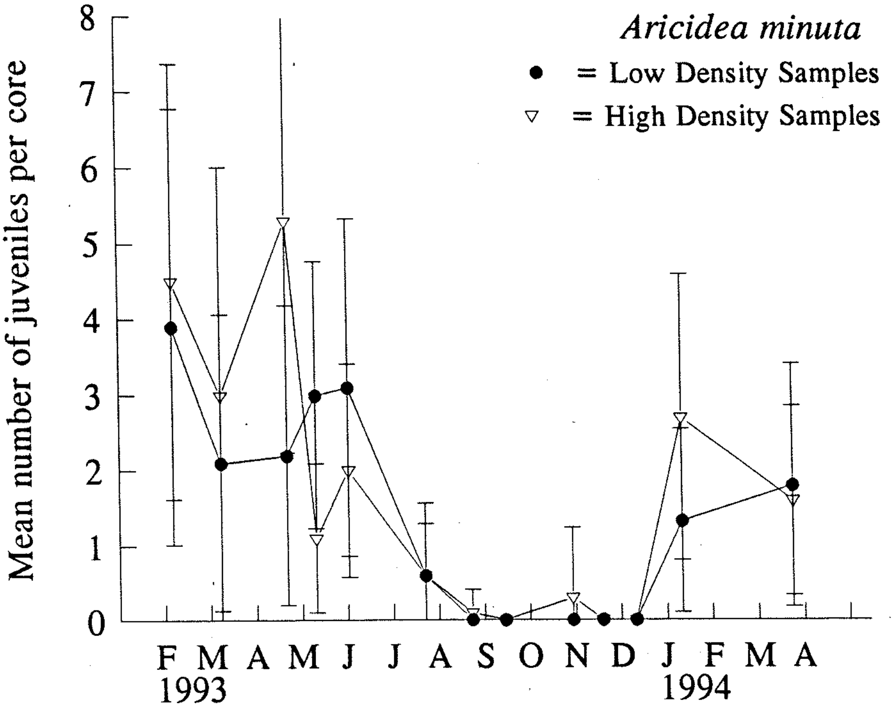


Figure 7.15 The Temporary Meiofauna. The five stages of development observed for *Aricidea minuta* at Solent Breezes.



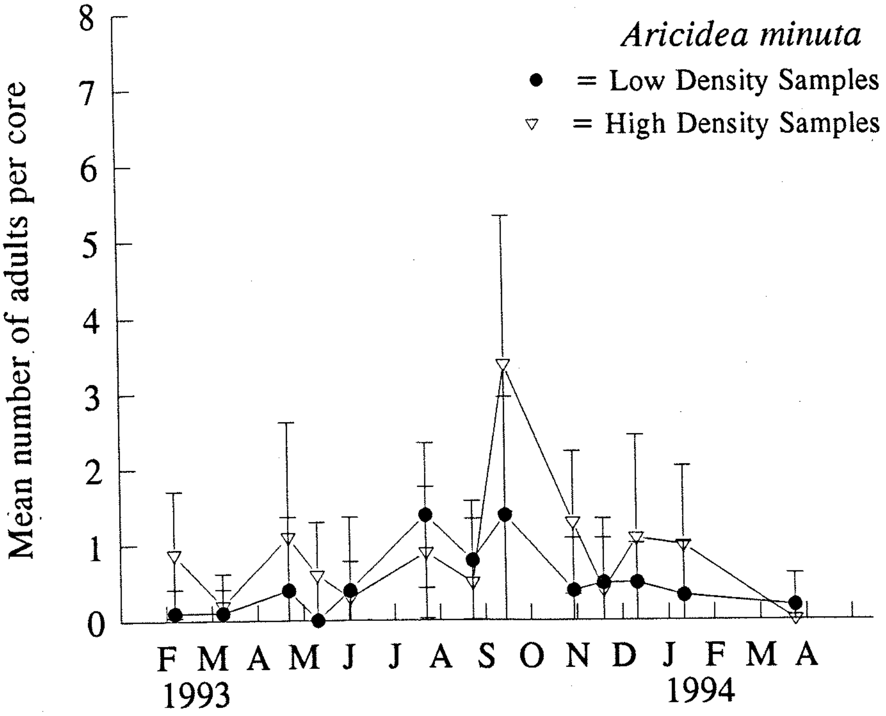


Figure 7.16 The Temporary Meiofauna. Temporal changes in the abundance of juvenile (upper graph) and adult (lower graph) *Aricidea minuta* in high and low *Lanice conchilega* tube density areas. Core size = 9.08cm^2 (surface area).

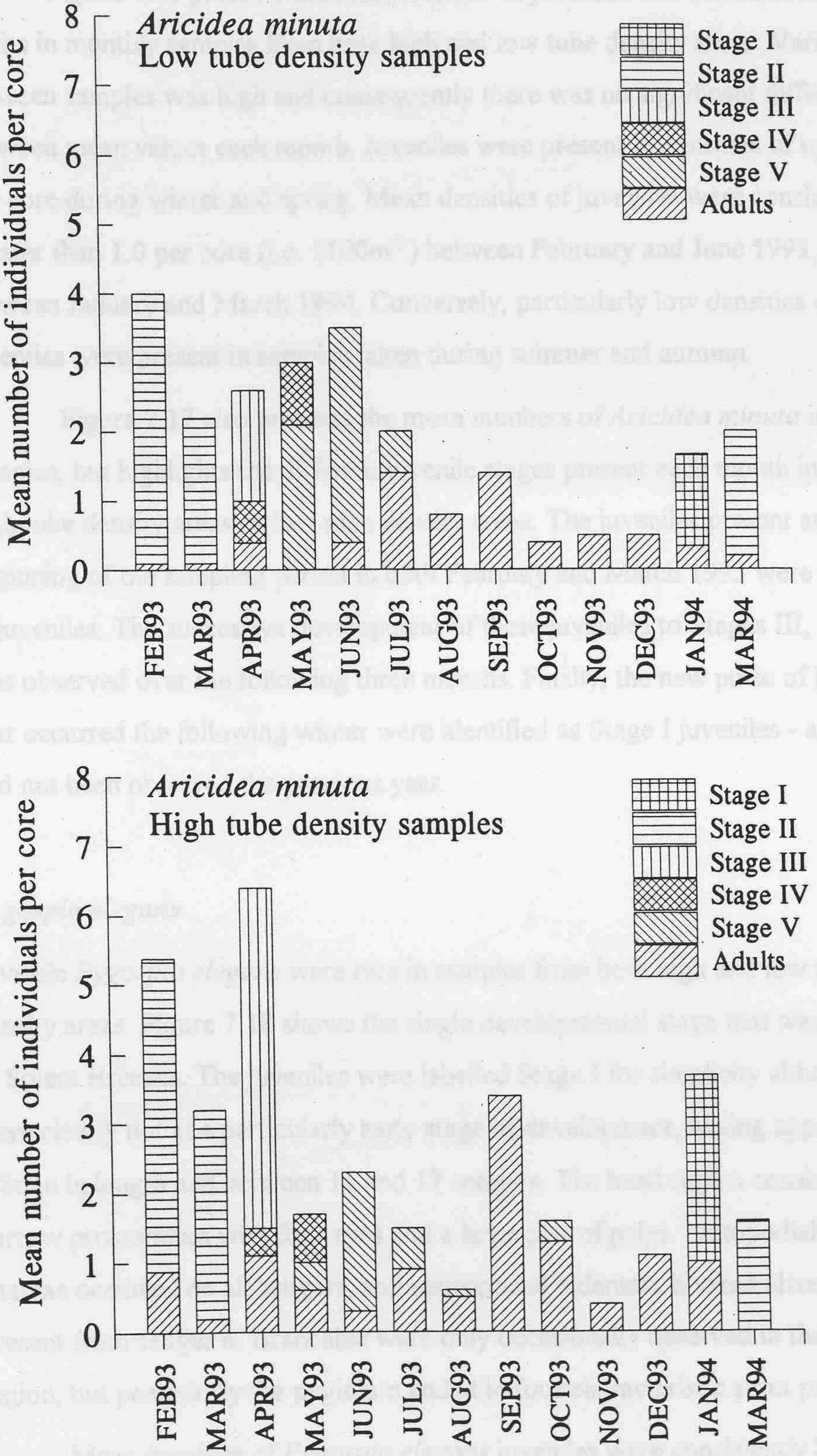


Figure 7.17 The Temporary Meiofauna. Temporal changes in the abundance of *Aricidea minuta* juvenile stages and adults in high and low *Lanice conchilega* tube density areas. Core size = 9.08cm^2 (surface area).

Figure 7.16 presents the mean number of juveniles and the mean number of adults in monthly samples from both high and low tube density areas. Variation between samples was high and consequently there was no significant difference between mean values each month. Juveniles were present in densities of up to 12 per core during winter and spring. Mean densities of juveniles were consistently greater than 1.0 per core (i.e. $1100m^{-2}$) between February and June 1993, and between January and March 1994. Conversely, particularly low densities of juveniles were present in samples taken during summer and autumn.

Figure 7.17 also presents the mean numbers of *Aricidea minuta* in monthly samples, but highlights the different juvenile stages present each month in either high tube density areas or low tube density areas. The juveniles present at the beginning of the sampling period in both February and March 1993 were all Stage II juveniles. The successive development of these juveniles to Stages III, IV and V was observed over the following three months. Finally, the new pulse of juveniles that occurred the following winter were identified as Stage I juveniles - a stage that had not been observed the previous year.

Pygospio elegans

Juvenile *Pygospio elegans* were rare in samples from both high and low tube density areas. Figure 7.18 shows the single developmental stage that was observed at Solent Breezes. The juveniles were labelled Stage I for simplicity although they were clearly not at a particularly early stage of development, having approximately 0.8mm in length and between 15 and 17 setigers. The head region consisted of a narrow prostomium with four eyes and a large pair of palps. Notopodial capillary chaetae occurred on all setigers, and neuropodial bidentate hooked chaetae were present from setiger 6. Branchiae were only occasionally observed in the mid-body region, but posteriorly the pygidium ended in four characteristic stout processes.

Mean densities of *Pygospio elegans* juveniles were consistently below 1.0 (Figure 7.19; upper graph). However, adult specimens were observed in greater densities, and the mean number of individuals in high tube density areas was often greater than in low tube density areas (Figure 7.19; lower graph).

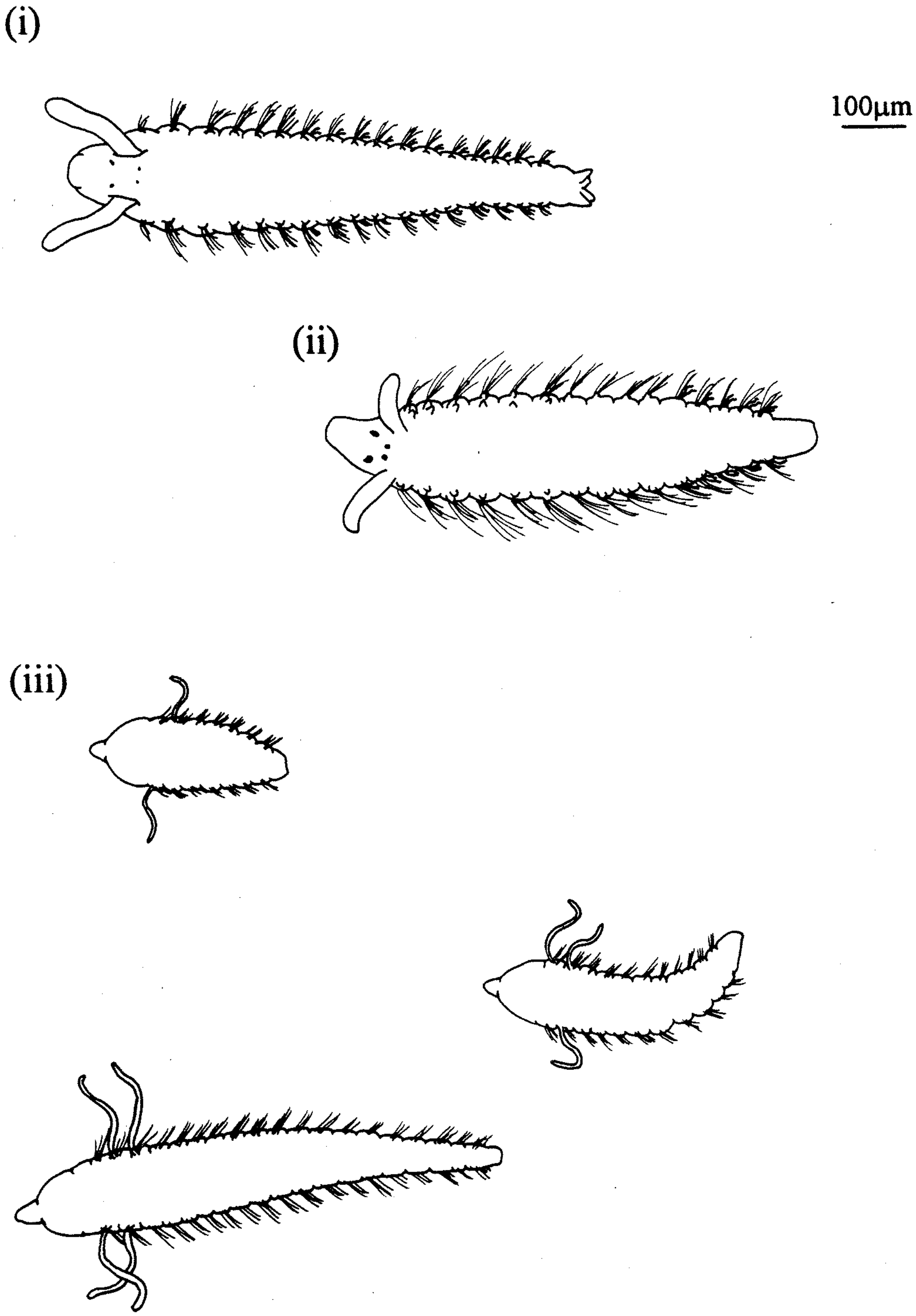
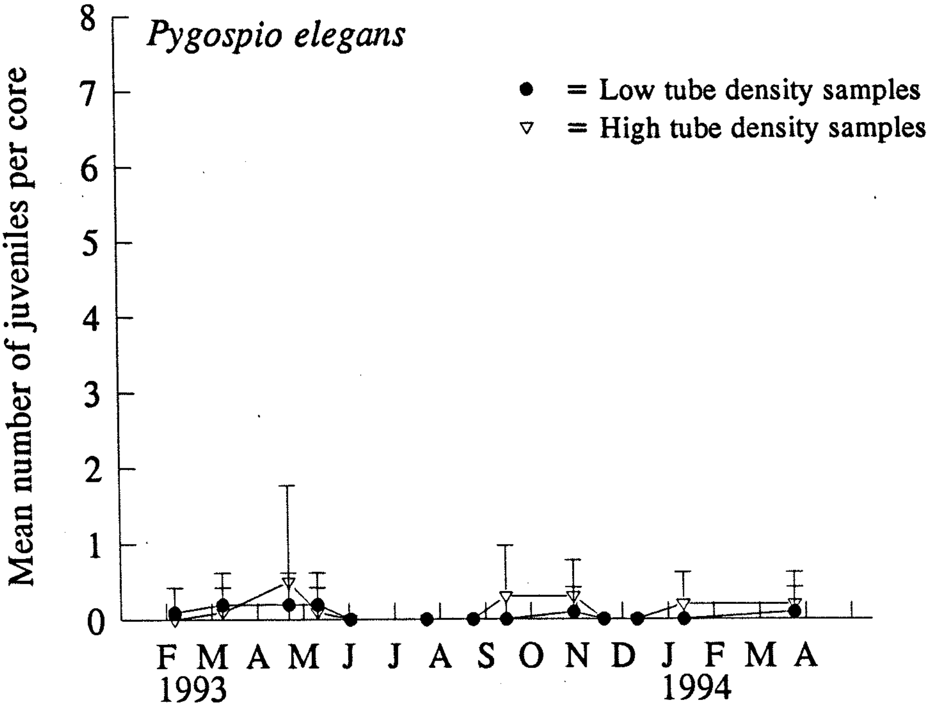


Figure 7.18 The Temporary Meiofauna. The developmental stages observed for (i) *Pygospio elegans*; (ii) *Spio martinensis*; and (iii) Cirratulidae at Solent Breezes.



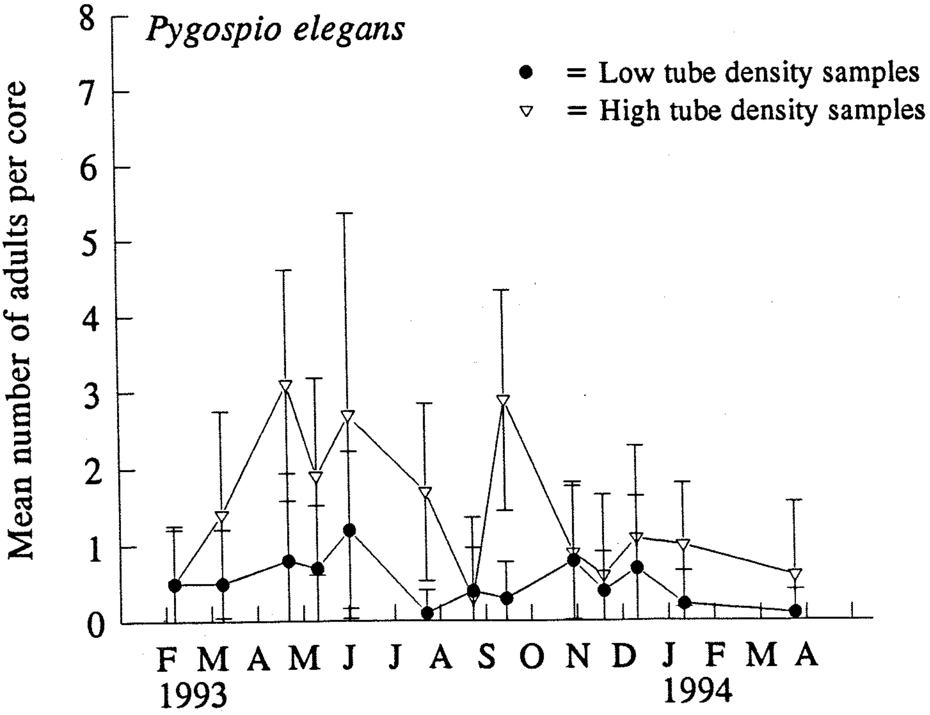


Figure 7.19 The Temporary Meiofauna. Temporal changes in the abundance of juvenile (upper graph) and adult (lower graph) *Pygospio elegans* in high and low *Lanice conchilega* tube density areas. Core size = 9.08cm^2 (surface area).

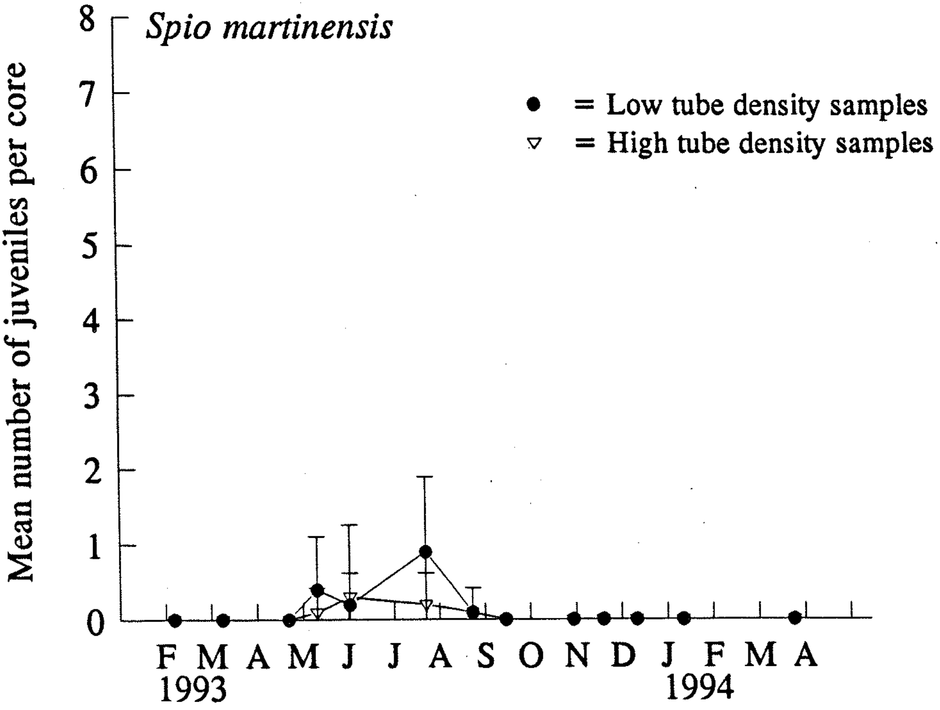
Spio martinensis

Juvenile specimens of *Spio martinensis* were also rare in samples from both high and low tube density areas. Figure 7.18 shows the single developmental stage that was observed at Solent Breezes. Juveniles were again labelled as Stage I for simplicity although they were clearly not at a particularly early stage of development. The juveniles were approximately 0.85mm in length for between 15 and 17 setigers. The head region had two pairs of eyes and a large pair of palps. Small branchiae were visible on anterior setigers and capillary chaetae were observed on all setigers. Finally, neuropodial bidentate hooked chaetae were present from setiger 11.

The density of adult specimens of *Spio martinensis* increased during the summer months, and the mean number of adults in low tube density areas was consistently greater than in high tube density areas during this period (Figure 7.20; lower graph). Mean densities of *Spio martinensis* juveniles were consistently below 1.0 (Figure 7.20; upper graph).

Cirratulidae

The 3 stages of development observed for members of the family Cirratulidae are shown in Figure 7.18. Accurate identification of juvenile cirratulids is often difficult because of the basic morphological changes that can occur during development. For example, the characteristic unidentate acicular spines of adult *Chaetozone setosa* are often weakly bidentate in the posterior neuropodia of juveniles. A similar progression from bidentate to unidentate spines is observed in the posterior neuropodia of *Caulleriella zetlandica* during its development (Woodham and Chamber, 1994). In *Tharyx killariensis*, the size and shape of posterior neurochaetae may depend on the age of specimens (*pers. obs.*). Consequently, the early stages of development observed for cirratulid juveniles could not be identified to species level.



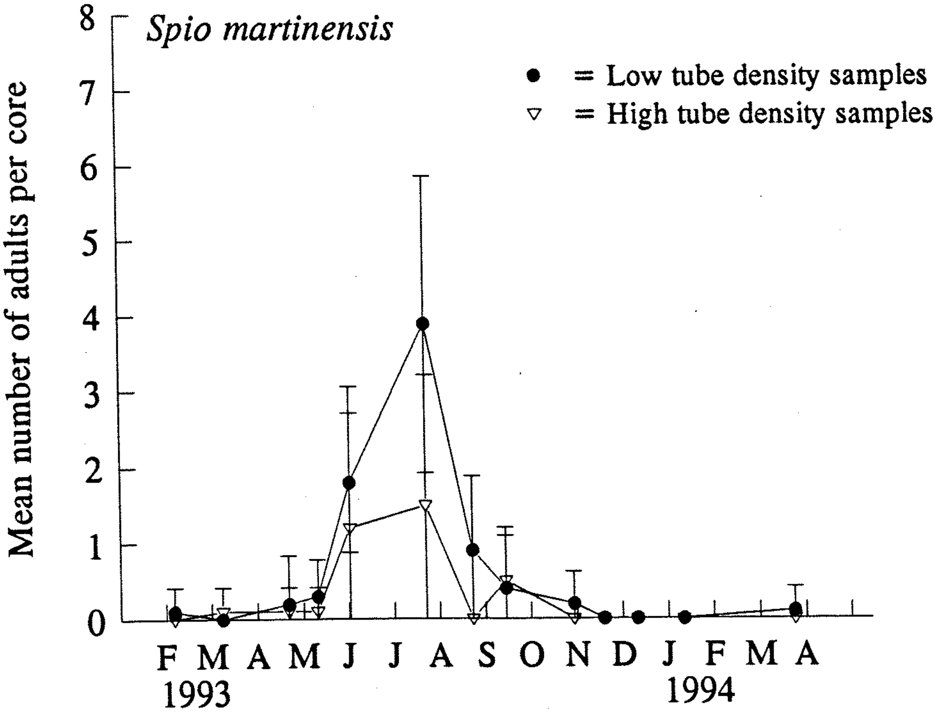
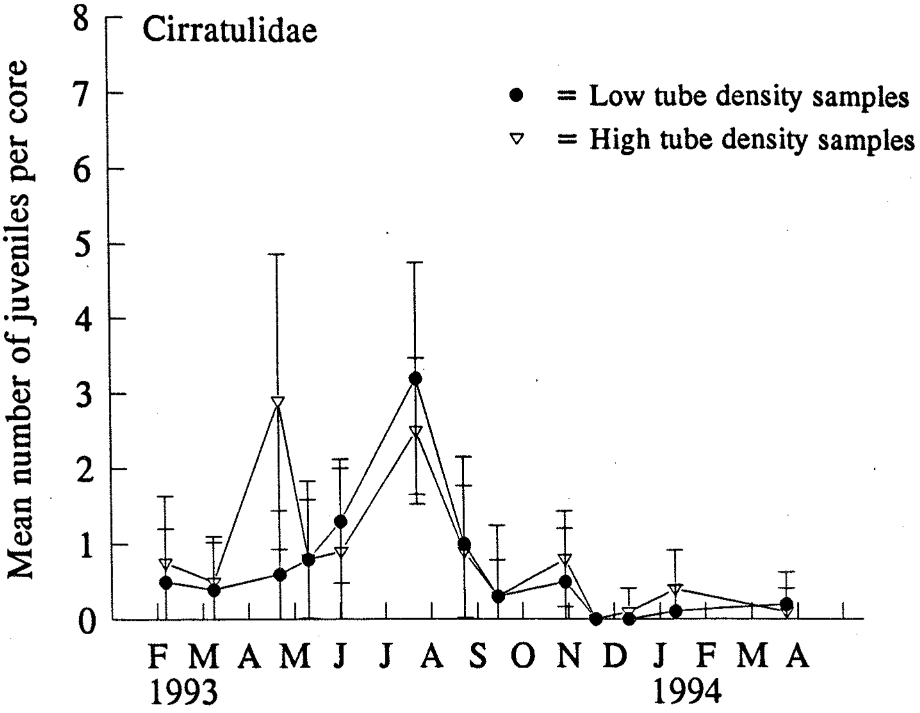


Figure 7.20 The Temporary Meiofauna. Temporal changes in the abundance of juvenile (upper graph) and adult (lower graph) *Spio martinensis* in high and low *Lanice conchilega* tube density areas. Core size = 9.08cm^2 (surface area).



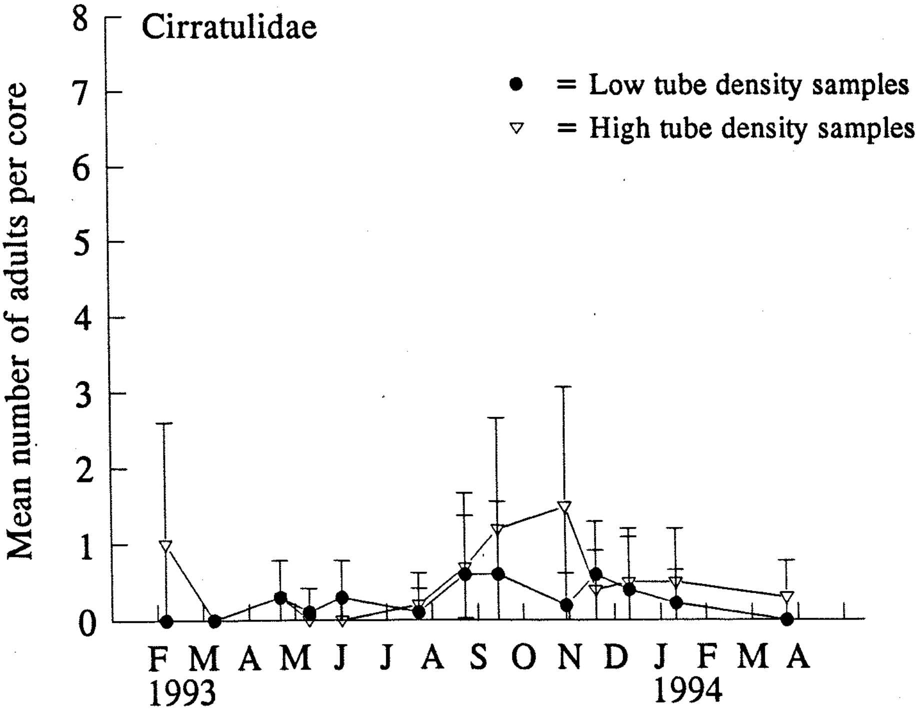


Figure 7.21 The Temporary Meiofauna. Temporal changes in the abundance of juvenile (upper graph) and adult (lower graph) Cirratulidae in high and low *Lanice conchilega* tube density areas. Core size = 9.08cm^2 (surface area).

Stage I juveniles had approximately 8 setigers and were between 0.30 and 0.35mm in length. Simple capillary chaetae were visible on all setigers and 2 or 3 tentacles were usually present in the anterior region. Stage II juveniles were defined as having approximately 12 setigers and were up to 0.55mm in length. Chaetal bundles were similar to those of Stage I specimens and 2 or 3 tentacles usually remained attached to the anterior region.

All cirratulid specimens with between 15 and 25 setigers were grouped together as Stage III juveniles. Capillary chaetae were visible on all setigers and additional stouter chaetae (spines) were present posteriorly. However, the exact configuration of these spines was usually indeterminable and their size and shape varied considerably.

Specimens that had more than 25 setigers but could not be identified were defined as immature adults, and some larger specimens were identified as either *Tharyx* sp. or *Chaetozone* sp.

Figure 7.21 presents the mean number of juveniles (± S.D.) and the mean number of adults (± S.D.) in monthly samples from both high and low tube density areas. Juveniles were present in relatively high abundance during April 1993 in high tube density areas. A subsequent increase in juvenile abundance occurred in July 1993 both in high tube density areas and low tube density areas.

Cirratulid juveniles were present in most months during the sampling period. In addition, *Chaetozone* sp. and *Tharyx* sp. adults occurred in both high and low tube density areas. However, mean numbers of adults were low throughout the sampling period because of the relatively small sample size used for this section of the study.

Crustacea

Representatives from the Amphipoda, the Tanaidacea and the Cumacea occurred in particularly low numbers. Consequently, no significant differences could be established between areas of high tube density and areas of low tube density.

Amphipods usually occurred in only 1 or 2 samples each month and mean densities were between zero and 0.3 per core. Four juvenile specimens could not be identified, but most amphipods were identified to genus or species level. No pulse of juveniles was observed for any of the amphipod species present at Solent Breezes.

The tanaid shrimp *Tanaissus lilljeborgi* was present in a number of the samples taken from areas of both high and low tube densities. Mean densities were between zero and 0.9 per core, and no significant increase in numbers occurred during the sampling period. Similarly, mean densities of the cumacean *Bodotria pulchella* were restricted to between zero and 0.7 per core. In addition, a single core sample contained 18 cumacean juveniles that could not be identified. However, these juveniles were assumed to have been recently released from a large adult female *Bodotria pulchella* that was present in the same sample.

7.4 Discussion

The meiofaunal sampling programme was designed to investigate temporal and spatial variations in the abundance of different meiofaunal groups at Solent Breezes, with the particular aim of comparing areas of sediment containing high and low densities of *Lanice conchilega* tubes. The following discussion first addresses the permanent meiofauna by analysing the population changes that occurred in its dominant component taxa, and examining any potential influences that *Lanice conchilega* and its tubes may have exerted on these main groups. Secondly, the macrofauna juveniles that constituted the temporary meiofauna are discussed with particular reference to the dominant polychaete species that were present in sufficient numbers to be considered individually. Temporal variations in the abundance of these polychaete juveniles and the potential influence of *Lanice conchilega* and its tubes on their distributions are examined.

(i) The permanent meiofauna

On a global scale, average densities of meiofaunal organisms are approximately $10^6 m^{-2}$, and densities are generally higher in intertidal sediments than in other areas (Coull and Bell, 1979). Meiofaunal assemblages are controlled by a variety of parameters and often display large temporal variability. The abundance of meiofauna at Solent Breezes was distinctly variable both in time and space. Average densities ranged between $0.4 \times 10^6 m^{-2}$ and $4.0 \times 10^6 m^{-2}$, and there was a degree of temporal variability in the form of seasonal changes in overall abundance, with maximum densities occurring in mid-summer. Similar mid-summer peaks in total meiofaunal abundance have previously been observed by Coull (1985) at a sandy estuarine site in South Carolina, USA. Although Coull acknowledged that accurate quantification of the mechanisms controlling meiofaunal abundance requires specifically designed experimentation, he was able to suggest that meiofaunal densities at this sandy site were mainly controlled by physical factors.

The patterns of change that occurred in overall meiofaunal abundance at Solent Breezes were clearly a reflection of the population changes that occurred in the major component taxa. Nematodes were usually the most abundant meiofaunal organisms, although between-sample variation was high. The abundance and diversity of nematodes in marine habitats is well documented (e.g. Heip *et al.*, 1985; Nybakken, 1997; Platt and Warwick, 1980; Warwick *et al.*, 1998), and the number of species living in any one habitat may be as much as an order of magnitude greater than for any other taxon (Platt and Warwick, 1980). Nematode densities are highest in estuarine muds and salt marshes (up to $20.0 \times 10^6 m^{-2}$) (Warwick and Price, 1979; Teal and Wieser, 1966), but diversity and species richness are greatest in sandy beaches (Heip *et al.*, 1985; Warwick *et al.*, 1998). The maximum abundance of nematodes in any single meiofaunal core taken from Solent Breezes was equivalent to $2.7 \times 10^6 m^{-2}$, and the highest mean abundance for a quadrat was equivalent to $1.9 \times 10^6 m^{-2}$. Similar maximum densities were observed by Coull (1985) at his sandy site, but densities at his muddy site reached as high as $6.3 \times 10^6 m^{-2}$. Clearly, the sandy characteristics of the sedimentary environment at Solent Breezes restricted overall nematode abundance to some degree (compared with muddy sediments), but it is likely that species richness would have been relatively high. Although individual species were not identified in the present study, the importance of nematodes in terms of both their overall contribution to production and their potential to interact with the other fauna at Solent Breezes is acknowledged.

The temporal variations in overall nematode abundance showed no distinct seasonality. It is probable that some of the nematode species present had peaks in abundance at specific times that remained undetected. Although seasonal variations in total nematode abundance have previously been observed by others, results vary between regions and between habitat types (see Heip *et al.*, 1985). Temperature and food availability are both important factors influencing patterns of abundance. Reproduction in nematodes is usually continuous, and both generation times and fecundity are temperature dependent (Warwick *et al.*, 1998). Fecundity has been shown to increase dramatically with increased temperature (Warwick, 1981), and consequently seasonal changes in ambient temperatures at Solent Breezes would be expected to have controlled levels of abundance in the absence of any other limiting factors. However, a direct correlation between temperature and overall nematode abundance did not exist. It is therefore conceivable that food availability played an important role in controlling nematode abundance.

Food resources that are potentially available to free-living marine nematodes include detritus, bacteria, benthic diatoms, other larger organisms (dead or living), and probably dissolved organic matter (Heip *et al.*, 1985; Warwick *et al.*, 1998). Although co-occurring species are potentially in competition for all these food resources, morphological differences in feeding structures allow a high level of selectivity and resource partitioning. Indeed, the high diversity of nematodes often observed in marine habitats is a reflection of this selectivity and consequent partitioning of potential food items between species. The gross measurement of total organic content used for the present study did not allow changes in the numerous types of potential food items to be monitored accurately. However, it is likely that the temporal changes observed in overall nematode abundance were largely an expression of the controlling influences exerted by different food resources on different component species. Similarly, spatial variation in nematode abundance both between samples and between quadrats may also have been linked to food resource heterogeneity.

Meiofaunal animals such as nematodes tend to exhibit a patchy horizontal distribution and individual nematode species tend to be distributed independently. The causes of meiofaunal patchiness have yet to be accurately quantified, but a number of suggestions have previously been offered. Although the general physical characteristics of a sediment (e.g. grain size distribution) may often appear to be relatively homogenous, small scale variations in the sedimentary environment may be present. Some workers have suggested that the potential food sources of nematodes (and other meiofauna) are patchily distributed, leading to the concentration of individuals around them (Coull and Bell, 1979; Lee *et al.*, 1977). At Solent Breezes average nematode abundance was consistently greater in samples taken from areas of high *Lanice conchilega* tube densities. However, it has been acknowledged that between-sample variation was high and abundance was only significantly greater in high tube density samples than in low tube density samples on three occasions.

Lanice conchilega tube density was therefore not necessarily the only factor influencing overall nematode abundance. However, tube density may well have significantly influenced some nematode species by affecting the availability of specific food resources. For example, a particular species may have been more abundant in high tube density areas if the concentration of potential food items available to that species was higher in those areas. Equally, a second species may have been relatively low in abundance because of a relative scarcity of suitable food resources. Again, it must be stressed that the gross measurement of total organic content gave no indication of the potential food resources available to individual species in each sample or set of samples. In addition, sandy sediments are known to contain high numbers of nematode species (typically more than 100), and none of the species are particularly dominant (Warwick *et al.*, 1998). Therefore, for tube density to have significantly influenced the overall abundance of nematodes from a food resource perspective, it would have needed to influence the amount of food available to a high proportion of the component species in the same way.

Localised predation events are also likely to decrease levels of meiofaunal abundance and influence patchiness, particularly if a predator selects individual taxa or a specific size range of prey organisms (Coull and Bell, 1979). In addition, Palmer (1988b) found that disturbance-induced drift of meiofaunal animals was significantly greater in the presence of predatory fish. Biogenic structures such as polychaete tubes may provide refuge areas for meiofaunal species and may also increase the heterogeneity of the sedimentary environment, both of which would affect abundance and patchiness (Lee *et al.*, 1977; Thistle, 1979). Reise and Ax (1979) observed relatively high numbers of nematodes adjacent to the burrows of *Arenicola*, as a result of the presence of "oxygen islands" around the burrows in a predominantly anaerobic environment. Although subsurface sediment layers at Solent Breezes were not anaerobic, *Lanice conchilega* tubes may have enhanced the levels of oxygen in the sedimentary environment directly adjacent to them through their direct link with the surface. This possible enhancement of oxygen levels is one way in which tubes may have affected local habitat heterogeneity, thus influencing nematode abundance. However, at this point it is important to consider the different spatial scales on which *Lanice conchilega* tubes were likely to exert an influence on the meiofauna at Solent Breezes.

The areas of sediment containing high tube densities that were sampled for the meiofaunal study all contained between 50 and 65 tubes per quadrat ($0.071m^2$). Therefore, individual tubes had between approximately 11 and $14cm^2$ (equivalent to circles with radii of 1.86cm and 2.13cm respectively) surrounding them, assuming a regular distribution. Clearly, the natural distribution of tubes would not have been regular (see Chapter 4), with some tubes being relatively close together and others with relatively large areas of unoccupied sediment surrounding them. The five permanent meiofauna cores taken from each quadrat only sampled a total of $7.7cm^2$ of the available space between the tubes (i.e. approximately 1% of the total quadrat area). The positioning of these core samples was as close to random as possible and consequently some samples would inevitably have been taken close to tubes and some at relatively remote positions. The potential influence of an individual tube on nematode abundance would arguably have decreased with distance from the tube. Therefore, the random positioning of samples in the available space between tubes could have contributed to the high levels of spatial variability observed in the abundance of nematodes and other meiofaunal taxa. For example, if tubes were acting as refuge areas protecting meiofauna from predation, their influence may only have been significant on a relatively small scale, with the risk of predation increasing with distance from the nearest tube. In addition, the influence of *Arenicola* burrows on nematode abundance observed by Reise and Ax (1979) was only significant on a relatively small scale (up to approximately 2cm from burrows). It is therefore conceivable that any comparable tube-induced influence on nematode abundance would probably have been restricted to a relatively small area around each *Lanice conchilega* tube.

In contrast, the increased production of mucus in dense patches of *Lanice conchilega* potentially influenced the meiofauna on a slightly larger scale. In Chapter 2 it was suggested that the mucus produced during tube building and feeding was a likely contributor to the relatively high concentrations of sedimentary bioavailable protein present in areas of high *Lanice conchilega* tube densities. The potentially stabilising influence of dense aggregations of tubes has also been attributed mainly to the mucus binding of sedimentary particles (see Chapter 6). This less localised influence of *Lanice conchilega* on the surrounding sedimentary environment may have been at least in part responsible for meiofaunal abundance being generally greater in high tube density areas. The meiofauna living in the dynamic environment of surface sediment layers are often re-suspended and dispersed by wave action and water currents. In general, passive re-suspension processes are responsible for meiofauna being present in the water column above beaches and unvegetated mudflats (Palmer, 1988a; Palmer and Gust, 1985). Nematodes generally inhabit deeper sedimentary layers and some species migrate away from the surface if water flow is present (Palmer and Molloy, 1986). However, those species that do inhabit surface layers (e.g. *Metachromadora* spp.) may be susceptible to passive suspension (Eskin and Palmer, 1985; Warwick and Gee, 1984). The stabilising influence of mucus binding therefore has the potential to reduce the intensity of such re-suspension events, thus reducing the impact of wave action on overall abundance. In addition, this mucus and its associated microbial populations may have constituted a potential food source for some species, which would also have affected overall abundance.

Harpacticoid copepods are generally the second most abundant component of the permanent meiofauna. Intertidal sediments usually contain densities of approximately $0.1 \times 10^6 m^{-2}$ to $1.0 \times 10^6 m^{-2}$, but maximum densities may be as high as $4.0 \times 10^6 m^{-2}$ in clean sand (Huys *et al.*, 1996). In a particular habitat type, species richness and diversity are relatively constant throughout the world, and intertidal sediments generally contain approximately 30 species with 3-5 of these containing the majority of individuals (Huys *et al.*, 1996). At Solent Breezes, harpacticoids were usually the second most abundant taxon. Temporal variability in overall harpacticoid abundance was high, with a major peak in abundance occurring in late summer. Maximum densities were in line with those quoted by Huys *et al.* (1996): the highest density in a core was equivalent to $2.0 \times 10^6 m^{-2}$, and the highest mean density for a quadrat was equivalent to $0.7 \times 10^6 m^{-2}$. In addition to the large numbers of adult harpacticoids present during August and September 1993, high densities of nauplii were also recorded, confirming a marked increase in the level of reproductive activity during this period.

Different species of harpacticoids produce broods of offspring for different lengths of time during the year, and at different times of the year. Some species (commonly those associated with algae) produce broods throughout the year, whilst others have a specific breeding season (Hicks, 1979; Huys *et al.*, 1996). Seasonal peaks in harpacticoid abundance are a function of a number of parameters. Rates of reproduction and development have been shown to be positively correlated with temperature (e.g. Heip and Smol, 1976; Palmer and Coull, 1980), and consequently most species reach maximum densities in warmer months. However, other parameters such as predation and food supply may also influence abundance in a local population. Harpacticoid densities can be dramatically reduced by fish predation, and food availability may be a significant factor superimposed on any temperature influence (Hicks and Coull, 1983). Coull and Dudley (1985) demonstrated significant differences in the levels of harpacticoid seasonality at two estuarine sites in South Carolina, USA. A variety of seasonal patterns were observed in the various dominant species, with some species having discrete breeding periods coinciding with their maximum abundance, and others being regarded as continuous breeders (Coull and Dudley, 1985; Coull and Vernberg, 1975). The major peak in overall harpacticoid abundance observed at Solent Breezes was therefore likely to have been caused by an increased level of reproductive activity in one or a few of the dominant species present. The overriding influence of temperature is clearly apparent, but the populations involved must also have been relatively free from any significant food availability or predation restraints. In addition, the virtual absence of nauplii in winter months indicates that reproductive activity was minimal during this winter period and that there were no continuous breeders among the dominant species.

Harpacticoid copepods, like all meiofauna, have a patchy spatial distribution (Hicks and Coull, 1983). This natural variability was evident throughout the sampling period at Solent Breezes, but on average harpacticoid abundance was consistently greater in areas containing high densities of *Lanice conchilega* tubes. Although between-sample variation was high and consequently the difference between high and low density areas was rarely significant, possible reasons for this overall trend must be explored. Many of the potential effects of

Lanice conchilega and its tubes discussed above with regard to nematode abundance also apply to harpacticoid abundance. In particular, the tubes are likely to have provided a source of habitat heterogeneity and potential areas of refuge from fish predation, both of which may have had a localised influence on harpacticoid abundance.

Similarly, the relatively large amounts of mucus present in areas of high tube density had the potential to positively influence harpacticoid copepod abundance by increasing the stability of the sedimentary environment. Meiobenthic copepods are the most common group found suspended in the water column above the sediment surface (Palmer and Gust, 1985; Walters and Bell, 1986), but the factors that determine where re-settlement occurs after a disturbance are difficult to quantify (Palmer, 1988a). Eckman (1983) suggested that meiofaunal settlement may simply be a passive process controlled by hydrodynamics. Similarly, Kern and Taghon (1986) found that harpacticoids exhibited increased levels of recruitment in areas where sediment accumulated (N.B. both juveniles and adults act as recruits in this case). They concluded that recruitment was mainly a passive process but swimming behaviour may have enhanced final settlement patterns. It has been shown in Chapter 2 that a degree of sediment accumulation was evident at Solent Breezes within dense patches of *Lanice conchilega* tubes (see also Muskananfola, 1994). Sediment stabilisation and accumulation in areas containing high tube densities could therefore have enhanced the settlement of both adult and juvenile harpacticoids.

The potentially stabilising influence of *Lanice conchilega* tubes would conceivably have affected harpacticoid abundance more during winter months when levels of wave-induced disturbance are likely to have been higher. Indeed, harpacticoid abundance in high tube density areas was only significantly greater than abundance in low tube density areas during late autumn and winter (i.e. November and December 1993, and January 1994), when levels of hydrodynamic disturbance are likely to have been higher.

The mucus produced by *Lanice conchilega* during feeding and tube building may also have influenced harpacticoid abundance from a food resource perspective. Potential sources of food for harpacticoids include organic detritus and its associated microbial populations, microalgae, ciliates and dissolved organic matter (Hicks and Coull, 1983; Huys *et al.*, 1996). In addition, extracellular polymer secretions such as mucus may provide important specialised sources of nutrition (Huys *et al.*, 1996). For example, the large quantities of mucilage produced by macroalgae, and its associated dense populations of bacteria, diatoms, fungi and blue-green algae, have been suggested as important resources for phytal-dwelling harpacticoids (e.g. Hicks, 1980). While some harpacticoids exhibit a high level of food specificity, others can utilise a wide variety of food sources (Huys *et al.*, 1996). It is therefore possible that the mucus produced by *Lanice conchilega* was a specific or additional potential food resource for one or more of the dominant harpacticoid species at Solent Breezes.

The potential influences of *Lanice conchilega* on harpacticoid distributions are also likely to have been dependent on the lifestyles and reproductive characteristics of the species present. Clearly, increased wave action and wave currents are likely to have disturbed epibenthic and near-surface populations more than sub-surface interstitial species. In addition, any stabilising influence exerted by *Lanice conchilega* on the sediment matrix would arguably have been more important to those harpacticoid species living nearer the sediment surface. Furthermore, epibenthic forms may have been detrimentally affected by the surface feeding activities of *Lanice conchilega*, as both juveniles and adults of these species are potential components of *Lanice conchilega*'s diet.

Most harpacticoid species have direct benthic development of their nauplii and copepodites. However, some species belonging to the families Longipediidae and Canuellidae have planktonic nauplii (Huys *et al.*, 1996) and it is conceivable that the physical presence of *Lanice conchilega* tubes would have influenced these nauplii during settlement. For example, the canuellid species *Canuella perplexa*, which was present at Solent Breezes, has planktonic nauplii and subsequent benthic copepodite stages (Vincx and Heip, 1979). The settlement of these juveniles may have been enhanced in areas of dense *Lanice conchilega* tubes as a result of the influence of tube crowns on small scale hydrodynamics at the sediment-water interface. Furthermore, although the nauplii and copepodites of the majority of harpacticoid species are benthic, horizontal dispersal can occur at all stages of development (including adults) and does not necessarily require a pelagic stage (Hicks and Coull, 1983). Therefore, the functioning of tube crowns as baffles (behind which transported material is deposited) may have influenced the resettlement of both juveniles and adults following any hydrodynamic disturbance.

The Ostracoda present at Solent Breezes exhibited a similar temporal pattern in overall abundance to the Harpacticoida during the sampling period. However, mean monthly densities were generally lower, and in particular the mid-summer increase in ostracod abundance was markedly smaller than the concurrent peak in harpacticoid abundance. Nevertheless a distinct peak in abundance was present during this mid-summer period (July and August). Marine ostracods generally have seasonal lifecycles and reproduction is restricted to relatively short periods in spring, summer or autumn (Athersuch *et al.*, 1989). In addition, temperature is documented as the main controlling mechanism that causes seasonality in marine ostracods, with juvenile development being relatively slow at lower temperatures (Athersuch *et al.*, 1989). Many ostracod species only produce one generation per year and most development takes place during spring and summer. However, some species have shorter lifecycles and may be able to produce more than one generation during this warmer period.

Throughout the majority of the sampling period, and notably during the mid-summer period of peak abundance, areas of high and low *Lanice conchilega* tube densities were relatively indistinguishable with respect to ostracod abundance. The spatial distributions of ostracod species are influenced by many physical and chemical parameters, including temperature, salinity, pH, oxygen concentration, substrate type and food supply (Athersuch *et al.*, 1989). Water temperature, salinity and substrate type are more likely to influence distributions on a large scale (i.e. between geographical regions) rather than on a local scale on a shore, and both pH and oxygen concentration are reported to be of minor significance in sedimentary environments (Athersuch *et al.*, 1989). However, food supply is likely to affect ostracod distributions on both large and small spatial scales. Most marine ostracods are thought to be scavengers feeding on dead animal or plant material, or herbivores that ingest diatoms (Athersuch *et al.*, 1989). Others may feed on the bacteria and microalgae that exist on the surface of sedimentary particles

(Whittaker, 1974), and the possibility remains that some species may adopt a carnivorous lifestyle (Athersuch *et al.*, 1989). Although information on the feeding habits of marine and brackish ostracods is relatively limited, it appears that they may not be able to utilise muco-proteins in the same way that nematodes and harpacticoids are able to. This may go some way towards explaining the relatively minor difference between ostracod densities in high and low tube density areas during the peak reproductive period.

Ostracod abundance at Solent Breezes was, however, significantly greater in high tube density areas during November and December 1993. It is conceivable that the stabilising influence of *Lanice conchilega* and its tubes may have affected abundance more during these two months, when the likelihood of wave-induced disturbance was greater. This potential influence has already been noted with respect to harpacticoid abundance during late autumn and winter (i.e. November and December 1993, and January 1994). Deep burrowing and non-swimming species of ostracod rarely occur in the water column (Palmer, 1988a), but near-surface swimming forms may well have reacted to hydrodynamic disturbance in a similar way to that described for harpacticoids. Re-settlement may therefore have been relatively enhanced in areas of high tube densities where sediment accumulation occurred.

Clearly, the level of influence exerted by *Lanice conchilega*, particularly from a stabilisation perspective, will vary according to the lifestyles of the meiofaunal species present. It is important to recognise that while overall meiofaunal abundance was consistently greater in high tube density areas, the difference was not always significant, even in winter. Species living nearer the sediment surface would obviously have been more susceptible to hydrodynamic disturbance, while other parameters may have had a more important role in controlling the distributions of deeper dwelling species. Questions relating to the mechanisms controlling spatial patterns in meiofaunal communities are far from being resolved, and such issues are especially problematic when addressing nematode distributions because of the relatively high levels of species diversity and the complex partitioning of resources along a multitude of axes. The identification of individual meiofaunal species and the investigation of temporal and spatial variations in these species had to remain beyond the scope of the present study. However, this discussion has highlighted a number of parameters that potentially influenced abundance in the three major meiofaunal taxa at Solent Breezes, with particular reference to *Lanice conchilega* and its tubes.

The two remaining meiofaunal taxa examined in this chapter (i.e. Foraminiferida and Tardigrada) were both present in relatively low numbers, and between-sample variation was high throughout the sampling period. No clear seasonal pattern existed in abundance, although mean values were relatively high in late-summer. In addition, no significant differences existed between areas of high and low tube densities, although average abundance was generally greater in high tube density areas. At least some of the controlling mechanisms described for the previous major taxa presumably also influenced forams and tardigrades. However, although individual species belonging to these two taxa may have varied significantly both temporally and spatially, the sampling programme was unable to detect any significant patterns in overall abundance.

Finally, the conspicuous absence of "soft" meiofaunal taxa such as turbellarians and gastrotrichs must be acknowledged. The groups of "hard" meiofauna discussed above all remain identifiable after standard preservation in 4% formalin, but other less robust taxa become unrecognisable (McIntyre and Warwick, 1984). The quantification of these more fragile animals requires live extraction and examination. Unfortunately, for such techniques to be successful they must be conducted as soon as possible after samples have been taken, and therefore samples cannot be stored for any significant length of time. The nature and scale of the study conducted at Solent Breezes did not allow meiofaunal samples to be processed immediately. The samples needed to be preserved and stored for long periods before they could be processed, and consequently soft meiofaunal taxa could not be studied.

(ii) The temporary meiofauna

The temporary meiofauna at Solent Breezes was dominated by juvenile polychaetes throughout the sampling period. The overall abundance of temporary meiofauna was highly variable both temporally and spatially, with mean values ranging across an order of magnitude. However, there was no clear seasonality in overall abundance because of differences in the timing of recruitment among the dominant component species. In addition, no consistent difference existed in overall abundance between areas of high *Lanice conchilega* tube density and areas of low tube density. Crustaceans from the Amphipoda, the Tanaidacea and the Cumacea occurred in very low densities, and no significant changes in abundance were observed either seasonally or between areas of high and low tube densities. The following discussion therefore concentrates on the dominant polychaete species that were present in sufficient numbers to be considered individually. The morphologies of the various developmental stages observed for these dominant species have been described in detail in the results section of this chapter, and are therefore not re-addressed here. However, temporal and spatial variations in the abundance of each species (or group of species) are discussed below with particular reference to any previously published material.

There are numerous ways in which *Lanice conchilega* and its tubes potentially influenced the larval and juvenile stages of other infaunal species at Solent Breezes. The relative importance of pre- and post-settlement processes in structuring soft-sediment communities is by no means well established, and it seems that the different adult-juvenile interactions that have been previously inferred from field and laboratory experiments are rarely universally applicable. The mechanisms through which *Lanice conchilega* might influence juvenile recruitment and survivorship include both facilitatory and inhibitory interactions. The effects of such antagonistic controlling mechanisms would conceivably counteract each other. This appears to have resulted in a lack of any consistently significant difference between areas of high and low tube density with respect to total juvenile abundance. Chapter 6 has outlined the important direct and indirect interactions that could have occurred between *Lanice conchilega* and the non-adult stages of the other infauna. These are re-described briefly below, after which the juveniles found in the temporary meiofaunal samples are considered in detail.

Local hydrodynamics are expected to influence larval settlement on at least some spatial scale (Snelgrove and Butman, 1994). Eckman (1979) concluded that larval distributions in the benthos are influenced by fine-scale hydrodynamics, and tube spacing and density have also been shown to affect recruitment (Eckman, 1983), but it has not been established whether or not passive deposition was entirely responsible for the larval patterns observed (Snelgrove and Butman, 1994). Although passive deposition of larvae operates on several spatial scales, inferences may be complicated by the ability of some larvae to actively respond to some aspect of the flow environment or to some resultant sedimentary variable (e.g. organic matter) (e.g. Snelgrove *et al.*, 1993).

At Solent Breezes, a net accumulation of sediment occurred in areas containing higher densities of *Lanice conchilega* tubes. Therefore, if passive deposition was a dominant factor controlling the settlement of planktonic larvae, settlement may have been enhanced in areas of high tube density as a result of small-scale hydrodynamics at the sediment-water interface. In addition, the presence of increased concentrations of muco-proteins on the sediment surface had the potential to influence the settlement of some larvae through active habitat selection mechanisms.

Juveniles may be also redistributed after settlement during the early stages of benthic life. Such redistribution may be a significant dispersal mechanism both for recently settled larvae and, perhaps more importantly, for the early developmental stages of species with entirely benthic lifecycles (i.e. direct developers) (Sigurdsson *et al.*, 1976). Juveniles living at or near the sediment-water interface at Solent Breezes were therefore particularly susceptible to disturbance and passive re-suspension caused by increased wave action. The stabilising influence of mucus binding in high tube density areas potentially reduced the impact of any wave-induced disturbances.

Woodin (1976) hypothesised that tube builders occupying a large proportion of the available space should effectively inhibit larvae through their feeding and defecation on the sediment surface. More specifically, Wilson (1980) demonstrated that the feeding activities of the terebellid polychaete *Eupolymnia heterobranchia* significantly lowered the survivorship of the larvae of *Nereis vexillosa* in the laboratory. Field experiments have often been unable to satisfactorily distinguish between avoidance of high adult densities by larvae and increased mortality in settling larvae caused by ingestion by the resident adults (Wilson, 1991b). Olafsson *et al.* (1994) reasoned that adult-juvenile interactions generally reduce rather than enhance recruitment, and the controlling influence of adults on juvenile density appears to operate mainly after settlement rather than while larvae are in the water column. Some studies have indicated that changes in sediment chemistry caused by the activities of adult invertebrates may alter the behaviour of settling larvae (e.g. Woodin, 1991). However, the most consistently influential adult-juvenile interactive mechanism is that between predatory infaunal species and recently settled juveniles.

The overall implication is that the activities of *Lanice conchilega* in high density areas are likely to have negatively affected the juveniles of other species, despite the fact that the majority of these juveniles remained in the benthos throughout their development. It is conceivable that changes in sediment chemistry (including an increase in muco-protein concentration) in high density areas altered the behaviour of potentially settling planktonic larvae, resulting in either a negative or positive effect depending on the behavioural response induced. In addition, if *Lanice conchilega* actively ingested small juvenile stages (as observed by Wilson (1980) for *Eupolymnia heterobranchia*), it would essentially have been acting as a predator and this would have had a significant influence on juvenile survivorship, even if the majority of juveniles were direct developers.

No evidence was found to suggest that total juvenile densities were either significantly higher or significantly lower in high tube density areas. Superficially this appears to imply that no significant interactions occurred between *Lanice conchilega* and the juvenile stages of other infaunal species. However, the physical interactions described above potentially facilitate larval recruitment or juvenile resettlement following re-suspension. In contrast, direct interactions between large tube building animals (rather than their tubes) and juvenile infauna are predominantly inhibitory, and therefore act in opposition to any facilitatory interactions. The following paragraphs focus on the polychaete juveniles that dominated the temporary meiofauna samples. Species are discussed individually, with particular reference to any available literature on juvenile morphology and ecology to illustrate the likely influences exerted on each species by *Lanice conchilega* and its tubes.

Streptosyllis websteri exhibited a major recruitment pulse in July 1993 and it has been estimated that this input of juveniles to the benthos first arrived soon after the June 1993 sampling visit (see Section 7.3.2). Early stage juveniles were present from February in 1993 and appeared again in March 1994, but achaetous larvae were not observed. In comparison, Garwood (1982) noted the presence of achaetous larvae and recognised the existence of an extended spawning season from April through to July with two peaks in spawning activity. Despite this he only observed a single recruitment pulse of juveniles with 2-4 setigers, which occurred at a similar time of year to the recruitment pulse observed at Solent Breezes (i.e. mid-July). It is therefore reasonable to assume that the Solent Breezes population had a similar reproductive cycle to Garwood's Northumberland population, with an extended spawning season and possibly two spawning peaks during spring.

Juvenile development in *Streptosyllis websteri* is largely benthic and it is unlikely that any prolonged pelagic phase exists (Garwood, 1982). However, fertilisation appears to occur in the water column and consequently some settlement of larvae must occur, albeit at a very early stage of development. *Lanice conchilega* and its tubes therefore had the potential to influence *Streptosyllis websteri* juveniles both during initial settlement and during the extended period of benthic development. Firstly, if settlement was entirely passive, *Lanice conchilega* tubes in high densities could have facilitated the accumulation of larvae. However, such a prediction is complicated by the possibility that larvae may have been able to actively select or reject settlement sites. Relatively high bioavailable protein concentrations in high tube density areas were perhaps more likely to have positively influenced settlement, but this theory remains unsubstantiated.

Both adult and juvenile *Streptosyllis websteri* are expected to inhabit surface sediments (to a depth of approximately 6cm) (Garwood, 1982) and therefore are potentially susceptible to disturbance and passive re-suspension caused by wave action. Consequently, individuals may have been positively influenced by the stabilising influence of mucus in high tube density areas. Finally, settling larvae and the early juvenile stages were potentially at risk from predation by *Lanice conchilega* in high density areas.

The potential interactions between *Lanice conchilega* and *Streptosyllis websteri* juveniles therefore include both facilitatory and inhibitory processes. Consequently, it is perhaps not surprising that there was no significant difference between high and low tube density areas with respect to juvenile *Streptosyllis websteri* abundance. In addition, *Streptosyllis websteri* is an active errant polychaete and as such would have been able to migrate relatively rapidly between areas at all stages of development. This species is known to feed on benthic diatoms and therefore the distribution of diatoms on the sediment surface may have significantly influenced both juvenile and adult distributions.

Exogone hebes juveniles were present throughout the sampling period in both high and low tube density areas, but there was no significant recruitment pulse. Similarly, Pocklington and Hutcheson (1983) observed no fixed breeding season in a population of *Exogone hebes* on the Grand Banks of Newfoundland. He suggested that the very successful viviparous mode of reproduction observed in the Newfoundland population facilitated the numerical dominance of *Exogone hebes* in this relatively cold northern part of its broad latitudinal distribution. Solent Breezes is actually further north than Pocklington and Hutcheson's sampling site, and it is therefore reasonable to suggest that the viviparous lifestyle was also dominant in the Solent Breezes population. This hypothesis is supported by the lack of any juveniles with less than 7 setigers (see Section 7.3.2).

Although the level of small-scale spatial variation was high and consequently differences between high and low tube density areas were rarely significant, mean abundances of both juvenile and adult *Exogone hebes* were consistently greater in high tube density areas. Chapter 6 has already discussed the significant positive correlation between *Exogone hebes* and tube density, and has suggested several possible mechanisms that might have been responsible for this relationship. Firstly, as it inhabits surface layers juvenile *Exogone hebes* would have been positively influenced by any stabilising effects of mucus binding in high tube density areas. In addition, a number of similarities exist between the food resources utilised by *Lanice conchilega* and *Exogone hebes* (despite their size difference), and therefore the two species may simply co-occur where suitable food resources are more abundant. Finally, the viviparous reproduction and direct development of *Exogone hebes* may have resulted in a reduction in predation pressure as the fully differentiated juveniles were arguably too large to be captured by the tentacles of *Lanice conchilega*. The elimination of this source of predation would have allowed any facilitatory mechanisms to predominate, resulting in the relative increase in *Exogone hebes* abundance observed in high tube density areas.

Scoloplos armiger juveniles were only present in the spring (i.e. March to May 1993 and March 1994), and a relatively large recruitment peak of Stage I juveniles occurred in March 1994. No significant difference existed between areas of high and low *Lanice conchilega* tube density, although the mean abundance of *Scoloplos armiger* juveniles in high tube density samples was approximately three times that in low density samples in March 1994.

Juvenile development in *Scoloplos armiger* has traditionally been described as entirely benthic, occurring initially within a stalked egg cocoon (Wilson, 1991a and references therein). These juveniles have been observed to leave the cocoon at the nine setiger stage (Anderson, 1959), after which development continues within the sediment. More recently, an alternative planktonic mode of juvenile development has been recorded (Plate and Husemann, 1992). The earliest pelagic stage is an ovoid trochophore which develops into a bentho-pelagic juvenile with approximately 10 setigers (0.9mm in length). The morphology of this settling planktonic stage is very similar to that of the benthic juveniles previously observed emerging from cocoons (Plate and Husemann, 1992), and consequently the Stage I juveniles observed in the present study could have been the product of either mode of development.

The relative importance of the different processes potentially influencing the distribution of *Scoloplos armiger* juveniles would have varied according to the mode of development employed by the Solent Breezes population. Egg cocoons were observed attached to the sediment surface at various times during this study, indicating the occurrence of direct benthic development, but the possibility of planktonic larval settlement cannot be dismissed. Any planktonic juveniles would have been influenced during settlement by alterations in the local hydrodynamic regime caused by *Lanice conchilega* tubes. In addition, active selection or rejection responses may have been influenced by any changes in the sedimentary environment generated by the activities of *Lanice conchilega*. Settling juveniles would also have been at risk from predation by *Lanice conchilega*, but their relatively large size (approximately 0.9mm) could have reduced their susceptibility. Conversely, benthic juveniles emerging from a cocoon would have avoided contact with the sediment surface, thereby minimising the risk of predation. These juveniles would also have been less susceptible to disturbance and redistribution caused by wave action as the would have remained in subsurface layers throughout their development to adulthood.

Details of the developmental biology of *Aricidea minuta* have not been previously documented. In fact little is known about the reproduction of paraonids in general (Strelzov, 1973; Wilson, 1991a). Direct development was first suggested by Hartman (1957), and this strategy still appears to be the most likely (Strelzov, 1973). The smallest juvenile stage observed at Solent Breezes occurred in January 1994, and this stage had presumably also been present prior to sampling in January 1993 as the development of juveniles through Stages II to IV was followed during the first five months of the sampling programme. Reproduction must therefore have taken place in winter months both prior to sampling (i.e. 1992-3) and during sampling (i.e. 1993-4).

Spatial variability in juvenile abundance was again high in *Aricidea minuta* and no significant difference existed between high and low tube density areas. Nevertheless, *Lanice conchilega* potentially influenced juvenile survivorship in a number of ways. Firstly, adult and juvenile *Aricidea minuta* live on or near the sediment surface. Consequently, juveniles would arguably have been susceptible to disturbance and passive re-suspension caused by increased wave action and would therefore have derived benefit from the stabilising influence of mucus in high tube density areas. Conversely, early developmental stages would potentially have been subject to an increased level of predation pressure by *Lanice conchilega* in high density areas. There may also have been a degree of protection from epibenthic predation through the provision of localised refuge areas around tubes, but this seems likely to have been counteracted by *Lanice conchilega* predation.

Juveniles belonging to the family Spionidae were present in very low densities, and there was no significant peak in juvenile recruitment in either *Pygospio elegans* or *Spio martinensis*. The *Pygospio elegans* juveniles that were recorded all had approximately 15 setigers and were between 0.8 and 1.0mm in length. Larval development in *Pygospio elegans* can be benthic (within an egg capsule) or planktonic (Gudmundsson, 1985; Wilson, 1991a). Direct developing benthic juveniles emerge from the egg capsule when they have between 14 and 20 setigers (Gudmundsson, 1985), and settlement of planktonic juveniles occurs at approximately the same stage (between 12 and 20 setigers; see Morgan, 1997). Therefore the *Pygospio elegans* juveniles recorded at Solent Breezes could have been the product of either mode of development. Juvenile development in *Spio martinensis* is predominantly planktonic and settlement occurs at the 30-setiger stage (Gudmundsson, 1985). Therefore, as the *Spio martinensis* juveniles observed at Solent Breezes had approximately 15 setigers they must have been at a pre-settlement stage, suggesting that they had been stranded on the shore and would return to the plankton on a subsequent tidal flood.

Any settling or emerging juveniles of *Pygospio elegans* or *Spio martinensis* would have been too large to be potential prey items for *Lanice conchilega*, but their surface dwelling habit would have rendered them susceptible to passive re-suspension and therefore they may have benefited from the stabilising influence of mucus in areas of high *Lanice conchilega* tube density. Differences between the physico-chemical environment in high and low density areas may also have influenced both passive and active settling processes. However, interactions between *Lanice conchilega* and the juveniles of these spionid species were likely to have been very infrequent because of the relative scarcity of the latter throughout the sampling period.

The adult populations of *Pygospio elegans* and *Spio martinensis* were variable both temporally and spatially, but both were recorded in significant numbers during the sampling period despite the absence of any significant juvenile recruitment. In particular, there was recruitment into the adult population of *Spio martinensis* during June and July 1993 without any previous or concurrent input of juveniles. This introduces the possibility that population densities were maintained or altered by a degree of adult migration onto the shore from subtidal regions.

Juveniles belonging to the family Cirratulidae could not be identified to species level and consequently had to be considered together (see Section 7.3.2). Cirratulid juveniles generally appeared to be more abundant in spring and summer, but no significant difference existed between high and low tube density areas. The processes potentially influencing the temporal and spatial distributions of cirratulid juveniles are difficult to predict because of the high number of component species that would have been present. At least eight species were recorded during the macrofaunal sampling period (see Appendix 1), and for the current chapter it was impossible to recognise which species were present as juveniles because of the general plasticity of basic morphological characteristics that exists in developing cirratulids. In addition, reproduction and juvenile ecology in cirratulids is decidedly variable both between and within genera (Wilson, 1991a). Consequently, a number of possible interactions between cirratulid juveniles and *Lanice conchilega* could have been present at different times and it is impossible to hypothesise about how these interactions would then influence adult distributions.

Finally, several of the dominant macrofaunal species recorded at Solent Breezes (see Table 4.1) were conspicuously absent from the temporary meiofauna samples. Perhaps most surprisingly, *Lanice conchilega* itself was rarely recorded. It was hoped that the sampling regime would have revealed evidence for intraspecific interactions between established adult *Lanice conchilega* and settling juvenile recruits. However, only two small adults were recorded throughout the sampling period (one in May 1993 and one in July 1993), and no newly settled juveniles were observed. Chapter 5 gives details of the significant recruitment of juvenile *Lanice conchilega* that occurred at Solent Breezes in June 1991, but also notes the absence of any significant recruitment the following year. It would appear that there was no quantifiable input of juveniles in 1993, suggesting that the *Lanice conchilega* population was maintained either by the movement of adults onto the shore from subtidal locations or because of a low level of mortality in the resident population. Some authors have suggested that *Lanice conchilega* exhibits little locomotory ability and is not expected to leave its tube or migrate between localities (Smith, 1988; 1989a; Beukema, 1985). However, Ropert (1996) described a *Lanice conchilega* population in the Baie de Seine in which there was almost a total absence of juveniles. The development and maintenance of this population relied on the transportation of adults to the study site from another population. The phenomenon of adult displacement observed by Ropert was reliant on the peculiar topography of the area under investigation. It is therefore possible that adults were transported onto the shore at Solent Breezes.

In addition, mortality in the *Lanice conchilega* population could have been minimal during 1992 and 1993. Unfortunately the longevity of this species has not yet been established. Beukema *et al.* (1978) described *Lanice conchilega* as a short-lived species that rarely survived a second winter on the tidal flats of the western part of the Dutch Wadden Sea. However, in subtidal or less harsh intertidal regions it is conceivable that this species would live longer. The young *Lanice conchilega* that arrived at Solent Breezes in June 1991 may have survived through two winters, particularly if an opportunity for spawning did not arise during this time.

The migration of adults is a process that potentially maintained population densities in several of the remaining dominant polychaete species at Solent Breezes. It has previously been documented that the planktonic larvae of *Nephtys hombergii* settle on subtidal sediments and subsequently migrate into adult littoral populations (Gibbs, 1969; Warwick and Price, 1975). In addition, rapid recolonisation of a naturally defaunated intertidal areas by adult polychaetes (including spionid species) has previously been observed by Dauer and Simon (1976). This process of recolonisation was not unexpected as the distributions of many intertidal polychaete species extend well into the subtidal zone.

(iii) Interactions between permanent and temporary meiofauna

Bell and Coull (1980) first suggested the possible existence of a "meiofaunal bottleneck" by which the permanent meiofauna present within a sediment might influence newly settled or recently settled juvenile macrofauna. There is no doubt that the body sizes of temporary and permanent meiofaunal taxa often overlap (Warwick, 1984), but the significance of any interactions between them remains unestablished. A number of observations indicate that interactions between juvenile macrofauna and the permanent meiofauna may be important. Firstly, juvenile macrofauna often arrive in the meiofaunal community during periods of increased abundance in the permanent meiofauna (e.g. Bell, 1979). In addition, many juveniles inhabit the upper 1cm of sediment where meiofaunal taxa are most abundant (Coull and Bell, 1979), and juvenile macrofauna and permanent meiofauna often potentially utilise similar food resources.

Experimental increases in meiofaunal densities have been shown to reduce recruitment success in the spionid polychaete *Streblospio benedicti*, but the mechanism behind this interaction was not identified (Bell and Coull, 1980). The sabellid polychaete *Manayunkia aestuarina* was included as a member of the permanent meiofauna in this study, and the interaction between this species and settling *Streblospio benedicti* juveniles was suggested as a possible cause of the reduction in recruitment success observed in the latter. However, although *Manayunkia aestuarina* is a relatively small species, it is often large enough to be categorised as macrofauna (*pers. obs.*) and therefore should perhaps not have been included in the permanent meiofauna. Another mechanism potentially causing a reduction in recruitment success in juvenile macrofauna is predation: polychaete and bivalve juveniles are ingested by predatory turbellarians and this interaction may result in significant post-settlement mortality in some taxa (Watzin, 1986). However, the influence of more dominant meiofaunal taxa (i.e. nematodes and harpacticoids) has yet to be clarified (Zobrist and Coull, 1992).

The meiofaunal bottleneck remains simply a hypothesis. Experiments conducted by Zobrist and Coull (1992) indicated that numerically dominant meiofauna such as nematodes and harpacticoid copepods did not significantly influence settlement in either *Streblospio benedicti* or *Mercenaria mercenaria*.

They concluded that if the bottleneck exists it is not an interaction that occurs during settlement, and suggested further work is needed to establish whether the bottleneck operates as a post-settlement phenomenon.

At Solent Breezes the survival of macrofaunal juveniles may have been influenced by the presence of permanent meiofauna via indirect competition for shared resources, but the intensity of any such interactions cannot be evaluated. In addition, the importance of the role played by predatory turbellarians cannot be assessed because the fixation method used did not allow these soft meiofaunal animals to be quantified. Nevertheless, it is recognised that if the meiofaunal bottleneck exists as a significant post-settlement phenomenon, interactions between the dominant meiofaunal groups (nematodes and harpacticoids) and the early developmental stages of macrofaunal species may have influenced subsequent macrofaunal populations and community structure. Clearly, the frequency and intensity of such potential interactions would have been greater during periods of peak meiofaunal abundance (i.e. July and August 1993) and in areas of sediment containing relatively high densities of meiofauna. Although meiofaunal abundance was generally greater in high tube density areas, small scale variability was high and a carefully designed sampling programme would be required to further examine whether relatively high meiofaunal abundance in high tube density areas significantly influenced the early developmental stages of macrofaunal species.

CHAPTER 8

Summary and Conclusions

The overall aim of this study was to investigate the interactive processes occurring in the intertidal soft-sediment community at Solent Breezes, with particular reference to the influence of *Lanice conchilega* on the other fauna. To this end, a series of sampling programmes were designed firstly to produce a detailed description of the environmental and biological characteristics of the shore at Solent Breezes, secondly to establish levels of background variability and examine the environmental parameters potentially influencing faunal patterns (particularly in relation to *Lanice conchilega*), and thirdly to specifically investigate the macrofauna and meiofauna in areas of sediment containing different densities of *Lanice conchilega*. This chapter summarises the main results and conclusions that have been presented in previous chapters, addressing each of the objectives described in Section 1.4 in turn.

(i) The first objective of this study was to describe in detail the background environmental and biological characteristics of the shore at Solent Breezes.

The transect sampling regime was designed to put the main mid-shore sampling site into context on a local scale, and to facilitate the characterisation of both the sedimentary environment and the faunal assemblages occurring at Solent Breezes in relation to other soft-sediment intertidal habitats. The hydrodynamics of the region and the local geology resulted in the shore profile at Solent Breezes incorporating two distinct physical zones (a steep-sloping region upper shore region of coarse material and an extensive shallow-sloping sediment flat). A relatively consistent assemblage of infaunal species was present across the main mid-shore area of shallow-sloping sediment flat. Towards the top of this relatively homogeneous region, species abundance and diversity declined, presumably as a result of gradual changes in environmental conditions (e.g. emersion factors). Interacting hydrodynamic and sedimentary conditions at the top of the shore appeared to influence the faunal assemblage found at the highest transect site.

Similarly, the hydrodynamic processes and associated sedimentary parameters close to the shingle bar at the bottom of the shore are thought to have resulted in an increase in the abundance of the facultative suspension feeder *Spio martinensis*.

The main mid-shore sampling site selected for the two year macrofaunal monitoring programme was physically representative of a large proportion of the intertidal sediment flat at Solent Breezes. In addition, the mid-shore infaunal community was considered to be representative of the majority of the sediment flat at Solent Breezes and much of the adjacent coastline along this eastern shore of Southampton Water. The basic habitat characteristics of the mid-shore area and the dominant species present at the sampling site corresponded to the "uncommon" LGS.Lan biotope description given in the Joint Nature Conservation Committee's MNCR littoral biotope classification guide (Connor *et al.*, 1997). The scale and intensity of the sampling programme undertaken for the current study generated a comprehensive list of the infaunal species at Solent Breezes, including almost 60 polychaete species and over 20 amphipod species. Previous studies of the benthic fauna of Southampton Water have been somewhat sporadic and there is still little information on the relative abundance of species (Tubbs, 1999). The list is therefore an important addition to current knowledge of the fauna occurring in the region.

(ii) The second objective of this study was to investigate temporal and spatial changes in the benthic community at the main mid-shore sampling site, and relate these changes to environmental parameters at the site.

The macrofaunal monitoring programme highlighted a moderate level of temporal stability in the infaunal community at Solent Breezes. A large proportion of monthly data sets were faunistically similar, although these were separable into two seasonal groups. The dense macroalgae that occurred on the sediment surface in some summer months significantly influenced the fauna at Solent Breezes, primarily by causing a seasonal pulse in weed-associated epifaunal amphipods. The exclusion of these species from the faunal matrix did not eliminate the seasonal signal in the data, but reduced its relative importance. In addition to the overall seasonal trend, several other important changes occurred in the infaunal community during the sampling period. Firstly, faunal abundance and diversity were both particularly low in March 1991. These observed minima were likely to have been a result of the relatively harsh environmental conditions that prevailed during the winter of 1990-1991 (i.e. exceptionally low minimum temperatures and physical disturbance arguably caused by increased wave action). In addition, relatively high levels of recruitment followed in the spring and summer of 1991 (this was most pronounced in *Lanice conchilega*). Distinct faunal changes also occurred towards the end of the sampling period, but it was unclear whether these changes were caused directly by a concurrent disturbance, or were a result of a natural decline in some populations following low recruitment levels and an opportunistic increase in other species, primarily *Capitella capitata*.

The use of a monitoring programme alleviates some of the intrinsic problems associated with single-point-in-time observations, but the data sets produced by a long term study are still time-specific to a degree, with each faunal data set having a unique suite of accompanying environmental observations. This restriction does not allow for the different time spans over which potentially controlling parameters may exert an influence. Time-specific correlations are therefore most useful for analysing the direct effects of more catastrophic disturbances that have a relatively rapid impact on the resident infaunal populations; e.g. severe weather or major predation events. However, it must also be recognised that such events may have a more long term influence on those individuals that are able to survive the period of disturbance. In addition, the level of response to a disturbance or change will be influenced by both the timing of the incident and events prior to it.

(iii) The third objective of this study was to describe the population dynamics and general ecology of the dominant species *Lanice conchilega* at Solent Breezes.

The analysis of the *Lanice conchilega* population was based on simple biometric techniques. Although many aspects of *Lanice conchilega* have previously been investigated, details of the dynamics of any one population have not been studied using body width measurements. Significant juvenile recruitment was only observed in the first year of the study. It has been suggested that relatively severe winter conditions in this year triggered a subsequent high level of reproductive "effort" in the spring. Initial settlement of recruiting juveniles was random across the mid-shore sampling site. The juveniles therefore showed no significant preference for particular areas of sediment. However, as the young individuals developed the overall distribution of the population returned to being significantly contagious. This pattern could have resulted from a higher level of post-settlement juvenile mortality between patches of adults or a post-settlement migration of juveniles away from unsuitable areas.

The lack of a significant supply of juveniles to replace older individuals in 1992 may have contributed to the subsequent decrease observed in overall abundance. Alternatively, the environment at Solent Breezes may have become temporarily less suitable for *Lanice conchilega*, resulting in both a decrease in the likelihood of juvenile settlement in the area and a gradual decline in numbers of established adults. The combined use of body width and tube width measurements allowed a direct comparison to be drawn between the two distributions each month. The presence of excess tubes during the last few months suggested that individual worms were dying, being removed or emigrating and leaving their tubes behind. The precise cause(s) of this observed pattern could not established but several potential mechanisms have been discussed (natural mortality, predation, environmental disturbance).

(iv) The fourth objective of this study was to highlight any effects that dense aggregations of *Lanice conchilega* had on the surrounding benthic environment.

The size distribution of particles in surface sediment layers did not alter significantly with increasing *Lanice conchilega* tube density. Furthermore, sediment samples taken from high tube density areas did not contain significantly higher or lower concentrations of total organic matter than areas with no tubes. However, dense aggregations of *Lanice conchilega* did influence certain other local sedimentary characteristics. Firstly, sediment stabilisation and net accumulation resulted in a significant increase in the depth of sediment above the underlying clay layer at higher tube densities. Secondly, mucus produced by *Lanice* *conchilega* was a likely cause of the relatively high concentrations of sedimentary bioavailable protein observed in areas of high tube density.

(v) The fifth objective of the study was to investigate the potential direct and indirect influences of *Lanice conchilega* and its tubes on both macrofaunal and meiofaunal animals.

A consistently significant positive relationship existed between *Lanice conchilega* tube density and macrofaunal abundance. The local environmental changes that occurred with increasing tube density were potentially responsible for this relationship. At higher tube densities, the increase observed in the depth of sediment above the underlying clay equated to an increase in the amount of space available for other macrofauna to inhabit. In addition, the mucus derived labile organic matter (bioavailable protein) and its associated microbes potentially enhanced levels of food resources available to deposit feeders. Species living at or near the sediment-water interface may also have been positively influenced by the stabilising affects of mucus binding in high tube density areas. Finally, a degree of localised protection from epibenthic predation may have been provided by *Lanice conchilega* tube crowns.

The potential interactions that occurred between *Lanice conchilega* and the juveniles of other macrofaunal species have been analysed and discussed in detail. Direct interactions were potentially inhibitory. In particular, predation by *Lanice conchilega* on newly settled or newly emerging juveniles on the sediment surface could have significantly influenced survivorship in these juveniles. In contrast, indirect interactions between *Lanice conchilega* and macrofaunal juveniles were predominantly facilitatory. The presence of increased quantities of food resources (including mucus and its associated microbes) in dense patches of *Lanice conchilega* could have enhanced levels of survival in infaunal juveniles. Juveniles living at or near the sediment-water interface were potentially susceptible to wave disturbance and passive re-suspension caused by increased wave action. The stabilising influence of mucus binding in high tube density areas could therefore have reduced the impact of any wave-induced disturbances. Passive deposition of planktonic larvae could have been increased in high density areas because of the net accumulation of particles. The presence of increased concentrations of muco-proteins on the sediment surface also had the potential to influence the settlement of larvae through active habitat selection mechanisms. Other changes in sediment chemistry in high density areas could have resulted in positive or negative behavioural responses in settling larvae.

The various potential influences of *Lanice conchilega* and its tubes on juvenile recruitment and survivorship therefore included both facilitatory and inhibitory interactions, the effects of which would be expected to counteract each other. This appears to have resulted in a lack of any significant difference between areas of high and low tube density with respect to juvenile abundance.

The presence of macroalgae in relatively high abundance evidently disrupted some of the effects of *Lanice conchilega* and its tubes in August 1993. The macroalgae provided a second source of mucus that would have been present in both high and low tube density areas, potentially influencing stability across the shore and providing another source of food for deposit feeders. In addition, the macroalgae itself was a potential source of food and refuge, which may have had a localised influence on the spatial distributions of macrofaunal animals.

Correlations between *Lanice conchilega* tube density and *Exogone hebes* abundance have been attributed to their potential utilisation of similar types of food (this relies on the absence of any significant competitive interaction), and relatively large "first stage" benthic juveniles of *Exogone hebes* being too big to be at risk from predation by *Lanice conchilega* (thus eliminating this potential inhibitory mechanism).

The meiofaunal sampling programme also provided detailed information on juvenile development in several polychaete species. The description of these juveniles was a slight digression from the main theme of this study. However, such specific details are commonly conspicuously absent from the published literature, despite a wealth of information often being available on the different reproductive modes exhibited by polychaetes. Perhaps most importantly, details of the development of *Aricidea minuta* have not been previously documented.

Patterns of change observed in the overall abundance of permanent meiofauna at Solent Breezes were clearly a reflection of the changes that occurred in the major component taxa (primarily Nematoda and Harpacticoida). Average nematode and harpacticoid densities were consistently greater in samples taken from areas of high *Lanice conchilega* tube densities, although it must be acknowledged that between-sample variation was high. The tubes are likely to have provided a source of habitat heterogeneity and potential areas of refuge from fish predation, both of which would have had a localised influence on meiofaunal abundance. Meiofauna living in the dynamic environment of surface sediment layers are often re-suspended and dispersed by wave action and water currents. The relatively large amounts of mucus present in areas of high tube density therefore had the potential to positively influence meiofaunal abundance by enhancing surface sediment stability. This mucus and its associated microbial populations also potentially provided a specific or additional food resource for some of the nematode and harpacticoid species present. Finally, the accumulation of particles in high tube density areas could also have influenced settlement (particularly in harpacticoid nauplii).

(vi) The final objective of the study was to assess the relative importance of *Lanice conchilega* among the interactive processes controlling spatial and temporal patterns in the fauna at Solent Breezes.

Lanice conchilega had an important structuring influence at Solent Breezes, affecting both macrofaunal and meiofaunal distributions. The consistently significant correlation between *Lanice conchilega* tube density and macrofaunal abundance seems to have been a result of direct or indirect adult-adult interactions, rather than any influence that *Lanice conchilega* or its tubes might have had on juvenile stages. Adult migration has been suggested as a process potentially maintaining some population densities at Solent Breezes. In a similar way, movements of adult macrofaunal animals could have maximised the utilisation of vertical space and available food resources, thereby increasing relative abundance in high tube density areas.

From a seasonal perspective, it is important to note that the influence of *Lanice conchilega* on macrofaunal abundance was maintained during winter. However, when relatively rare species were lost from the shore during winter through mortality or emigration, this loss occurred from both high and low tube density areas. Therefore, it seems the influence of temperature on these rarer species was not mitigated by the effects of *Lanice conchilega* on the sedimentary environment. In addition, although *Lanice conchilega* had a stabilising influence on the substratum, sporadic extreme physical disturbances have the potential to override at least some of this influence by causing significant changes in the sedimentary regime across the region. The relative importance of *Lanice conchilega* and its tubes in controlling the spatial distributions of other species may therefore be reduced during any periods of intense disturbance. However, in the relatively sheltered environment at Solent Breezes, such catastrophic disturbances (caused by either natural events or anthropogenic activities) are expected to be infrequent.

The low background levels of wave-induced disturbance at Solent Breezes are most likely to significantly influence the distributions of meiofaunal animals living close to the sediment-water interface as these are often re-suspended and dispersed by wave action and water currents. Therefore, sediment stabilisation by *Lanice conchilega* would be expected to exert a greater influence on meiofaunal distributions during winter when background levels of wave action are higher. This hypothesis is supported by the fact that harpacticoid, ostracod and, to a lesser extent, nematode abundance was significantly greater in high tube density areas during winter months.

Finally, the macrofaunal survey initially highlighted the transient impact that macroalgae had on faunal characteristics because of the co-occurrence of high densities of epifaunal amphipod species. Subsequently, it became apparent that some of the faunal characteristics related to *Lanice conchilega* tube density (perhaps most importantly the relationship between tube density and *Exogone hebes*) were partially overridden by the presence of macroalgae on the shore. However, the macroalgae present during August 1993 did not interfere with the overall relationship between *Lanice conchilega* and total macrofaunal abundance.

This implies that one of the most important factors affecting abundance in high tube density areas was the depth of sediment above the underlying clay (i.e. sediment volume), as this seems unlikely to have been significantly influenced by the short-term occurrence of macroalgae on the sediment surface.

In summary, the positive influence of *Lanice conchilega* and its tubes on the other fauna at Solent Breezes has been attributed primarily to sediment-mediated adult-adult interactions. Superficially this appears to contradict previous indications that tube-builders may limit burrowing organisms through the restriction of movement and the pre-emption of space. However, the densities of *Lanice conchilega* occurring at the sampling site were clearly not high enough to cause such a negative interaction. To the contrary, sediment accumulation and stabilisation in *Lanice conchilega* patches actually increased space availability. The overall influence of *Lanice conchilega* on pre- and post-settlement juvenile stages at Solent Breezes was neutral (i.e. neither facilitatory nor inhibitory). The macrofaunal distributions observed therefore appear to have been a result of post-juvenile processes rather than an expression of any juvenile recruitment patterns.

Many of the interactive processes highlighted by the present study would benefit from further research. More detailed analysis of the sedimentary environment both within and between *Lanice conchilega* patches may provide useful additional information relating to the mechanisms through which *Lanice conchilega* influences other animals. For example, accurate characterisation of sedimentary organic material, particularly the increased bioavailable organic component present in high tube density areas, may help to establish the relative importance of mucus and its associated microbes in determining faunal distributions.

The effects of *Lanice conchilega* and its tubes on sediment stability and accumulation could be analysed more closely using laboratory flume experiments. For example, individual tubes and aggregations of tubes at different densities could be tested to establish their effects on near-bed hydrodynamics, and interactions between flow and variables such as tube-crown structure could be examined.

Accurate quantification of epibenthic predation at Solent Breezes would require the use of carefully designed exclusion experiments supported by gut content analyses and laboratory experiments. Additional field work could also be used to clarify the different spatial scales on which *Lanice conchilega* exerts an influence. For example, precise ***in situ*** sectioning of small cores could yield further information on small scale meiofaunal distributions in relation to *Lanice conchilega*. The causes of the correlation between *Lanice conchilega* and *Exogone hebes* could be explored further by investigating small scale distributions of *Exogone hebes* around individual tubes and specifically analysing the feeding ecology of these two species.

Finally, the lack of any significant difference between high and low tube density areas with respect to juvenile abundance indicates that any facilitatory and inhibitory *Lanice conchilega*-juvenile interactions were counteracting each other to produce an overall neutral interaction. The potential interactions discussed in detail in Chapters 6 and 7 therefore require confirmation. For example, the role of *Lanice conchilega* in determining larval deposition and substrate-selection patterns could be more closely analysed using laboratory-based experimentation. Similarly, it would be appropriate to confirm the potential impact of *Lanice conchilega* predation on juvenile survivorship.

APPENDIX 1

The Macrofauna at Solent Breezes

A complete list of the macrofauna at Solent Breezes. Each species is listed with its authority and its designated code as given in the Species Directory of the Marine Fauna and Flora of the British Isles and Surrounding Seas (Howson and Picton, 1997).

Species	**MCS Code**	**Authority**
Harmothoe sp. indet.	P50	Kinberg, 1855
Pholoe inornata	P92	Johnston, 1839
Phyllodocidae sp. indet.	P114	
Eteone longa	P118	(Fabricius, 1780)
Anaitides mucosa	P145	(Oersted,1843)
Eumida sp. indet.	P163	Malmgren, 1865
Eumida bahusiensis	P164	Bergstrom, 1914
Eumida sanguinea	P167	(Oersted,1843)
Glycera sp. indet.	P255	Savigny, 1818
Glycera tridactyla	P265	Schmarda, 1861
Kefersteinia cirrata	P305	(Keferstein, 1862)
Syllidia armata	P321	Quatrefages, 1866
Ehlersia cornuta	P349	(Rathke, 1843)
Syllis sp. indet.	P358	Savigny, 1818
Syllis gracilis	P360	Grube, 1840
Streptosyllis websteri	P405	Southern, 1914
Syllides benedicti	P407	Banse, 1971
Exogone hebes	P421	(Webster and Benedict, 1884)
Exogone naidina	P422	Oersted, 1845
Sphaerosyllis sp. indet.	P424	Claparède, 1863
Sphaerosyllis erinaceus	P426	Claparède, 1863
Autolytus sp. indet.	P434	Grube, 1850
Neridiidae sp. indet.	P458	
Nereis longissima	P475	Johnston, 1840
Perinereis cultrifera	P480	(Grube, 1840)
Platynereis dumerilii	P484	(Audouin and Milne-Edwards, 1833)
Websterinereis glauca	P487	(Claparède, 1870)
Nephtys assimilis	P495	Oersted, 1843
Nephtys caeca	P496	(Fabricius, 1780)

Species	**MCS Code**	**Authority**
Nephtys cirrosa	P498	Ehlers, 1868
Nephtys hombergii	P499	Savigny, 1818
Parougia caeca	P633	(Webster and Benedict, 1884)
Protodorvillea kefersteini	P638	(McIntosh, 1869)
Scoloplos armiger	P672	(O F Müller, 1776)
Aricidea minuta	P677	Southward, 1956
Poecilochaetus serpens	P718	Allen, 1904
Polydora sp. indet.	P748	Bosc, 1802
Polydora caeca	P750	(Oersted, 1843)
Polydora ciliata	P752	(Johnston, 1838)
Pseudopolydora antennata	P772	(Claparède, 1870)
Pseudopolydora pulchra	P774	(Carazzi, 1895)
Pygospio elegans	P776	Claparède, 1863
Spio decorata	P789	Bobretzky, 1870
Spio martinensis	P791	Mesnil, 1896
Spiophanes bombyx	P794	(Claparède, 1870)
Aphelochaeta sp. "A"	(P823)	
Aphelochaeta sp. indet.	P823	Blake, 1991
Aphelochaeta marioni	P824	(Saint-Joseph, 1894)
Caulleriella alata	P829	(Southern, 1914)
Caulleriella zetlandica	P831	(McIntosh, 1911)
Chaetozone gibber	P833	Woodham and Chambers, 1994
Chaetozone setosa	P834	Malmgren, 1867
Cirriformia tentaculata	P839	(Montagu, 1808)
Tharyx sp. "A"	(P845)	
Tharyx killariensis	P846	(Southern, 1914)
Capitella capitata	P907	(Fabricius, 1780)
Notomastus latericeus	P921	M Sars, 1851
Arenicola sp. indet.	P929	Lamarck, 1801

Species	**MCS Code**	**Authority**
Clymenura sp. indet.	P955	Verrill, 1900
Euclymene oerstedii	P964	(Claparède, 1863)
Pectinariidae sp. indet.	P1100	
Lanice conchilega	P1195	(Pallas, 1766)
Hydroides sp. indet.	P1330	Gunnerus, 1768
Hydroides ezoensis	P1333	Okuda
Pomatoceros lamarcki	P1340	(Quatrefages, 1866)
Pomatoceros triqueter	P1341	(Linnaeus, 1758)
Tubificidae sp.	P1425	
Anoplodactylus pygmaeus	Q45	(Hodge, 1864)
Balanus balanus	R76	(Linnaeus, 1758)
Harpacticoida sp. indet.	R785	
Hersiliodes sp. indet.	R1923	Canu, 1888
Gammarellus angulosus	S115	(Rathke, 1843)
Pontocrates arenarius	S135	(Bate, 1858)
Amphilochus neapolitanus	S159	Della Valle, 1893
Leucothoe sp. indet.	S176	Leach, 1814
Leucothoe incisa	S177	Robertson, 1892
Leucothoe lilljeborgi	S178	Boeck, 1861
Leucothoe procera	S179	Bate, 1857
Urothoe poseidonis	S250	Reibisch, 1905
Parametaphoxus fultoni	S265	(T Scott, 1890)
Atylus swammerdamei	S412	(H Milne-Edwards, 1830)
Dexamine spinosa	S415	(Montagu, 1813)
Ampelisca brevicornis	S427	(Costa, 1853)
Bathporeia guilliamsoniana	S454	(Bate, 1856)
Bathyporeia sarsi	S458	Watkin, 1938
Gammarus sp. indet.	S471	J C Fabricius, 1775
Gammarus locusta	S478	(Linnaeus, 1758)

Species	**MCS Code**	**Authority**
Cheirocratus sp. indet.	S503	Norman, 1867
Melita palmata	S525	(Montagu, 1804)
Microprotopus maculatus	S550	Norman, 1867
Ericthonius sp. indet.	S561	H Milne-Edwards, 1830
Ericthonius punctatus	S564	(Bate, 1857)
Aoridae sp. indet.	S577	
Aora gracilis	S579	(Bate, 1857)
Corophium arenarium	S609	Crawford, 1937
Pariambus typicus	S651	(Kröyer, 1845)
Phtisica marina	S657	Slabber, 1769
Sphaeroma monodi	S870	Bocquet Hoestlandt & Levi, 1954
Tanaissus lilljeborgi	S1169	Stebbing, 1891
Bodotria pulchella	S1196	(G O Sars, 1879)
Bodotria scorpioides	S1197	(Montagu, 1804)
Eudorellopsis deformis	S1210	(Kroeyer, 1846)
Crangon crangon	S1385	(Linnaeus, 1758)
Pagurus bernhardus	S1457	(Linnaeus, 1758)
Macropodia sp. indet.	S1529	Leach, 1814
Liocarcinus arcuatus	S1578	(Leach, 1814)
Carcinus maenas	S1594	(Linnaeus, 1758)
Decapoda megalopa larva		
Gibbula umbilicalis	W165	(da Costa, 1778)
Hydrobia ulvae	W385	(Pennant, 1777)
Hinia reticulata	W745	(Linnaeus, 1758)
Nucula sp. indet.	W1565	Lamarck, 1799
Cerastoderma edule	W1961	(Linnaeus, 1758)
Mercenaria mercenaria	W2102	(Linnaeus, 1758)
Chironomid larva		
Callionymus sp. indet.	ZG451	Linnaeus, 1758

APPENDIX 2

This Appendix presents complete lists of the macrofauna and meiofauna identified for each section of the study in the following order:

1. The Transect Macrofauna;
2. The Monthly Time Series Macrofauna;
3. Macrofaunal Lists for the *Lanice conchilega* Density Experiments;
4. The Permanent Meiofauna Samples;
5. The Temporary Meiofauna Samples.

This raw data is included on an accompanying CD-ROM. Details of the data files and formats are given in the **readme.txt** file in the root directory.

REFERENCES

ALLEN, P.L. and MOORE, J.J. (1987) Invertebrate macrofauna as potential indicators of sandy beach instability. *Estuarine, Coastal and Shelf Science,* **24**, 109-125.

ALLER, R.C. (1980) Relationships of tube-dwelling benthos with sediment and overlying water chemistry. In: *Marine Benthic Dynamics*. Ed. Tenore, K.R. and Coull, B.C. Belle W. Baruch Library in Marine Science No. 11. Publ. University of Southern California Press, Columbia. 285-310.

ALLER, R.C. and YINGST, J.Y. (1978) Biogeochemistry of tube-dwellings: A study of the sedentary polychaete *Amphitrite ornata* (Leidy). *Journal of Marine Research*, **36**, 201-254.

ANDERSON, D.T. (1959) The embyology of the polychaete *Scoloplos armiger*. *Quarterly Journal of Microscopical Science*, **100**, 89-166.

ATHERSUCH, J., HORNE, D.J. and WHITTAKER, J.E. (1989) Marine and brackish water ostracods. *Synopses of the British Fauna, (N.S.)*, **43**. Publ. E.J. Brill. 343pp.

BALLY, R (1983) Intertidal zonation on sandy beaches of the west coast of South Africa. *Cahiers de Biologie Marine*, **24**, 85-103.

BAMBER, R.N. (1993) Changes in the infauna of a sandy beach. *Journal of Experimental Marine Biology and Ecology*, **172**, 93-107.

BAMBER, R.N. and STOCKWELL, T. (1988) *The littoral sedimentary fauna around Fawley*. Unpubl. Central Electricity Research Laboratories. (Report No. TPRD/L/3291/R88.)

BARNES, R.S.K. (1973) *Contributions towards a fauna list for Southampton Water. Part 1: Species recorded from the intertidal mudflats*. Unpubl. Central Electricity Research Laboratories. (Laboratory Note, No. RD/L/N 183/71.)

BARRY, J.P. (1989) Reproductive response of a marine annelid to winter storms: an analog to fire adaptation in plants? *Marine Ecology Progress Series*, **54**, 99-107.

BATTEN, S.D. (1994) *Correlative studies of the ecophysiology and community structure of benthic macrofauna*. PhD Thesis, University of Southampton.

BELL, S.S. (1979) Short- and long-term variation in a high marsh meiofaunal community. *Estuarine and Coastal Marine Science*, **9**, 331-350.

BELL, S.S. and COULL, B.C. (1980) Experimental evidence for a model of juvenile macrofauna-meiofauna interactions. In: *Marine Benthic Dynamics*. Ed. Tenore, K. and Coull, B.C. Belle W. Baruch Library in Marine Science No. 11. Publ. University of Southern California Press, Columbia. 179-188.

BEUKEMA, J.J. (1979) Biomass and species richness of macrobenthic animals living on a tidal flat area in the Dutch Wadden Sea: effects of a severe winter. *Netherlands Journal of Sea Research*, **13(2)**, 203-223.

BEUKEMA, J.J. (1982) Annual variation in reproductive success and biomass of the major macrozoobenthic species living in a tidal flat area of the Wadden Sea. *Netherlands Journal of Sea Research*, **16**, 37-45.

BEUKEMA, J.J. (1985) Zoobenthos survival during severe winters on high and low tidal flats in the Dutch Wadden Sea. In: *Marine Biology of Polar Regions and Effects of Stress on Marine Organisms*. Ed. Gray, J.S. and Christiansen, M.E. Publ. J.Wiley and Sons Ltd. 351-361.

BEUKEMA, J.J. (1990) Expected effects of changes in winter temperature on benthic animals living in soft sediments in coastal North Sea areas. In: *Expected Effects of Climatic Change on Marine Coastal Ecosystems*. Ed. Beukema, J.J. *et al*. Publ. Kluwer, Dordrecht. 83-92.

BEUKEMA, J.J., DE BRUIN, W. and JANSEN, J.J.M. (1978) Biomass and species richness of the macrobenthic animals living on the tidal flats of the Dutch Wadden Sea: long term changes during a period with mild winters. *Netherlands Journal of Sea Research*, **12(1)**, 58-77.

BEUKEMA, J.J. and DE VLAS, J. (1979) Population parameters of the lugworm *Arenicola marina*, living on the tidal flats of the Dutch Wadden Sea. *Netherlands Journal of Sea Research*, **13**, 331-353.

BHAUD, M. (1988) The two planktonic larval periods of *Lanice conchilega* (Pallas, 1766) Annelida Polychaeta, a peculiar example of the irreversibility of evolution. *Ophelia*, **29(2)**, 141-152.

BHAUD, M. and CAZAUX, C.P. (1990) Buoyancy characteristics of *Lanice conchilega* (Pallas) larvae (Terebellidae). Implications for settlement. *Journal of Experimental Marine Biology and Ecology*, **141**, 31-45.

BISHOP, G.M.and HOLME, N.A. (1980) Survey of the littoral zone of the coast of Great Britain. Final report - part 1: The sediment shores - an assessment of their conservation value. (Contractor: Marine Biological Association / Scottish Marine Biological Association.) *Nature Conservancy Council, CSD Report No. 326.*

BLAKE, J.A. (1991) Revision of some genera and species of Cirratulidae (Polychaeta) from the western North Atlantic. In: *Systematics, Biology and Morphology of World Polychaeta. Proceedings of the Second International Polychaete Conference, Copenhagen, 1986.* Ed. Petersen M.E. and Kirkegaard J.B., *Ophelia,* **Supplement 5**, 17-30.

BONSDORFF, E. and PEARSON, T.H. (1997) The relative impact of physical disturbance and predation by *Crangon crangon* on population density in *Capitella capitata*: an experimental study. *Ophelia*, **46(1)**, 1-10.

BORDOVSKIY, O.K. (1965) Accumulation and transformation of organic substances in marine sediments. 3. Accumulation of organic matter in bottom sediments. *Marine Geology*, **3**, 33-82.

BRENCHLEY, G.A. (1982) Mechanisms of spatial competition in marine soft bottom communities. *Journal of Experimental Marine Biology and Ecology*, **60**, 17-33.

BROWN, A.C. (1971) Ecology of the sandy beaches of the Cape Peninsula, South Africa. Part 1. Introduction. *Transactions of the Royal Society of South Africa*, **39**, 237-279.

BROWN, A.C. (1973) The ecology of sandy beaches of the Cape Peninsula, South Africa. Part 4. Observations on two intertidal Isopoda, *Eurydice longicornis* (Stüder) and *Exosphaeroma truncatitelson* Barnard. *Transactions of the Royal Society of South Africa*, **40**, 381-404.

BROWN, A.C. and McLACHLAN, A. (1990) *Ecology of Sandy Beaches*. Publ. Elsevier, Amsterdam.

BUCHANAN, J.B. (1984) Sediment Analysis. In: *Methods for the Study of Marine Benthos. I.B.P. Handbook, No. 16*. Ed. Holme N.A. and McIntyre A.D. Publ. Blackwell Scientific Publications, Oxford. 41-65.

BUCHANAN, J.B. and MOORE, J.J. (1986) Long term studies at a benthic station off the coast of Northumberland. *Hydrobiologia*, **142**, 121-127.

BUHR, K.J. (1976) Suspension-feeding and assimilation efficiency in *Lanice conchilega* (Polychaeta). *Marine Biology*, **38**, 373-383.

BUHR, K.J. (1979) A mass population of *Lanice conchilega* (Polychaeta: Terebellidae) in the Weser Estuary, Germany. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven*, **17**, 101-149.

BUHR, K.J. (1981) Effects of the cold winter 1978/79 on the macrobenthos of the *Lanice* - association in the Weser Estuary. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven*, **19**, 115-131.

BUHR, K.J. and WINTER, J.E. (1977) Distribution and maintenance of a *Lanice conchilega* association in the Weser Estuary (FRG), with special reference to the suspension-feeding behaviour of *Lanice conchilega*. In: *Biology of Benthic Organisms, 11th European Symposium on Marine Biology, Galway 1976.* Ed. Keegan B.F., Ceidigh, P.O. and Boaden P.J.S. Publ. Pergamon Press. New York. 101-114.

CAREY, D.A. (1983) Particle re-suspension in the benthic boundary layer induced by flow around polychaete tubes. *Canadian Journal of Fisheries and Aquatic Science*, **40(Suppl. 1)**, 301-308.

CAREY, D.A. (1987) Sedimentological effects and palaeoecological implications of the tube building polychaete *Lanice conchilega* (Pallas). *Sedimentology*, **34**, 49-66.

CASWELL, H. (1976) Community structure: a neutral model analysis. *Ecological Monographs*, **46**, 327-354.

CHAMBERS, S.J. and MUIR, A.I. (1997) Polychaetes: British Chrysopetaloidea, Pisionoidea and Aphroditoidea. *Synopses of the British Fauna, (N.S.)*, **54**. Publ. Field Studies Council. 202pp.

CHAMBERS, S.J. and GARWOOD, P.R. (1992) *Polychaetes from Scottish waters. Part 3: Family Nereidae.* Publ. National Museums of Scotland. 65pp.

CLARKE, K.R. and AINSWORTH, M. (1993) A method of linking multivariate community structure to environmental variables. *Marine Ecology Progress Series*, **92**, 205-219.

CLARKE, K.R. and WARWICK, R.M. (1994) *Changes in marine communities: an approach to statistical analysis and interpretation*. Publ. Natural Environment Research Council, UK. 144pp.

CLARK, R.B. (1962) Observations on the food of *Nephtys. Limnology and Oceanography*, **7**, 380-385.

CLAVIER, J. (1983) Biological cycle of *Euclymene oerstedii* (Annelida; Polychaeta) in the Rance Basin. *Comptes rendus Academie Science Series III*, **296**, 483-486.

CODLING, I.D. and ASHLEY, S.J. (1992) Development of a biotic index for the assessment of pollution status of marine communities. *WRc Report No. NR 3102/1/2404/4280*. © WRc plc. 78pp.

CONNOR, D.W., BRAZIER, D.P., HILL, T.O. and NORTHEN, K.O. (1997) Marine Nature Conservation Review: Marine biotope classification for Britain and Ireland. Volume 1 - Littoral biotopes. Version 97.06. *Joint Nature Conservation Committee Report No. 229.*

COULL, B.C. (1985) Long-term variability of estuarine meiobenthos: an 11 year study. *Marine Ecology Progress Series*, **24**, 205-218.

COULL, B.C. and BELL, S.S. (1979) Perspectives in marine meiofaunal ecology. In: *Ecological Processes in Coastal and Marine Ecosystems*. Ed. Livingston, R.J. Publ. Plenum Press, New York and London. 189-216.

COULL, B.C. and DUDLEY, B.W. (1985) Dynamics of meiobenthic copepod populations: a long term study (1973-1983). *Marine Ecology Progress Series*, **24**, 219-229.

COULL, B.C. and VERNBERG, W.B. (1975) Reproductive periodicity of meiobenthic copepods: seasonal or continuous. *Marine Biology*, **32**, 289-293.

COVEY, R. (1998) Eastern Channel (Folkstone to Durlston Head) (MNCR Sector 7). In: *Marine Nature Conservation Review. Benthic Marine Ecosystems of Great Britain and the North-east Atlantic*. Ed. Hiscock, K. Publ. Joint Nature Conservation Committee, Peterborough. (Coasts and seas of the United Kingdom. MNCR series.) 199-218.

CRISP, D.J. (1964) The effects of the severe winter of 1962-63 on marine life in Britain. *Journal of Animal Ecology*, **33**, 163-210.

CROKER, R.A. and HATFIELD, E.B. (1980) Space partitioning and interactions in an intertidal sand-burrowing amphipod guild. *Marine Biology*, **61**, 79-88.

DAHL, E. (1952) Some aspects of the ecology and zonation of the fauna on sandy beaches. *Oikos*, **4**, 1-27.

DALE, N.G. (1974) Bacteria in intertidal sediments: factors related to their distribution. *Limnology and Oceanography*, **19**, 509-518.

DALES, R.P. (1955) Feeding and digestion in Terebellid polychaetes. *Journal of the Marine Biological Association of the United Kingdom*, **34**, 55-79.

DAUER, D.M. and SIMON, J.L. (1976) Habitat expansion among polychaetous annelids repopulating a defaunated marine habitat. *Marine Biology*, **37**, 169-177.

DAY, J.H. (1967) *A monograph of the Polychaeta of southern Africa*. British Museum (Natural History), London.

DEAN, D. (1978) Migration of the sand worm *Nereis virens* during winter nights. *Marine Biology*, **45**, 168-173.

DE VLAS J. (1979) Annual food intake by plaice and flounder in a tidal flat area in the Dutch Wadden Sea, with special reference to consumption of regenerating parts of macrobenthic prey. *Netherlands Journal of Sea Research*, **13**, 117-153.

DE VLAS J. (1981) On cropping and being cropped: the regeneration of body parts by benthic organisms. *Marine Science*, **15**, 173-177.

DEXTER, D.M. (1972) Comparison of the community structure in a Pacific and Atlantic Panamanian sandy beach. *Bulletin of Marine Science*, **2**, 449-462.

DIXON, I.M.T. and MOORE, J. (1987) Surveys of harbours, rias and estuaries in southern Britain: the Solent system. (Contractor: Field Studies Council, Oil Pollution Research Unit, Pembroke.) *Nature Conservancy Council, CSD Report No. 723.*

DUCHÊNE J.C. and BHAUD, M. (1988) Uncinial patterns and age determination in terebellid polychaetes. *Marine Ecology Progress Series*, **49**, 267-275.

DYER, K.R. (1986) *Coastal and estuarine sediment dynamics*. Publ. John Wiley, Chichester, England. 342pp.

EAGLE, R.A. (1975) Natural fluctuations in a soft bottom benthic community. *Journal of the Marine Biological Association of the United Kingdom*, **55**, 865-78.

ECKMAN, J.E. (1979) Small-scale patterns and processes in a soft-substratum intertidal community. *Journal of Marine Research*, **37**, 437-457.

ECKMAN, J.E., NOWELL, A.R.M. and JUMARS, P.A. (1981) Sediment destabilisation by animal tubes. *Journal of Marine Research*, **39**, 361-374.

ECKMAN, J.E. (1983) Hydrodynamic processes affecting benthic recruitment. *Limnology and Oceanography*, **28**, 241-257.

EIBYE-JACOBSEN, D. (1991) A revision of *Eumida* Malmgren, 1865 (Polychaeta: Phyllodocidae). *Steenstrupia*, **17(3)**, 81-140.

ELEFTHERIOU, A. and JONES, D.A. (1976) The genus *Eurydice* on the west coast of India. *Journal of Zoology*, **178**, 385-394.

ELEFTHERIOU, A. and NICHOLSON, M.D. (1975) The effects of exposure on beach fauna. *Cahiers de Biologie Marine* (suppl.), **16**, 695-710.

ELLIOTT, J.M. (1971) *Some methods for the statistical analysis of samples of benthic invertebrates; FBA Scientific Publication*. Publ. Freshwater Biological Association. 144pp.

ESKIN, R.A. and PALMER, M.A. (1985) Suspension of marine nematodes in a turbulent tidal creek: species patterns. *Biological Bulletin of the Marine Biological Laboratory, Woods Hole*, **169**, 615-623.

FAUCHALD, K. (1977) The polychaete worms. Definitions and keys to the orders, families and genera. *Natural History Museum of Los Angeles County, Science Series,* **28**, 1-190.

FAUCHALD, K. and JUMARS, P.A. (1979) The diet of worms: a study of polychaete feeding guilds. *Oceanography and Marine Biology: an Annual Review*, **17**, 193-284.

FAUVEL, P. (1923) Polychètes errantes. *Faune de France*, **5**. 488pp.

FAUVEL, P. (1927) Polychètes sedentaires, Addenda aux errantes, archiannelides, myzostomaires. *Faune de France*, **16**. 494pp.

FERAL, P. (1992) Paleoecological implications of the polychaete *Lanice conchilega* (Pallas) on the intertidal zone of sandy shores. *Geobios*, **25**, 753-765.

FISH, J.D. and FISH, S. (1989) *A student's guide to the seashore*. Publ. Unwin, Hyman, London. 473pp.

FOLK, R.L. (1974) *Petrology of Sedimentary Rocks.* Publ. Hemphill Publishing Co., Austin, Texas. 182pp.

GARWOOD, P.R. (1982) The life-cycle and population dynamics of *Streptosyllis websteri* (Polychaeta: Syllidae) from a Northumberland beach. *Journal of the Marine Biological Association of the United Kingdom,* **62**, 783-798.

GARWOOD, P.R. (1991) Reproduction and the classification of the family Syllidae (Polychaeta). *Ophelia*, **Supplement 5**, 81-87.

GARWOOD, P.R. (1992) Segment counting in the genus *Nephtys* : its relevance to *N. hombergii*. *Polychaete Research Newsletter*, **14**, 7-8.

GEORGE, J.D. and HARTMANN-SCHRÖDER, G. (1985) Polychaetes: British Amphinomida, Spintherida and Eunicida. *Synopses of the British Fauna, (N.S.)*, **32**. Publ. E.J. Brill / Dr. W. Backhuys, London-Leiden-Köln-København. 221pp.

GIBBS, P.E. (1969) A quantitative study of the polychaete fauna of certain fine deposits in Plymouth Sound. *Journal of the Marine Biological Association of the United Kingdom*, **49**, 311-326.

GOERKE, H and WEBER, K. (1990) Locality-dependent concentrations of bromophenols in *Lanice conchilega* (Polychaeta, Terebellidae). *Comparative Biochemistry and Physiology,* **97B(4)**, 741-744.

GOERKE, H and WEBER, K. (1991) Bromophenols in *Lanice conchilega* (Polychaeta, Terebellidae): the influence of sex, weight and season. *Bulletin of Marine Science*, **48(2)**, 517-523.

GOSS-CUSTARD, J.D., JONES, R.E. and NEWBERY, P.E. (1977) The ecology of The Wash. I. Distribution and diet of wading birds (Charadrii). *Journal of Applied Ecology*, **14**, 681-700.

GRAHAM, A. (1988) Molluscs: prosobranch and pyramidellid gastropods. *Synopses of the British Fauna, (N.S.)*, **2**. Publ. E.J. Brill / Dr. W. Backhuys. viii + 662pp. (2nd edition).

GRANT, J. (1981) Sediment transport and disturbance on an intertidal sandflat: infaunal distribution and recolonisation. *Marine Ecology Progress Series*, **6**, 249-255.

GRASSLE, J.P. and GRASSLE, J.F. (1976) Sibling species in the marine pollution indicator *Capitella* (Polychaeta). *Science*, **192**,567-69.

GREMARE, A. (1986) A comparative study of reproductive energetics in two populations of the terebellid polychaete *Eupolymnia nebulosa* Montagu with different reproductive modes. *Journal of Experimental Marine Biology and Ecology*, **96**, 287-302.

GREMARE, A. (1994) What describes fecundity of *Capitella* sp. 1 better: macro- or micro-nutrient availability? *Marine Biology*, **119**, 367-374.

GREMARE, A., MARSH, A.G. and TENORE, K.R. (1989) Fecundity and energy partitioning in *Capitella capitata* Type I (Annelida, Polychaeta). *Marine Biology*, **100**, 365-371..

GUDMUNDSSON, H. (1985) Life history patterns of polychaete species of the family Spionidae. *Journal of the Marine Biological Association of the United Kingdom*, **65**, 93-111.

HALL, S.J. (1994) Physical disturbance and marine benthic communities: life in unconsolidated sediments. *Oceanography and Marine Biology: an Annual Review*, **32**, 179-239.

HARTLEY, J.P. (1981) The family Paraonidae (Polychaeta) in British waters: a new species and new records with a key to species. *Journal of the Marine Biological Association of the United Kingdom*, **61**, 133-149.

HARTMAN, O. (1957) Orbiniidae, Apistobranchidae, Paraonidae and Longosomidae. *Allan Hancock Pacific Expedition Reports*, **15**, 3.

HARTMANN-SCHRÖDER, G. (1971) Annelida, Borstenwurmer, Polychaeta. *Die Tierwelt Deutschlands und der angrenzenden Meeresteile*, **58**. 594pp.

HAYWARD, P.J. and RYLAND, J.S. (1990a) *The marine fauna of the British Isles and North-West Europe. Volume I: Introduction and Protozoans to Arthropods.* Publ. Oxford University Press. 627pp.

HAYWARD, P.J. and RYLAND, J.S. (1990b) *The marine fauna of the British Isles and North-West Europe. Volume II: Molluscs to Chordates.* Publ. Oxford University Press. 368pp.

HEIP, C. and SMOL, N. (1976) Influence of temperature on the reproductive potential of two brackish water harpacticoids (Crustacea: Copepoda). *Marine Biology*, **35**, 327-334.

HEIP, C., VINCX, M. and VRANKEN, G. (1985) The ecology of marine nematodes. *Oceanography and Marine Biology: an Annual Review*, **23**, 399-489.

HERBERT, R. (1991) Autumn field meeting at Osborne Bay, Isle of Wight (8th September 1991). *Porcupine Newsletter*, **5(3)**, 53-58.

HICKS, G.R.F. (1979) Pattern and strategy in the reproductive cycles of benthic harpacticoid copepods. In: *Cyclic Phenomena in Marine Plants and Animals*. Ed. Naylor E., Hartnoll, R.G. Pergamon Press, Oxford. 139-147.

HICKS, G.R.F. (1980) Structure of phytal harpacticoid copepod assemblages and the influence of habitat complexity and turbidity. *Journal of Experimental Marine Biology and Ecology*, **44**, 157-192.

HICKS, G.R.F. and COULL, B.C. (1983) The ecology of marine meiobenthic harpacticoid copepods. *Oceanography and Marine Biology: an Annual Review*, **21**, 67-175.

HILL, S.D., FERKOWICZ, M.J. and GRASSLE, J.P. (1988) Effects of tail regeneration on early fecundity in *Capitella* sp.I and sp.II (Polychaeta). *Biological Bulletin of the Marine Biological Laboratory, Woods Hole*, **175**, 311-312.

HOLDICH, D.M. and JONES, J.A. (1983a) Tanaids. Keys and notes for the identification of the species. *Synopses of the British Fauna, (N.S.)*, **27**. Publ. Cambridge University Press. 98pp.

HOLDICH, D.M. and JONES, J.A. (1983b) The distribution and ecology of British shallow-water tanaid crustaceans (Peracarida, Tanaidacea). *Journal of Natural History*, **17**, 157-183.

HOLDICH, D.M. and BIRD, G.J. (1986) Tanaidacea (Crustacea) from sublittoral waters off West Scotland, including the description of two new genera. *Journal of Natural History,* **20**, 79-100.

HOLME, N.A. and BISHOP, G.M. (1980) Survey of the littoral zone of the coast of Great Britain. 5. Report on the sediment shores of Dorset, Hampshire and the Isle of Wight. (Contractor: Scottish Marine Biological Association / Marine Biological Association.) *Nature Conservancy Council, CSD Report No. 280.*

HOLME, N.A. and MCINTYRE, A.D. (1984) *Methods for the Study of Marine Benthos. I.B.P. Handbook, No. 16.* 2nd Edition. Publ. Blackwell Scientific Publications, Oxford. 334pp.

HOLTHE, T. (1986) Polychaeta Terebellomorpha. *Marine Invertebrates of Scandinavia*, *7*, 1-194.

HOWSON, C.M. and PICTON, B.E. (1997) *The species directory of the marine fauna and flora of the British Isles and surrounding seas.* Ulster Museum and The Marine Conservation Society, Belfast and Ross-on-Wye. Ulster Museum Publication No. 276. 508pp.

HUYS, R., GEE, J.M., MOORE, C.G. and HAMOND, R. (1996) Marine and Brackish Water Harpacticoid Copepods. Part 1. *Synopses of the British Fauna, (N.S.)*, **51**. Publ. Field Studies Council. 352pp.

INGLE, R.W. (1996) Shallow Water Crabs. *Synopses of the British Fauna, (N.S.)*, **25** (Second Edition). Publ. Field Studies Council. 206pp.

JONES, N.S. (1976) British Cumaceans. *Synopses of the British Fauna, (N.S.)*, **7**. Publ. Academic Press, London and New York. 62pp.

JONES, N.S. and HOLDICH, D.M. (1983) A new species of the tanaid genus *Tanaissus* Norman and Scott from British waters. *Crustaceana,* **45(2)**, 214-219.

KERN, J.C. and TAGHON, G.L. (1986) Can passive recruitment explain harpacticoid copepod distribution in relation to epibenthic structure? *Journal of Experimental Marine Biology and Ecology*, **101**, 1-23.

KING, G.M. (1986) Inhibition of microbial activity in marine sediments by a bromophenol from a hemichordate. *Nature*, **323**, 257-259.

KING, P.E. (1986) Sea Spiders. A revised key to the adults of littoral pycnogonids in the British Isles. *Field Studies*, **6**, 493-516.

LAURISTON, W. (1977) *Littoral infaunal communities at Royal Pier, Southampton Water*. Unpubl. MSc. Thesis, University of Southampton.

LEE, J.J., TIETJEN, J.H., MASTROPAOLO, C. and RUBIN, H. (1977) Food quality and heterogeneous spatial distribution of meiofauna. *Helgoländer wissenschaftliche Meeresuntersuchungen*, ***30***, 272-282.

LEVIN, L.A. (1982) Interference interactions among tube-dwelling polychaetes in a dense infaunal assemblage. *Journal of Experimental Marine Biology and Ecology*, **65**, 107-119.

LEVINGTON, J.S. and BIANCHI, T.S. (1981) Nutrition and food limitation of deposit feeders. I. The role of microbes in the growth of mud snails (Hydrobiidae). *Journal of Marine Research*, **39**, 531-556.

LINCOLN, R.J. (1979) *British Marine Amphipoda: Gammaridea.* Publ. British Museum (Natural History), London. 658pp.

LOREZ, G.R. and LEVINGTON, J.S. (1987) Ecology of deposit feeding animals in marine sediments. *Quarterly Review of Biology*, **62**, 235-260.

LOPEZ, G.R., TANTICHODOK, P. and CHENG, I-J. (1989) Radiotracer methods for determining utilisation of sedimentary organic matter by deposit feeders. In: *Ecology of Marine Deposit Feeders; Lecture Notes on Coastal and Estuarine Studies, No. 31*. Ed. Lopez G.R., Taghon G.L. and Levington J.S. Publ. Springer-Verlag, New York. 149-170.

MARGALEF, D.R. (1951) Diversidad de especies en les communidades naturales. *Publ. Inst. Biol. apl., Barcelona*, **9**, 5-27.

MARSH, A.G., GREMARE, A. and TENORE, K.R. (1989) Effects of food type and ration on growth of juvenile *Capitella* sp. 1 (Annelida: Polychaeta): macro- and micro-nutrients. *Marine Biology*, **102**, 519-527.

MARSHMAN, N.A. and MARSHALL K.C. (1981) Bacterial growth on proteins in the presence of clay minerals. *Soil Biology and Biochemistry*, **13**, 127-134.

MATTIN, V.J. (1992) *The Seasonal Variation in Bioavailable Sedimentary Organics at Solent Breezes, Southampton Water.* Unpublished BSc. Hons. Thesis, University of Southampton.

MAYER, L.M. (1989) The nature and determination of non-living sedimentary organic matter as a food source for deposit feeders. In: *Ecology of Marine Deposit Feeders; Lecture Notes on Coastal and Estuarine Studies, No. 31*. Ed. Lopez G.R., Taghon G.L. and Levington J.S. Publ. Springer-Verlag, New York. 98-113.

MAYER, L.M., MACKO, S.A, MOOK, W.H. and MURRAY, S. (1981) The distribution of bromine in coastal sediments and its use as a source indicator for organic matter. *Organic Geochemistry*, **3**, 37-42.

MAYER, L.M., RAHAIM, P.T., GUERIN, W., MACKO, S.A., WATLING, L. and ANDERSON, F.E. (1985) Biological and granulometric controls on sedimentary organic matter of an intertidal mudflat. *Estuarine and Coastal Shelf Sciences*, **20**, 491-503.

MAYER, L.M., SCHICK, L.L. and SETCHELL, F.W. (1986) Measurement of protein in nearshore marine sediments. *Marine Ecology Progress Series*, **30**, 159-165.

McCALL, P.A. (1977) Community patterns and adaptative strategies of the infaunal benthos of Long Island Sound. *Journal of Marine Research*, **35**, 221-266.

McINTYRE, A.D. and WARWICK, R.M. (1984) Meiofaunal techniques. In: *Methods for the Study of Marine Benthos. I.B.P. Handbook, No. 16*. Ed. Holme N.A. and McIntyre A.D. Publ. Blackwell Scientific Publications, Oxford. 217-244.

McLACHLAN, A. (1990) Dissipative beaches and macrofauna communities on exposed intertidal sands. *Journal of Coastal Research*, **6(1)**, 57-71.

MEADOWS, P.S. and ANDERSON, J.G. (1966) Microorganisms attached to marine and freshwater sand grains. *Nature*, **212**, 1059-1060.

MILLER, D.C., BOCK, M.J. and TURNER, E.J. (1992) Deposit and suspension feeding in oscillatory flows and sediment fluxes. *Journal of Marine Research*, **50**, 489-520.

MÖLLER, P. (1986) Physical factors and biological interactions regulating infauna in shallow boreal areas. *Marine Ecology Progess Series*, **30**, 33-47.

MORGAN, T.S. (1997) *The formation and dynamics of* Pygospio elegans *tube-beds in the Somme Bay, France*. PhD Thesis, University of Southampton.

MORISITA, M. (1962) I_δ-index, a measure of dispersion of individuals. *Research in Population Ecology*, **4**, 1-7.

MUSKANANFOLA, M.R. (1994) *The influence of biological, sedimentological and physical factors on sediment stability in intertidal waters*. PhD Thesis, University of Southampton.

MYERS, A.A. and COSTELLO, M.J. (1984) The amphipod genus *Aora* in British and Irish waters. *Journal of the Marine Biological Association of the United Kingdom,* **64**, 279-283.

MYERS, A.A. and COSTELLO, M.J. (1986) The Amphipod sibling pair *Leucothoe lilljeborgi* Boeck and *L. incisa* Robertson in British and Irish waters. *Journal of the Marine Biological Association of the United Kingdom,* **66**, 77-82.

MYERS, A.A. and McGRATH, D. (1982) Taxonomic studies on British and Irish Amphipoda. Re-establishment of *Leucothoe procera*. *Journal of the Marine Biological Association of the United Kingdom,* **62**, 693-698.

MYERS, A.A. and McGRATH, D. (1984) A revision of the north-east Atlantic species of *Ericthonius* (Crustacea: Amphipoda). *Journal of the Marine Biological Association of the United Kingdom,* **64**, 379-400.

NAYLOR, E. (1972) British Marine Isopods. *Synopses of the British Fauna, (N.S.)*, **3**. Publ. Academic Press, London and New York. 86pp.

NEWELL, G.E. (1964) The South-East coast, Whitstable area. In: The effects of the severe winter of 1962-63 on marine life in Britain. Ed. CRISP D.J. *Journal of Animal Ecology*, **33**, 178-179.

NYBAKKEN, J.W. (1997) *Marine Ecology. An Ecological Approach. Fourth Edition*. Publ. A. W. Longman Inc. 481pp.

O'CONNOR, B.D.S. (1987) A review of the Glyceridae (Polychaeta) from the north east Atlantic with descriptions of two new species. *Journal of Natural History, 21*, 167-189.

OLAFSSON, E.B., PETERSON, C.H., and AMBROSE, W.G. (1994) Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft-sediments: the relative significanceof pre- and post-settlement processes. *Oceanography and Marine Biology: an Annual Review*, **32**, 65-109.

OLIVE, P.J.W. (1977) The life-history and population structure of the polchaetes *Nephtys caeca* and *Nephtys hombergii* with special reference to the growth rings in the teeth. *Journal of the Marine Biological Association of the United Kingdom,* **57**, 133-150.

OLIVER, J.S., SLATTERY, P.N., HULBERG, L.W. and NYBAKKEN, J.W. (1980) Relationships between wave disturbance and zonation of benthic invertebrate communities along a subtidal high-energy beach in Monterey Bay, California. *Fisheries Bulletin of the United States,* **78**, 437-454.

PALMER, M.A. (1988a) Dispersal of marine meiofauna: a review and conceptual model explaining passive transport and active emergence with implications for recruitment. *Marine Ecology - Progress Series*, **48**, 81-91.

PALMER, M.A. (1988b) Epibenthic predators and marine meiofauna: separating predation, disturbance and hydrodynamic effects. *Ecology*, **69**, 1251-1259.

PALMER, M.A. and COULL, B.C. (1980) The prediction of development rate and the effect of temperature for the meiobenthic copepod *Microarthidion littorale* (Poppe). *Journal of Experimental Marine Biology and Ecology*, **48**, 73-83.

PALMER, M.A. and GUST G. (1985) Dispersal of meiofauna in a turbulent tidal creek. *Journal of Marine Research*, **43**, 179-210.

PALMER, M.A. and MOLLOY, R.M. (1986) Flow and the vertical distribution of meiofauna: a flume experiment. *Estuaries*, **9**, 225-228.

PETERSON, C.H. (1977) Competitive organisation of the soft-bottom macrobenthic communities of southern California lagoons. *Marine Biology*, **43**, 343-359.

PETERSON, C.H. (1979) Predation, competitive exclusion, and diversity in the soft-sediment benthic communities of estuaries and lagoons. In: *Ecological Processes in Coastal and Marine Ecosystems*. Ed. Livingston, R.J. Publ. Plenum Press, New York and London. 233-263.

PHILLIPS, N.W. (1984) Roles of different microbes and substrates as potential suppliers of specific essential nutrients to marine detritivores. *Bulletin of Marine Science*, **12**, 33-47.

PIELOU, E.C. (1966) The measurement of diversity in different types of biological collections. *Journal of Theoretical Biology*, **13**, 131-144.

PLATE, S. and HUSEMANN, E. (1992) An alternative mode of development in *Scoloplos armiger* (O. F. Mueller, 1776) (Polychaeta, Orbiniidae). *Helgoländer Meeresuntersuchungen*, **44**, 487-492.

PLATE, S. and HUSEMANN, E. (1994) Identification guide to the planktonic polychaete larvae around the island of Helgoland (German Bight). *Helgoländer Meeresuntersuchungen*, **48**, 1-58.

PLATT, H.M. and WARWICK, R.M. (1980) The significance of freeliving marine nematodes to the littoral ecosystem. In: *The Shore Environment, Volume 2 - Ecosystems*. Ed. Price, J.H., Irvine, D.E.G., Farnham, W.H. Publ. Academic Press, London. 727-759.

PLEIJEL, F. (1993) Polychaeta Phyllodocidae. *Marine Invertebrates of Scandinavia*, **8**, 1-158.

POCKLINGTON, P. and HUTCHESON, M.S. (1983) New record of viviparity for the dominant benthic invertebrate *Exogone hebes* (Polychaeta: Syllidae) from the Grand Banks of Newfoundland. *Marine Ecology - Progress Series*, **11**, 239-244.

POSEY, M.H. (1986) Changes in a benthic community associated with dense beds of a burrowing deposit feeder, *Callianassa californiensis*. *Marine Ecology Progress Series*, **31**, 15-22.

RAFFAELLI, D. and HAWKINS, S. (1996) *Intertidal Ecology*. Publ. Chapman and Hall, London. 356pp.

RAFFAELLI, D., KARAKASSIS, I. and GALLOWAY, A. (1991) Zonation schemes on sandy shores: a multivariate approach. *Journal of Experimental Marine Biology and Ecology*, **148**, 241-253.

RAFFAELLI, D., RICHNER, H., SUMMERS, R. and NORTHCOTT, S. (1990) Tidal migrations in the flounder (*Platichthys flesus*). *Marine Behaviour and Physiology*, **16**, 249-260.

RAINER, S.F. (1989) Redescrition of *Nephtys assimilis* and *N. kersivalensis* (Polychaeta: Phyllodocida) and a key to *Nephtys* from northern Europe. *Journal of the Marine Biological Association of the United Kingdom,* **69**, 875-889.

RAINER, S.F. (1990) The genus *Nephtys* (Polychaeta: Phyllodocida) of northern Europe: A review of species including the description of *N. pulchra* sp.n. and a key to the Nephtyidae. *Helgoländer wissenschaftliche Meeresuntersuchungen,* ***45***, 65-96.

REES, E.I.S., NICHOLAIDOU, A. and LASKARIDOU, P. (1977) The effects of storms on the dynamics of shallow water associations. In: *Biology of Benthic Organisms, 11th European Symposium on Marine Biology, Galway 1976.* Ed. Keegan B.F., Ceidigh, P.O. and Boaden P.J.S. Publ. Pergamon Press, New York. 465-474.

REISE, K. (1983) Biotic enrichment of intertidal sediments by experimental aggregates of the deposit-feeding *Macoma balthica*. *Marine Ecology Progress Series*, **12**, 229-236.

REISE, K. and AX, P. (1979) A meiofaunal "thiobios" limited to the anaerobic sulphide system of marine sand does not exist. *Marine Biology*, **54**, 225-237.

ROPERT, M. (1996) Particularities of recruitment and renewal of a *Lanice conchilega* population (Polychaeta, Terebellidae) associated with mussel farming in the "Baie des Veys" (Western Part of the Bay of Seine). *Journal Recherche Océanographique*, **21**, 118-125.

SALVAT, B. (1964) Les conditions hydrodynamiques interstitielles des sédiments meubles intertidaux et la répartition verticale de la faune endogée. *C.R. Acaademie Sciences Paris*, **259**, 1567-1579.

SALVAT, B. (1967) La macrofaune carcinologique endogée des sédiments meubles intertidaux (Tanaidaces, Isopodes et Amphipodes) éthologie, bionomie et cycle biologique. *Mémoires du Muséum National d'Histoire Naturelle* Series A, **45**, 1-275.

SCHNEIDER, D. (1985) Migratory shorebirds: resource depletion in the tropics? In: *Neotropical Ornithology*. Ed. Buckley, P.A., Foster, M.S., Morton, E.S., Ridgely, R.S. and Buckley, F.G. Publ. American Ornithologist's Union, Washington DC. 520-558.

SCHUBERT, A. and REISE, K. (1986) Predatory effects of *Nephtys hombergii* on other polychaetes in tidal flat sediments. *Marine Ecology Progress Series*, **34**, 117-124.

SCHULTE, E. and RIEHL, R. (1976) Electron microscope studies on the tentacles of *Lanice conchilega* (Polychaeta, Sedentaria). *Helgoländer wissenschaftliche Meeresuntersuchungen*, **28**, 191-205.

SHANNON, C.E. and WEAVER, W. (1963) *The mathemathical theory of communication*. Publ. University of Illinois Press, Urbana. 125pp.

SHORT, A.D. and WRIGHT, L.D. (1983) Physical variability of sandy beaches. In: *Sandy Beaches As Ecosystems*. Ed. McLachlan, A. and Erasmus, T. Publ. Junk, The Hague, The Netherlands.

SIGURDSSON, J.B., TITMAN, C.W. and DAVIES, P.A. (1976) The dispersal of young post-larval bivalve molluscs by byssus threads. *Nature (London)*, **262**, 386-387.

SMALDON, G., HOLTHUIS, L.B. and FRANSEN, C.H.J.M. (1993) Coastal shrimps and prawns. *Synopses of the British Fauna, (N.S.)*, **15**. Publ. Field Studies Council. 142pp.

SMITH, R.I. (1988) Mixonephridia or nephromixia in terebellid polychaetes? A clarification. *Comparative Biochemistry and Physiology*, **91C**, 265-272.

SMITH, R.I. (1989a) Observations on the spawning behaviour of *Eupolymnia nebulosa*, and comparisons with *Lanice conchilega* (Annelida, Polychaeta, Terebellidae). *Bulletin of Marine Science*, **45(2)**, 406-414.

SMITH, R.I. (1989b) Notes on gamete production in *Lanice conchilega* (Annelida, Polychaeta, Terebellidae). *Invertebrate Reproduction and Development*, **15**, 7-12.

SNELGROVE, P.V.R. and BUTMAN, C.A. (1994) Animal-sediment relationships revisited: cause versus effect. *Oceanography and Marine Biology: an Annual Review*, **32**, 111-177.

SNELGROVE, P.V.R., BUTMAN, C.A. and GRASSLE, J.P. (1993) Hydrodynamic enhancement of larval settlement in the bivalve *Mulinia lateralis* (Say) and the polychaete *Capitella* sp. I in micro-depositional environments. *Journal of Experimental Marine Biology and Ecology*, **168**, 71-109.

SPOONER, G.M. (1947) The distribution of *Gammarus* species in estuaries. *Journal of the Marine Biological Association of the United Kingdom*, **27**, 1-52.

STEPHEN, A.C. (1929) Studies on the Scottish marine fauna: the fauna of the sandy and muddy areas of the tidal zone. *Transactions of the Royal Society of Edinburgh*, **56**, 291-306.

STEPHEN, A.C. (1930) Studies on the Scottish marine fauna. Additional observations of the fauna of the sandy and muddy areas of the tidal zone. *Transactions of the Royal Society of Edinburgh*, **56**, 521-535.

STRELZOV, V.E. (1973) *Polychaete worms of the family Paraonidae Cerruti, 1909 (Polychaeta, Sedentaria)*. Translated from Russian by I. Kohli (1979). Publ. Oxonian Press Pvt. Ltd., New Delhi.

TAGHON, G.L. and JUMARS P.A. (1984) Variable ingestion rate and its role in optimal foraging behaviour of marine deposit feeders. *Ecology*, **65**, 549-558.

TAGHON, G.L., NOWELL, A.R.M. and JUMARS, P.A. (1980) Induction of suspension feeding in spionid polychaetes by high particulate fluxes. *Science*, **210**, 562-564.

TAMAKI, A. (1987) Comparison of resistivity to transport by wave action in several polychaete species on an intertidal sand flat. *Marine Ecology Progress Series*, **37**, 181-189.

TEAL, J.M. and WIESER, W. (1966) The distribution and ecology of nematodes in a Georgia salt marsh. *Limnology and Oceanography*, **11**, 217-222.

TEBBLE, N. (1976) *British Bivalve Seashells,* 2nd edition. Publ. Her Majesty's Stationery Office, Edinburgh. 212pp.

TENORE, K.R. (1983) Organic nitrogen and calorific content of detritus III. Effect on growth of a deposit feeding polychaete, *Capitella capitata*. *Estuarine and Coastal Shelf Sciences*, **17**, 733-742.

TENORE, K.R. (1989) Some ecological perspectives in the study of the nutrition of deposit feeders. In: *Ecology of Marine Deposit Feeders, Lecture Notes on Coastal and Estuarine Studies, No. 31*. Ed. LOPEZ G.R., TAGHON G.L. and LEVINGTON J.S. Publ. Springer-Verlag, New York Inc., 309-317.

TENORE, K.R. and CHESNEY, E.J. (1985) The effects of interaction of rate of food supply and population density on the bioenergetics of the opportunistic polychaete *Capitella capitata* Type 1. *Limnology and Oceanography*, **30**, 1188-1195.

THISTLE, D. (1979) Harpacticoid copepods and biogenic structures: implications for deep-sea diversity maintenance. In: *Ecological Processes in Coastal and Marine Ecosystems*. Ed. Livingston, R.J. Publ. Plenum Press, New York and London. 217-232.

TUBBS, C. (1999) *The Ecology, Conservation and History of the Solent.* Publ. Packard Publishing Limited, Chichester. 184pp.

VINCX, M. and HEIP, C. (1979) Larval development and biology of *Canuella perplexa* T. and A. Scott, 1893 (Copepoda, Harpacticoida). *Cahiers de Biologie Marine*, **20**, 281-299.

WALTERS, K. and BELL, S.S. (1986) Diel patterns of active vertical migration in seagrass meiofauna. *Marine Ecology - Progress Series*, **34**, 95-103.

WARWICK, R.M. (1981) The influence of temperature and salinity on energy partitioning in the marine nematode *Diplolaimelloides bruciei*. *Oecologia*, **51**, 318-325.

WARWICK, R.M. (1984) Species size distributions in marine benthic communities. *Oecologia*, **64**, 32-41.

WARWICK, R.M. and GEE, J.M. (1984) Community structure of estuarine meiobenthos. *Marine Ecology - Progress Series*, **18**, 97-111.

WARWICK, R.M., JOINT, I.R. and RADFORD, P.J. (1979) Secondary production of the benthos in an estuarine environment. In: *Ecological Processes in Coastal Environments*. Ed. Jefferies, R.L. and Davy, A.J. Publ. Blackwell Scientific, Oxford, UK. 429-450.

WARWICK, R.M., PLATT, H.M. and SOMERFIELD, P.J. (1998) Free-living Marine Nematodes. Part III - Monhysterids. *Synopses of the British Fauna, (N.S.)*, **53**. Publ. Field Studies Council. 296pp.

WARWICK, R.M. and PRICE, R. (1975) Macrofauna production in an estuarine mud flat. *Journal of the Marine Biological Association of the United Kingdom*, **55**, 1-18.

WARWICK, R.M. and PRICE, R. (1979) Ecological and metabolic studies on free-living nematodes from an estuarine mud-flat. *Estuarine and Coastal Marine Science*, **9**, 257-271.

WATKIN, E.E. (1939) The pelagic phase in the life history of the amphipod genus *Bathyporeia*. *Journal of the Marine Biological Association of the United Kingdom*, **23**, 467-481.

WATKIN, E.E. (1941) Observations on the night tidal migrant Crustacea of Kames Bay. *Journal of the Marine Biological Association of the United Kingdom*, **25**, 81-96.

WATKIN, E.E (1942) The macrofauna of the intertidal sand of Kames Bay, Millport, Buteshire. *Transactions of the Royal Society of Edinburgh*, **60**, 543-561.

WATZIN, M.C. (1986) Larval settlement into soft-bottom systems: interactions with the meiofauna. *Journal of Experimental Marine Biology and Ecology*, **98**, 65-113.

WENDT, G.E. and McLACHLAN, A. (1985) Zonation and biomass of the intertidal macrofuana along a South African sandy beach. *Cahiers de Biologie Marine*, **26**, 1-14.

WHITTAKER, J.E. (1974) On *Semicytherura sella* (Sars). *Stereo-Atlas Ostracod Shells*, **2**, 85-92.

WILSON, D.P. (1954) The attractive factor in the settlement of *Ophelia bicornis* Savigny. *Journal of the Marine Biological Association of the United Kingdom*, **33**, 361-380.

WILSON, D.P. (1955) The role of micro-organisms in the settlement of *Ophelia bicornis* Savigny. *Journal of the Marine Biological Association of the United Kingdom*, **34**, 531-543.

WILSON, W.H. (1980) A laboratory investigation of the effect of a terebellid polychaete on the survivorship of Nereid polychaete larvae. *Journal of Experimental Marine Biology and Ecology*, **46**, 73-80.

WILSON, W.H. (1981) Sediment mediated interactions in a densely populated infaunal assemblage: the effects of the polychaete *Abarenicola pacifica*. *Journal of Marine Research*, **39**, 735-748.

WILSON, W.H. (1991a) Sexual reproductive modes in polychaetes: classification and diversification. *Bulletin of Marine Science*, **48(2)**, 500-516.

WILSON, W.H. (1991b) Competition and predation in marine soft-sediment communities. *Annual Review of Ecology and Systematics*, **21**, 221-241.

WITHERS, R.G. (1977) Soft-shore macrobenthos along the south-west coast of Wales. *Estuarine and Coastal Marine Science*, **5**, 467-484.

WITHERS, R.G. (1979) Observations on the macrofauna of intertidal sands at Ryde and Bembridge, Isle of Wight. *Proceedings of the Isle of Wight Natural History and Archaeology Society*, **7**, 81-89.

WITHERS, R.G. and THORPE, C.H. (1978) The macrobenthos inhabiting sandbanks in Langstone Harbour, Hampshire. *Journal of Natural History*, **12**, 445-455.

WOODHAM, A. and CHAMBERS, S. (1994) A new species of *Chaetozone* (Polychaeta, Cirratulidae) from Europe, with a re-description of *Caulleriella zetlandica* (McIntosh). In: *Actes de la 4ème Conference Internationale des Polychètes*. Ed. Dauvin J.-C., Laubier L. and Reish D. J. *Mémoires du Muséum National d'Histoire Naturelle*, Paris, **162**, 307-316.

WOODIN, S.A. (1974) Polychaete abundance patterns in a marine soft-sediment environment: the importance of biological interactions. *Ecological Monographs*, **44**, 171-187.

WOODIN, S.A. (1976) Adult-larval interactions in dense infaunal assemblages: patterns of abundance. *Journal of Marine Research*, **34**, 25-41.

WOODIN, S.A. (1981) Disturbance and community structure in a shallow water sand flat. *Ecology*, **59**, 274-284.

WOODIN, S.A. (1984) Effects of browsing predators: activity changes in infauna following tissue loss. *Biological Bulletin*, **166**, 558-573.

WOODIN, S.A. (1991) Recruitment of infauna: Positive or negative cues? *American Zoologist*, **31**, 797-807.

WORD, J.Q. (1978) The Infaunal Trophic Index. *Coastal Water Research Project Annual Report.* Southern California Coastal Water Research Project, El Segundo, CA. 19-39.

WORD, J.Q. (1990) *The Infaunal Trophic Index: a functional approach to benthic community analysis.* PhD Thesis, University of Washington. 297pp.

WRIGHT, L.D., NIELSEN, P., SHORT, A.D. and GREEN, M.O. (1982) Morphodynamics of a macrotidal beach. *Marine Geology*, **50**, 97-128.

YAMAMOTO, N. and LOPEZ G.L. (1985) Bacterial abundance in relation to surface area and organic content of marine sediments. *Journal of Experimental Marine Biology and Ecology*, **90**, 209-220.

ZAJAC, R.N. and WHITLACH, R.B. (1982a) Responses of estuarine infauna to disturbance. I. Spatial and temporal variation of initial recolonisation. *Marine Ecology Progress Series*, **10**, 1-14.

ZAJAC, R.N. and WHITLACH, R.B. (1982b) Responses of estuarine infauna to disturbance. II. Spatial and temporal variation of succession. *Marine Ecology Progress Series*, **10**, 15-27.

ZAJAC, R.N. and WHITLACH, R.B. (1991) Demographic aspects of marine, soft sediment patch dynamics. *American Zoologist*, **31**, 808-820.

ZIEGELMEIER, E. (1969) New investigations on the mode of tube-building of *Lanice conchilega* (Polychaeta, Sedentaria). *Helgoländer wissenschaftliche Meeresuntersuchungen*, **19**, 216-229.

ZOBRIST, E.C. and COULL, B.C. (1992) Meiobenthic interactions with macrobenthic larvae and juveniles: an experimental assessment of the meiofaunal bottleneck. *Marine Ecology - Progress Series*, **88**, 1-8.

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