AN INVESTIGATION INTO THE PROCESSES RESPONSIBLE FOR THE GENERATION OF THE SPATIAL PATTERN OF THE SPIONID POLYCHAETE *PYGOSPIO ELEGANS* CLAPARÈDE

STEFAN GEORGE BOLAM

A thesis submitted in partial fulfilment of the requirements of Napier University for the degree of Doctor of Philosophy.

July 1999

I declare that this thesis was written by me and that the work contained herein is my own.

Stefan G. Bolam

ABSTRACT

The spionid polychaete *Pygospio elegans* Claparède (1863) is a small, tube-building opportunist. On the intertidal sandflat Drum Sands, Firth of Forth, Scotland, this species is numerically dominant and forms areas of increased density or 'patches'.

Grid surveys, together with mapping and spatial autocorrelation analysis, revealed that these patches were areas of statistically significant higher numbers of *P. elegans* compared with surrounding areas where this species was present in very low numbers. These patches, 1-1.5m^2, could be seen as areas of smooth, raised sediment within an otherwise wave-rippled sandflat. The majority of the other macrobenthic invertebrate species also exhibited small- or meso-scale patchiness, but none of these patches were spatially coincident with those of *P. elegans*.

Although life history characteristics and disturbance have previously been postulated as being responsible for the generation of spionid patches, these have never been explicitly tested. The *P. elegans* population on Drum Sands was studied with respect to its population structure and reproductive biology and its response to macroalgal mat establishment and sediment disturbance. The possible role of these in the formation of small-scale patches of *P. elegans* are discussed.

The *P. elegans* population on Drum Sands displayed reproductive activity for the majority of the year although intense larval recruitment was confined to two acute periods, April/May and November/December. *P. elegans* reproduced exclusively via planktotrophic larvae: no evidence of asexual proliferation or benthic larval production was found. This life history provides a large larval availability for patch formation.

The role of macroalgal mat establishment in structuring the spatial distribution of *P. elegans* was investigated by a controlled, weed-implantation experiment and a comparative survey. Implanted *Enteromorpha prolifera* and naturally establishing *Vaucheria subsimplex* caused underlying sediments to have increased silt/clay fractions, increased organic and water contents and increased sorting coefficients and medium grain size. The sediment below these macroalgal mats also became significantly more reduced. While the communities under *E. prolifera* mats became dominated by *C. capitata*, those under *V. subsimplex* mats were dominated by *P. elegans*.

The effect of sediment disturbance on the faunal communities of Drum Sands was investigated by studying the initial colonisation of defaunated sediments. *P. elegans* numerically dominated the early stages of succession only during periods of high larval availability, *C. capitata* dominated at other times. Furthermore, *P. elegans* larval recruitment and adult immigration to defaunated sediments within *P. elegans* patches were higher compared with non-patch defaunated sediments.

The micro-scale spatial distribution of *P. elegans* within small-scale patches was examined. *P. elegans* was found to be non-randomly distributed throughout the year, patches formed were commonly less than $3cm^2$. Correlation analyses implied that these micro-scale patches may have been generated and maintained by adult-juvenile interactions and/or sediment heterogeneity.

Small-scale *P. elegans* patches were found to be distinct ecological areas when compared with surrounding sediments. Sediment properties and invertebrate community structure of *P. elegans* patches were significantly different to those of non-patch areas. These findings emphasise the ecological importance of patches of tube-building spionid polychaetes in allowing certain species to occur in habitats where they would otherwise be unable to survive.

ACKNOWLEDGEMENTS

I am indebted to my supervisors Dr. Teresa Fernandes, Professor Paul Read and Dr. Dave Raffaelli for their guidance, encouragement and constructive criticism throughout the course of this study.

I am also very grateful to a number of other people for their help in various aspects of my study. These are namely Mike Richards for his help in the field, Jill Sales for her help with statistical analyses, Peter Gibson for helping with faunal identification, Dr. Richard Ladle for reading through and commenting on the thesis, Marina Marcogni for her invaluable help with computing and Dagmar Rothaug and Karen Miller for helping me with fieldwork and sample sorting.

I must also thank a number of other people who I have contacted for specialist advice. These are Dr. Simon Thrush for his help during the early stages of my research, Dr. Helgi Gudmundsson and Dr. Torin Morgan for information about *Pygospio elegans*, Dr. Pierre Legendre for advice about numerical analyses, Dr. Martin Wilkinson for identifying my weed samples and Dr. Steve Hull for his advice about macroalgal mat implantation.

I would like to acknowledge my colleagues in the laboratory, my thanks go to them for keeping me 'entertained' over the years.

My last thanks, but by no means least, go to Thi for her enduring patience and understanding over the past couple of years.

CONTENTS

CHAPTER 4. THE EFFECTS OF MACROALGAL COVER ON THE SPATIAL DISTRIBUTION OF MACROBENTHIC INVERTEBRATES : AN EXPERIMENTAL STUDY. . . 83

CHAPTER 5. THE EFFECTS OF MACROALGAL COVER ON THE SPATIAL DISTRIBUTION OF MACROBENTHIC INVERTEBRATES: A SURVEY APPROACH . . 109

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1

INTRODUCTION

BACKGROUND

Aquatic and terrestrial environments may be viewed as being primarily structured by large-scale physical processes (currents and winds in aquatic systems) that cause gradients on the one hand and patchy structures separated by discontinuities on the other (Platt and Sathyendranath, 1992). These large-scale patches and gradients induce the formation of similar responses in biological systems, both spatially and temporally (Legendre and Fortin, 1989; Raffaelli *et al.*, 1993). For example, within the relatively homogeneous zones within large-scale patches, smaller-scale biological processes such as reproduction, predator-prey interactions and parasitism take place resulting in more spatial structuring. Legendre (1990) stated that several theories and models, such as those for predator-prey interactions, implicitly or explicitly assume that elements of an ecosystem that are close to one another in space are more likely to be influenced by the same process. Spatial heterogeneity is therefore functional in ecosystems and not the result of some random, noise-generating process (Legendre, 1993). The realisation that almost every ecological variable, biotic or abiotic, has a non-random spatial distribution (Valiela, 1984; Addicott *et al.*, 1987; Caswell and Cohen, 1991) has resulted in ecologists not treating spatial heterogeneity as a 'nuisance' in ecological studies (Legendre, 1993) which hinders the estimation of population densities (Reise, 1979; Valiela, 1984; McArdle *et al.*, 1990), but as a useful tool in assessing the processes operating within a particular system (Hall *et al.*, 1993). Observing patterns of variation in space helps with the understanding of population processes which occur over time scales too long to be amenable to studies (Sokal and Wartenberg, 1981). More fundamentally, assessment of spatial patterns also helps to determine suitable study areas (Livingston, 1987), appropriate sampling-scales (Downing, 1979; Eckman, 1979; Taylor, 1984) and the optimisation of mathematical models (Hanski, 1994; Petersen and DeAngelis, 1996).

The large increase in interest concerning the study of spatial patterns of species and communities has undoubtedly partly resulted from the expansion of techniques available for quantitatively and qualitatively assessing patterns. Most of these techniques, for example, quadrat-variance (Greig-Smith, 1952; Upton and Fingleton, 1985), spatial autocorrelation analysis (Cliff and Ord, 1973), mapping (Burrough, 1987), spatially-constrained clustering (Legendre and Fortin, 1989) and ordination (Wartenberg, 1985; Ter Braak, 1986) and semi-variogram analysis (see review by Legendre and Fortin, 1989) were developed by plant ecologists and have been adapted for use in other areas of ecology. Many of these techniques have been employed in the study of spatial patterns in the marine benthic environment.

Pattern and observational scale are intrinsically linked (Addicott *et al.*, 1987; Levin, 1992; Platt and Sathyendranath, 1992; Hall *et al.*, 1993; Lawrie, 1996). Patterns evident at one scale can either disappear or appear as noise when viewed at other scales (Eckman, 1979; Valiela, 1984; McArdle *et al.*, 1990; Dutilleul and Legendre, 1993; Thrush *et al.*, 1997a). This is because the processes which give rise to patterns in nature are scale-dependent (Legendre *et al.*, 1997; Thrush *et al.*, 1997b). For example, non-overlapping distributions of two species at one scale may reflect interspecific competition while at larger scales, a positive association between the two species may result from habitat selection (Wiens, 1989). Consequently, studying the relationship between the pattern observed and the process creating that pattern is problematical (McArdle *et al.*, 1997; Thrush *et al.*, 1997a, 1997b). Levin (1992) and Thrush *et al.* (1997c) suggested that recognition that different processes are relevant at different scales precludes the reductionist approach of sampling at the 'right' scale (e.g., Wiens, 1989; Kotliar and Wiens, 1990). Consequently, they proposed that ecologists should ask the question of how we can draw conclusions from one scale to another. Often, however, the scale at which one samples depends upon the questions one is attempting to answer within a particular study or upon logistical constraints. McArdle and Blackwell (1989) and Legendre *et al.* (1997) suggested that a good starting point before planning an experiment is the identification of the patterns that can be detected at one or several spatial scales.

The scales of observation, or the scales at which one 'views' the environment, obviously impose a limit as to the processes which can be investigated in any one study. This limitation is particularly pertinent to soft-bottom marine benthic studies where the organisms in question are often found exclusively below the sediment surface (Thrush, 1991): since only relatively small areas can be sampled the range of scales studied are small. Observational scales are varied by changing one or more of three aspects of a survey (Kotliar and Wiens, 1989; Legendre and Fortin, 1989; Wiens, 1989; Allen and Hoekstra, 1991; He *et al.*, 1994; Thrush *et al.*, 1997b):

- grain - the size of the sampling unit, limits the smallest scale which can be investigated;

- lag - distance between sampling units;

- extent - area covered by the study, determines the largest scale viewed.

The greatest amount of information will undoubtedly be gained from an investigation with zero lag and a grain which approaches the size of the organism (i.e., small contiguous cores), but logistically this can only be achieved to a very small extent. The majority of ecological studies carried out in the marine benthic environment have been conducted at scales with grains and lags determined by practical, logistic or other factors and many of them have therefore tended to miss the most suitable scales at which to study. Furthermore, most studies are conducted without any prior knowledge of the spatial scales of patterning which Taylor (1984) suggested leads to non-viable results. In many environmental impact studies for example, patchiness at any spatial scale between that of the sampling units and the location sampled will not be revealed by the sampling design: within-location variation will not have been adequately estimated by the replicate samples thus preventing valid comparisons among locations (Morrisey *et al.*, 1992).

Marine soft-bottom infaunal species have been shown to exhibit patchiness at a range of scales. In general, clumped distributions tend to be most common while regular spacing is only apparent at the micro-scale. Studies which have been carried out to determine the micro-scale (millimetres to centimetres) spatial distributions of marine macro-invertebrates, mostly using small, contiguous cores, have given important insights into the proximal factors determining population regulation. Thrush (1991) reviewed such studies and stated that biological processes were important in giving rise to patterns at this scale. These processes could be categorised into two groups: life history characteristics and biotic interactions (e.g., competition, predation and feeding modes). An example whereby processes from the first category, life history characteristics, can give rise to micro-scale patterning is the study by Eckman (1979). Using experimental manipulations and direct observations he showed that the micro-scale patchiness of several species of the Skagit Bay benthic community was created and maintained by the hydrodynamic effects of animal tubes affecting the settlement of new recruits. Lawrie (1996) found that the micro-scale patchiness of *Corophium volutator* on the Ythan estuary, Scotland, was generated and maintained by a negative adult-juvenile association. Competition has been found to result mostly in uniform distributions in invertebrate species. Levin (1981) observed that the large spionid *Pseudopolydora* cf. *paucibranchiata* had a regular distribution that was firstly initiated by uniform recruitment patterns and then enhanced by subsequent aggressive interactions (palp-fighting and biting) between individuals. Similarly, Connell (1963) suggested that the regular distribution of the amphipod *Ericthonius brasiliensis* was due to territorial avoidance by the new recruits and Reise (1979) proposed that the regular distribution he observed in *Hediste diversicolor* in the intertidal benthos of the Wadden Sea was also maintained by adult territoriality. However, Reise (1979) also suggested that the micro-scale patches found in most of the other polychaete species he studied could be related to their feeding modes. For example, patches of the carnivorous *Anaitides mucosa* were correlated with carrion and adult *Scoloplos armiger* and *Capitella capitata* distributions were presumed to result from a heterogeneous food resource.

The sampling strategies employed to ascertain the spatial patterns of macrobenthic invertebrate taxa at the small- to meso-scale (meters-10's of meters) have been more varied. Furthermore, the processes responsible for the patterns observed have been more difficult to determine but evidence suggests that environmental variables tend to be predominantly responsible. For example, McArdle and Blackwell (1989) used a systematic sampling design to investigate the density variability of the bivalve *Chione stutchburyi* in Ohiwa Harbour, New Zealand. The 5-15m areas of increased densities found using two-dimensional spatial autocorrelation analysis were suggested to have been due to an environmental gradient. The spionid polychaete *Marenzelleria viridis* was found to form patches of 0.04m^2-9m^2 in the Southern Baltic by Zettler and Bick (1996) which were attributed to result from changes in sediment structure. Gage and Coghill (1977) found that many invertebrate species in Scottish sea-lochs were patchily distributed. For example, the bivalve *Abra alba* formed patches of 3.5m and the polychaete *Diplocirrus glaucus* formed patches around 2-3.5m in length. They suggested that these patches probably resulted from environmental heterogeneity such as that created by patches of seaweed debris.

However, the most visually discernible small- to meso-scale patches formed by marine macro-invertebrates are probably the dense arrays of tube-beds formed by certain polychaete species. The tube-beds of several infaunal polychaete species have been studied such as *Lanice conchilega* (Carey, 1982, 1987; Ragnarsson, 1996), *Owenia fusiformis* (Fager, 1964) and *Clymenella torquata* (Sanders *et al.*, 1962). However, it is within the family Spionidae that many of the tube-bed forming species of polychaetes are found, such as *Spiophanes* cf. *wigleyi* (Featherstone and Risk, 1977), *Marenzelleria viridis* (Zettler and Bick, 1996), *Polydora ciliata* (Daro and Polk, 1973; Noji, 1994) and *Pygospio elegans* (Dupont, 1975; Morgan, 1997). The features which make spionids particularly capable of mass development and patch formation together with the ecological significance of such patches have been reviewed by Noji and Noji (1991).

The sizes of such patches have been found to vary greatly between taxa, for example, one of the large *C. torquata* tube-beds noted by Sanders *et al.* (1962) in Barnstable Harbour, Massachusetts, was estimated to cover 150,000m^2, while those formed by *M. viridis* varied between 0.04-9m^2 (Zettler and Bick, 1996). Often, these patches can readily be seen as large mounds or plateaus of smooth, raised sediment with numerous tube-heads protruding from the sediment surface. Within such patches, where worm densities can be very high (e.g., 200,000 *P. elegans*/m^2; Morgan, 1997), sediment stabilisation may occur due to the hydrodynamic effects of the tubes acting as roughness elements (Nowell and Church, 1979; Nowell *et al.*, 1981) and/or the indirect effect of increased microbial sediment-binding (Eckman *et al.*, 1981). The altered physical, chemical, physico-chemical and biological conditions encountered within these tube-beds have been shown to result in different infaunal macrobenthic (Sanders *et al.*, 1962; Fager, 1964; Ragnarsson, 1996) and meiobenthic (Reise, 1985; Noji, 1994) communities compared with non-patch areas.

The processes responsible for the formation and maintenance of such patches, in contrast to micro-scale patches, have not been explicitly studied. Relating observed patterns to the underlying processes which help to create them is difficult, even at the tractable scale at which manipulative experiments can be conducted (Hall *et al.*, 1993). However, several authors have proposed that sediment disturbance and the appropriate life history characteristics for their particular environment are prerequisites for patch formation. Carey (1987) suggested that there was an association between *L. conchilega*, macroalgal mat establishment and intermittently high sedimentation rates for *L. conchilega* mound development on St. Andrews Bay, Scotland. Fager (1964), however, suggested that a period of calm conditions after larval settlement could have led to the formation of the *O. fusiformis* patches. Morgan (1997) postulated that in view of the reproductive strategy possessed by the *P. elegans* population in the Baie de Somme, France, gregarious larval settlement and increased adult immigration into, or lower adult emmigration and/or lower mortality within patches, were important prerequisites for the formation of tube-beds. Many spionid polychaetes are capable of reaching very high numbers following a disturbance and have been described as opportunists (Grassle and Grassle, 1974; Pearson and Rosenberg, 1978). How this relates to formation of the observed patches is not clear. However, it would appear that for spionid tube-bed formation, some sediment disturbance is likely to be an important prerequisite.

THE PRESENT STUDY

On Drum Sands, Firth of Forth, Scotland, the tube-building, spionid polychaete *Pygospio elegans* forms small-scale patches which can be seen as areas of smooth, raised sediment within an otherwise wave-rippled sandflat. This study has 3 main aims, these are:

- To determine the spatial distribution of *P. elegans* on Drum Sands;
- To investigate the processes affecting *P. elegans* densities and the possible role of these processes in the formation and maintenance of small-scale patches;
- To assess the ecological importance of the spatial distribution of *P. elegans* on Drum Sands.

These 3 aims were addressed by carrying out surveys and experimental manipulations on Drum Sands, these are discussed in more detail below.

In Chapter 2, the small- to meso-scale (metres-10's metres) spatial patterns of *P. elegans* within a relatively homogeneous area of Drum Sands were investigated to explicitly determine the sizes of the *P. elegans* patches, their position, and worm density within them. The spatial patterns of other common taxa were also determined, together with sediment variables, in order to assess whether interspecific interactions and/or abiotic factors were likely to be important processes affecting the spatial distribution of *P. elegans*.

The population dynamics and reproductive biology of *P. elegans* on Drum Sands were considered in Chapter 3 together with their possible role in patch formation and maintenance. An understanding of the population dynamics and reproductive biology of this population was necessary in view of the reproductive variability found within this species.

The ecological effects of macroalgal mat formation on intertidal sandflats were investigated in Chapters 4 and 5. In these chapters, the potential role of macroalgal mat establishment in the formation and maintenance of *P. elegans* patches is discussed. This was achieved by both a controlled weed-implantation experiment (Chapter 4) and a descriptive survey (Chapter 5).

In Chapter 6, the role of sediment disturbance on intertidal sandflats is addressed. Using small-scale patches of *P. elegans*, the effects of dense assemblages of biogenic polychaetes on the initial successional dynamics and colonisation mode of the most abundant invertebrate taxa are addressed.

Chapter 7 considers the micro-scale spatial heterogeneity of *P. elegans*. Specifically, the spatial distribution of *P. elegans* within small-scale patches was monitored through the year and the importance of adult-juvenile interactions, interspecific interactions and abiotic variables in determining micro-scale patterns are discussed.

In Chapter 8, the ecological significance of the small-scale *P. elegans* patches were investigated. In particular, the structures of patch and non-patch communities were compared using univariate and multivariate analyses using data from samples taken at various times during this study. In this chapter, the community structure during the decline of these patches are studied, giving an insight into the possible causes of their demise.

Chapter 9 is a general discussion in which the findings of all the preceding chapters are brought together.

PYGOSPIO ELEGANS

Pygospio elegans Claparède is a small, sedentary, tube-building polychaete. This species is particularly interesting to study since various studies have suggested that it possesses a wide habitat tolerance, a variety of feeding mechanisms and displays a remarkable diversity of reproductive strategies (Morgan, 1997), in addition to its ability to form patches of increased density, or tube-beds.

Pygospio elegans has been found in a wide range of habitats from vertical rock crevices (Gudmundsson, 1985) to hard sand and gravel, but reaches its highest densities in sandy or mixed sediments (Smidt, 1951; Muus, 1967). The species is common in both marine and brackish waters although the highest densities are found in the latter, being abundant at salinities as low as 2ppt (Hempel, 1957).

Fauchald and Jumars (1979) described *P. elegans* as the most versatile of spionids with respect to its feeding mechanisms. It can filter-feed by building a mucus net within its tube, suspension-feed by trapping plankton with its palps or it can feed as a selective deposit-feeder (Hannerz, 1956; Hempel, 1957; Sanders *et al.*, 1962; Fauchald and Jumars, 1979).

Reproduction in *P. elegans* is varied and different strategies are employed by different populations. The species can reproduce sexually, producing either planktotrophic larvae (3-6 setigers) which spend several weeks in the water column (Hannerz, 1956; Anger *et al.*, 1986) or benthic larvae (12-20 setigers, Hannerz, 1956; Hempel, 1957; Rasmussen, 1973). The type of larvae produced mainly depends upon the population, although some populations have been shown to produce both types depending on the time of year (e.g., Gudmundsson, 1985; Ragnarsson, 1996). Furthermore, in most studies investigating sexual reproduction in *P. elegans* the timing of reproductive activity has been shown to vary. *P. elegans* can also reproduce asexually by individuals fragmenting into several sections, each fragment being capable of forming a new individual within 8 days at 20°C (Rasmussen, 1953). Fragmentation has been experimentally shown to depend upon the population density and food supply (Wilson, 1985) and in the field to depend upon season (Gudmundsson, 1985). Asexual reproduction has been reported as being essentially the sole method of reproduction in some populations (Hobson and Green, 1968). The reproductive strategies of *P. elegans* are discussed in more detail in Chapter 3.

THE STUDY SITE

The Firth of Forth is situated on the east coast of Scotland (Figure 1.1), separating Edinburgh and the Lothians to the south from the Kingdom of Fife to the north. The Firth of Forth stretches from the Forth Bridges in the west to Dunbar/Fifeness in the east and contains several harbours and boatyards for commercial and pleasure craft. The Firth is a channel for the passage of large vessels to and from Grangemouth, Rosyth and Leith. The oil industry has an oil-exporting terminal at Houndpoint and several construction/repair yards on the north coast of the Firth of Forth. Treated sewage and industrial effluent are disposed of at numerous outfalls along the coasts of the Firth of Forth. There are also numerous recreational uses and the Firth is an important area for nature conservation.

The Firth of Forth is monitored and regulated by the Scottish Environment Protection Agency (SEPA), duties formerly carried out by the Forth River Purification Board (FRPB). Annual nutrient and phytoplankton levels in the Firth of Forth are typical of those found in British estuarine and coastal waters (FRPB, 1993). Salinity shows annual variability between 29-33ppt due to seasonal weather conditions (Webb and Metcalfe, 1987; FRPB, 1993). The water temperature also varies between 5-15^{0}C following the annual cycle of irradiance levels and ambient air temperature (Webb and Metcalfe, 1987; FRPB, 1993).

All the sampling for the present study was carried out on Drum Sands which is a large, intertidal sandflat (Figure 1.2). The majority of the sandflat is relatively flat and a large proportion lies below mid-tide level (Figure 1.3). Personal observations have shown that the sediments vary on a large scale over the beach: although most of the sandflat can be described as clean beach sand it varies from mud at the top to coarse sand/gravel in patches towards the lower end of the sandflat. Monitoring programmes have shown the biological and chemical water qualities at nearby Cramond to be generally good with no detectable effects from the oil exporting terminal and treated ballast water outfall at Houndpoint (Griffiths, 1987; FRPB, 1988; 1992). Traces of sewage solids along the strandline of Drum Sands have been found during several studies which were presumed to result from both the septic tank discharge from

Dalmeny House and sewage discharged to below low water mark from Cramond (FRPB, 1988; 1992).

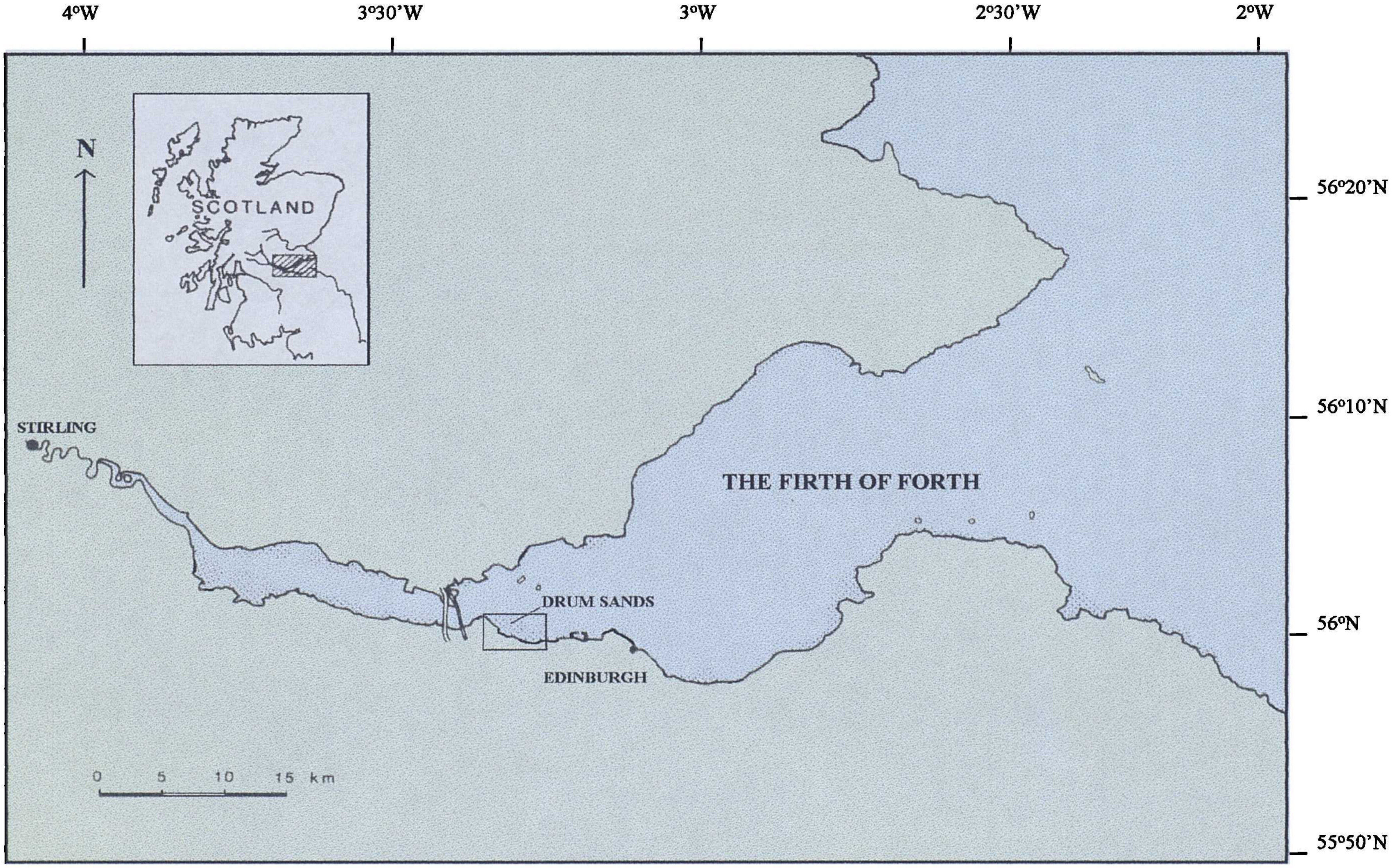


Figure 1.1 : Map of the Firth of Forth showing the location of Drum Sands.

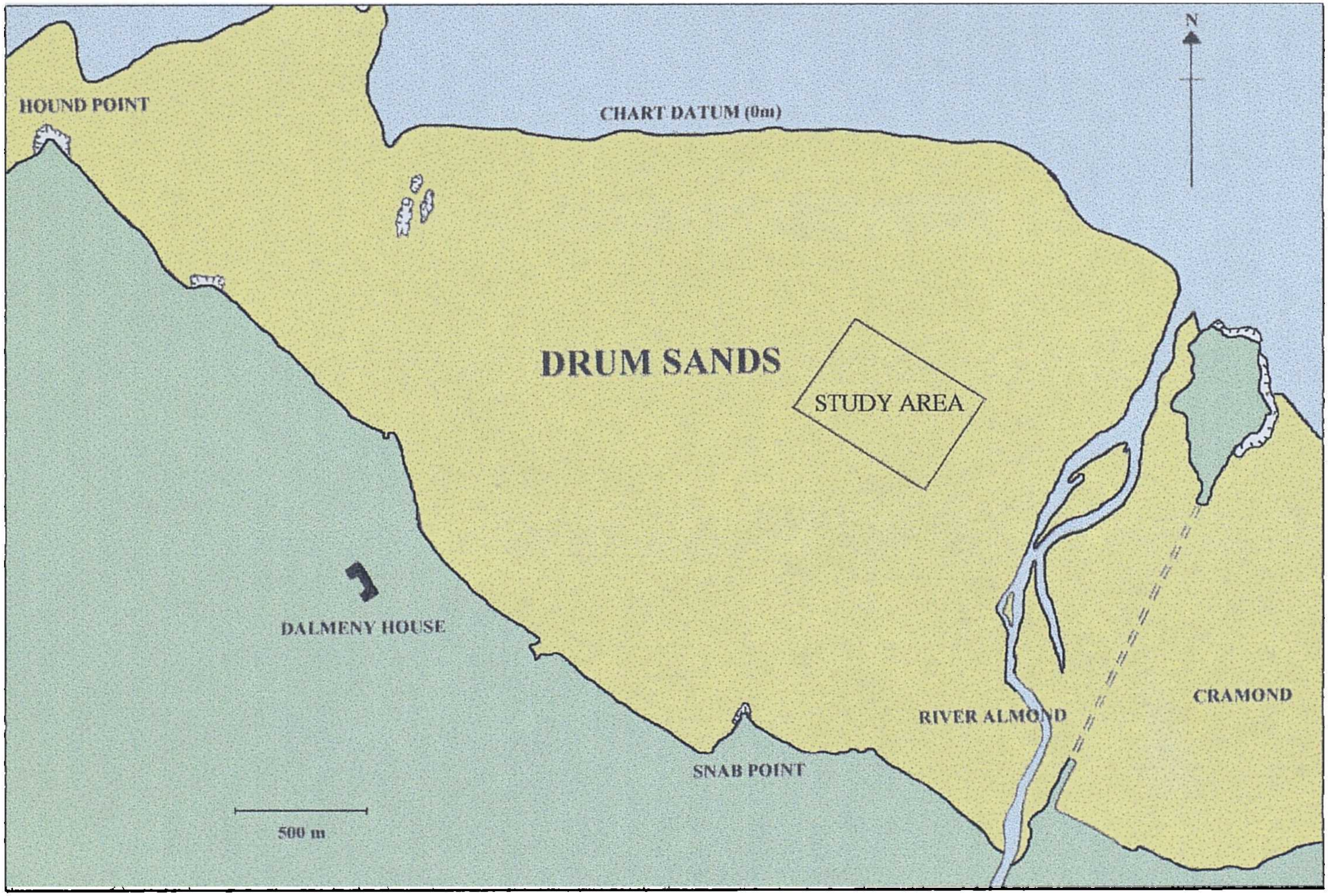


Figure 1.2 : Arial map of Drum Sands showing position of study area

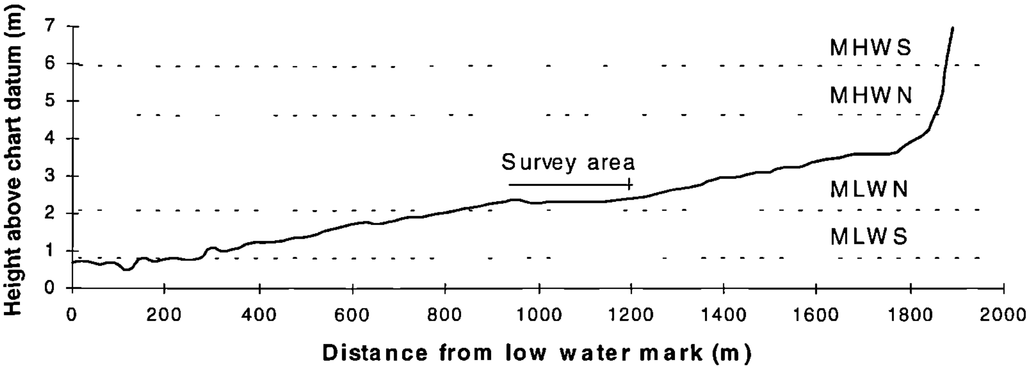


Figure 1.3 : Profile of Drum Sands in relation to height above chart datum, showing the position of the study area.

All the sampling was carried out within the 250×400m study area shown in Figure 1.2, just above mean low water neap tide level (Figure 1.3). This location was chosen since preliminary sampling revealed that *P. elegans* patches occurred in this region and that the sedimentary conditions were relatively constant. The tide covers the whole survey area in about 15 minutes (spring tide) so tidal effects on species distributions can essentially be ignored.

Very little macrobenthic data were available for Drum Sands. The sandflat is not monitored by the FRPB and the area has not previously been used for benthic studies. Stephen (1929) reported a *Cerastoderma edule* community on Drum Sands, but his samples were taken near Barnbougle Castle where the sediments are quite different from those found within the present study area.

CHAPTER 2

THE SMALL- TO MESO-SCALE SPATIAL DISTRIBUTION OF MARINE BENTHIC INVERTEBRATES ON DRUM SANDS, WITH PARTICULAR REFERENCE TO *PYGOSPIO ELEGANS*

INTRODUCTION

Spatial heterogeneity is a fundamental characteristic of animal and plant populations (Connell, 1963; Taylor, 1984), as well as the physical environment which the organisms inhabit. The assessment of the spatial variability of some variable, e.g., abundance of an organism, is often the starting point from which questions and hypotheses about important processes on the population or community level are generated (Andrew and Mapstone, 1987; Myers and Giller, 1988; Levin, 1992). Furthermore, Hall *et al.* (1993) recommended that an analysis of spatial pattern in both field experiments and survey programmes should be a priority for benthic ecologists.

There are numerous techniques available for the identification of spatial pattern, such as spectral analysis (Renshaw and Ford, 1984), quadrat-variance (Greig-Smith, 1952), spatial autocorrelation analysis (Cliff and Ord, 1973; Legendre and Fortin, 1989), dispersion indices (Morisita, 1962; Elliot, 1977; Krebs, 1989) and nested hierarchical analysis of variance (Morrisey *et al.*, 1992; Lindegarth *et al.*, 1995). These different techniques all provide different information on spatial pattern, require different sampling strategies and are more or less suitable at different spatial scales. For example, while a hierarchical nested analysis of variance requires a nested sampling design and is most suitable for determining large-scale (100m-kms) variation (Lindegarth *et al.*, 1995), spatial autocorrelation analysis, which requires a more regular sampling design (Thrush *et al.*, 1989) determines the underlying spatial structure and is more suitable for smaller-scale investigations (Morrisey *et al.*, 1992). Methods such as Greig-Smith's (1952) quadrat-variance technique, or related techniques such as the paired-quadrat variance (PQV) and two-term local quadrat variance (TTLQV) techniques (see Ludwig and Reynolds, 1988) assess patch sizes from a grid (or transect) of contiguous samples only.

Characterisation of populations in space requires the definition of both 'intensity' and 'form' (Pielou, 1969; Thrush *et al.*, 1989; Thrush, 1991). The intensity of a spatial distribution refers to whether it is clumped, regular or not significantly different from random, while the form of a pattern describes the size of the patches or gradients (Thrush, 1991). Methods which sort distributions into clumped, regular or random, e.g., dispersion indices, rely on the distribution of density estimates about the mean rather than the actual spatial arrangement of individuals and are therefore dependent on the size of the sampling unit. Dispersion indices, although only giving information about the intensity of the pattern, have been widely used by benthic ecologists for assessing the degree of aggregation or uniformity of species distributions (e.g., Gage and Geekie, 1973; Levin, 1981; Volckaert, 1987; Meire *et al.*, 1989; Thrush *et al.*, 1989; Lamont *et al.*, 1995; Lawrie, 1996). Indices such as the variance to mean ratio or index of dispersion (I), Morisita index (I_d), the standardised Morisita index (I_p) and Green's coefficient have been commonly applied to species data from a wide variety of sampling designs. Such indices are simple to calculate and the majority of them can be easily tested for significance using the Chi-square distribution. However, none of these indices on their own are ideal since they tend to be affected by population density and/or sample size (Elliot, 1977; Taylor, 1984; Andrew and Mapstone, 1987; Meire *et al.*, 1989; Hurlbert, 1990). Myers (1978) suggested that several indices should be used in conjunction and when their results correspond, a stronger statement can be made about the dispersion.

Dispersion indices give an indication of the intensity of pattern only, since they do not utilise the information contained in the arrangement of individuals in space they cannot give any idea as to the form of a pattern. Consequently, two distributions which may have a similar intensity of pattern may have very different spatial arrangements (Thrush, 1991; Hall *et al.*, 1993). Furthermore, such indices give no indication of the scales at which pattern might be found other than the scale at which the data used to calculate them were gathered (Hill, 1973).

Spatial autocorrelation analysis assesses whether the abundance of a species from one sample is significantly dependent on the abundances in neighbouring samples using Moran's *'i'* and/or Geary's *'c'* coefficients, or the Mantel coefficient for the multivariate situation (Sokal, 1986; Sokal and Thomson, 1987; Legendre and Fortin, 1989; Wartenberg, 1989). Correlograms, or graphs of these autocorrelation coefficients for various distance classes, allow inferences to be made on a variety of spatial patterns, heterogeneity in abundance, patch size and density gradients (Sokal and Oden, 1978; Sokal, 1979). Oden and Sokal (1986) and Sokal (1986) suggested that since correlograms describe the underlying spatial relationships of a pattern rather than its appearance, they may be closer guides to some of the processes that have generated these patterns than the patterns themselves. Consequently, spatial autocorrelation analysis has been widely used in many areas of ecology (Legendre and Trousellier, 1988; Leduc *et al.*, 1992; Hinch *et al.*, 1993; Diniz-Filho and Bini, 1994; Burgman and Williams, 1995) as well as in marine benthic studies (Jumars, 1978; Eckman, 1979; McArdle and Blackwell, 1989; Thrush *et al.*, 1989; Lawrie, 1996; Hewitt *et al.*, 1997) to describe the spatial pattern exhibited by macrobenthic populations and to help elucidate the processes producing them. The pattern observed depends upon the grain, lag and the extent and, therefore, there is a limit to the scales of patterns detected within any one survey.

Since correlograms may only ambiguously correspond to a single type of spatial structure (Sokal and Oden, 1978) their interpretation should be complemented by maps representing the spatial variation of the variable(s) of interest (Legendre, 1993). The easiest way to obtain a contour map of a single variable is to use inverse-square distance or other interpolation methods, such as kriging. However, interpretation of interpolation plots may be subjective: the patterns produced depend to a certain extent on the interpolation method and the distance classes chosen.

This study involved a detailed investigation into the spatial patterns exhibited by macrobenthic invertebrate species on an intertidal sandflat using some of the above described numerical techniques including the variance to mean ratio, Morisita index and standardised Morisita index, mapping with kriging and spatial autocorrelation analysis using Moran's and Geary's coefficients. An initial assessment of the spatial patterns of *P. elegans* will help identify which processes possibly determine this species' spatial distribution on Drum Sands and therefore the focus of successive research. The main aims of this study were:

1 - to investigate the small- and meso-scale spatial distributions of macrobenthic invertebrate species and sediment variables on an intertidal sandflat;

2 - to determine whether the abundance of this dominant species was associated with the spatial pattern of other species.

This was accomplished firstly by an investigation into the scales of spatial variability using analysis of variance; this 'transect' survey was also to serve as a pilot survey. A pilot survey was considered necessary to assess the macrofaunal densities and the scales of variability present. A more detailed investigation of spatial patterns was then carried out using three grid surveys, each conducted at different spatial scales. Since patchiness may occur at many scales (Kotliar and Wiens, 1990) it is necessary to sample as many scales as possible since whether a pattern is detected or not is a function of the sampling regime (Legendre and Fortin, 1989). For example, with spatial autocorrelation analysis, patches can only be detected if the spacing of the samples is on average less than the average diameter of a patch (Sokal and Wartenberg, 1981).

METHODS

Scales of Spatial Variability - Transect Survey

Survey design - The 'transect' survey for investigating the scales of spatial variability was carried out between the 17 and 18th of March, 1996. This survey used 16 plots arranged as shown in Figure 2.1. This design enabled the investigation of different scales of variation (patchiness) within the site using replicates within plots. The design can be described as 4 transects, 133m apart, with 4 plots along each, separated by 20m, 80m and 150m. Therefore, maximum scales of variability, in one direction only, within the area of relatively homogeneous sediments outlined in Figure 1.2 were investigated with this design.

Within each plot (1×1m), 3 randomly positioned box-core samples (25×25cm, 15cm depth) were taken and the sediments sieved through a 0.5mm mesh sieve. The samples were then fixed and preserved with saline formaldehyde solution (10%), neutralised with 0.2% sodium tetraborate (Borax) with a Rose Bengal (0.01%) stain and stored. The samples were later washed with water to remove the formaldehyde and the fauna sorted in a sorting tray with the aid of a magnifying lens and stored in 70% ethyl alcohol before identification. The fauna were identified to the lowest possible taxonomic level and counted. *Capitella* spp., which is known to be comprised of a morphologically similar but genetically distinct, sibling species were recorded as *Capitella capitata* (Grassle, 1984) for all of the studies carried out on Drum Sands. Pleijel and Dales (1991) suggested that *Eteone flava* and *Eteone longa* could represent two sibling species and that it is difficult to distinguish between them with preserved samples. Consequently, these individuals are called *Eteone* cf *flava* for this study.

Sediment samples were taken for organic carbon analysis and particle size analysis using a corer (2.4cm internal diameter) to a depth of 3cm and frozen at -20°C for storage. These samples were taken to 3cm depth since preliminary studies found the majority of the fauna inhabited sediments above this depth. Three randomly placed sediment samples were taken within each plot and pooled. Organic carbon content determination was done by weight loss on ignition at 480°C for 4 hours. Particle size distribution analysis was performed using the 'clean beach sand' method described in

Holme and McIntyre (1984). Percentage silt/clay (% <63μm), median particle size (Md phi (or ϕ)) and sorting coefficient (Inclusive Graphic Standard Deviation, I.G.S.D.) were obtained from the particle size distributions.

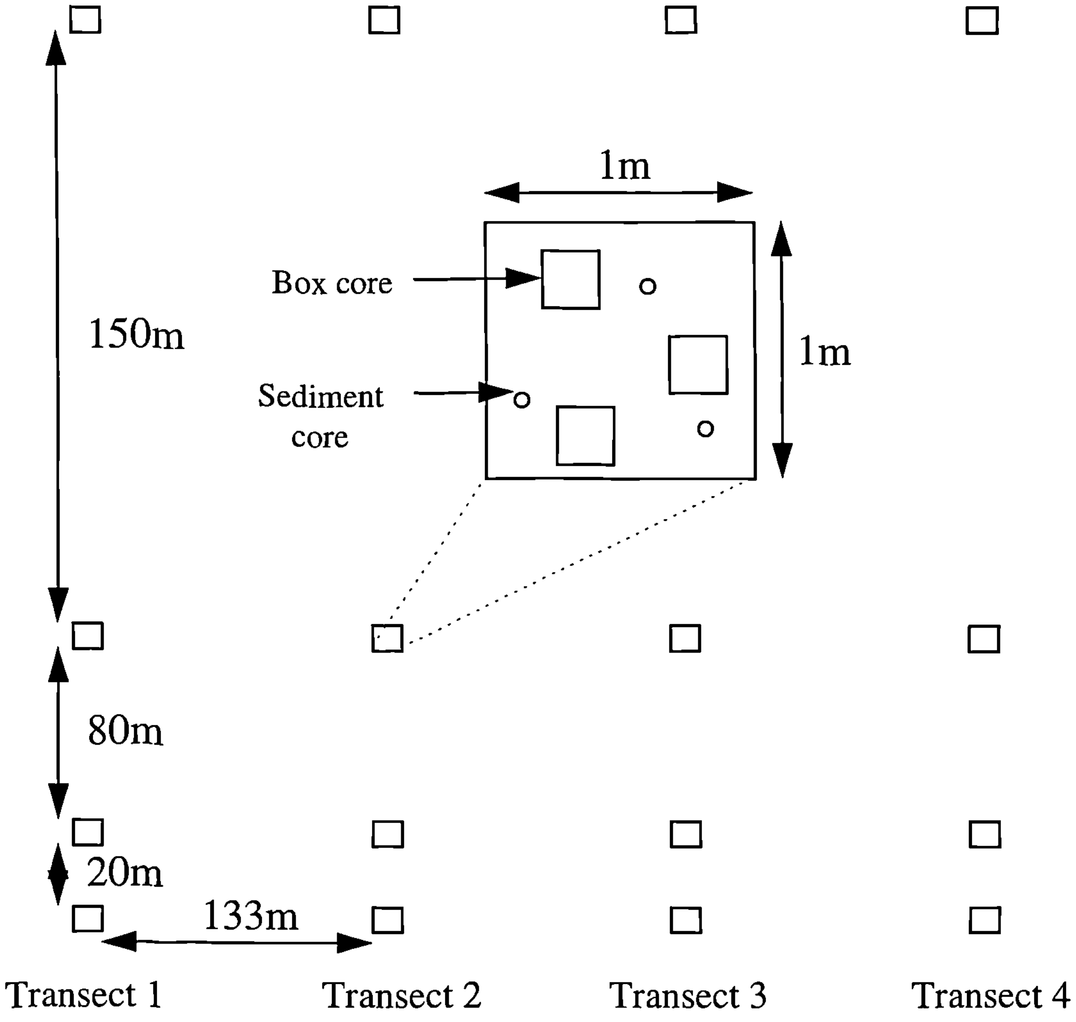


Figure 2.1 : Layout of plots for the transect survey. Within each plot (1×1m), three replicate box-cores (25×25cm, 15cm depth) were taken. Sediments were sampled by three randomly placed cores (2.4cm internal diameter, 3cm depth) and pooled.

In many marine soft-sediment studies the cores for sediment analyses are usually taken using smaller cores from within the larger faunal cores. Such sampling at different scales (grain) for the fauna and sediments is usually unavoidable. It is acknowledged that any small-scale sediment variability between the sampling unit used for the sediments ($4.5cm^2$) and that used for the fauna ($625cm^2$) is homogenised in this study. However, this was overcome to a certain extent by pooling the 3 random sediment cores. This concern for the mis-match of sampling-scales for the sediments and fauna applies to all the studies described in this thesis.

Data analyses - The data for each species with a mean abundance of 2 or more individuals per core for any one transect were checked for normality using the Anderson-Darling test and for homogeneity of variance using the Bartlett test. Any data not complying with these tests were log(x+1)-transformed before statistical analysis. Any species data with a non-normal distribution or a heterogeneous variance after transformation were analysed using non-parametric statistics. Variability along each transect was assessed by either a One-way ANOVA test with a Tukey multiple comparison test or a Kruskal-Wallis test using Minitab 10.0. In the event of a significant Kruskal-Wallis test, a *post hoc* Tukey test was performed on the log(x+1)-transformed data to indicate which plots were significantly different from each other.

Pattern Analysis - Grid Surveys

Survey design - Statisticians have usually condemned systematic sampling in favour of random sampling (Krebs, 1989). However, McArdle and Blackwell (1989) stated that when investigating spatial patterns a systematic sampling design (e.g., grid sampling) will usually provide the smallest sampling error of the mean (Milne, 1959). The possibility of a periodic variation in the variable being studied leading to a biased estimate of the mean is negligible (Milne, 1959; Krebs, 1989). Another advantage of grid sampling is the ease with which spatial patterns can be detected and displayed (McArdle and Blackwell, 1989). Consequently, this type of sampling is recommended in pattern analysis studies (Greig-Smith, 1952; Angel and Angel, 1967; Pielou, 1969; Hill, 1973; Elliot, 1977; Jumars *et al.*, 1977).

Pattern analysis was carried out by performing 3 separate surveys, each at a different scale (lag). The sample designs for each of these grid surveys were very similar to each other (Figure 2.2), except the lags were different in each case. The lags used for the 3 surveys were 1m, 8m and 40m and, from here-on will be referred to as the 1m, 8m and 40m surveys respectively. These lags were chosen so that spatial patterns could be investigated at a relatively small scale (1m survey), at an intermediate scale (8m survey) and at a relatively large scale (40m survey) within the 400×250m study area. The 1m and 8m surveys were composed of plots forming an 8×8 array while those of the 40m survey formed a 9×7 array so that the design could be positioned within the study area. The positions of the 1m and 8m surveys were determined by random co-ordinates while the 40m survey covered the majority of the 250m×400m survey area.

At each plot faunal abundances were assessed in two ways. A single box-core sample (625cm^2) was taken in an identical manner as described for the pilot survey: this method sampled the majority of the faunal species present. The results from the transect survey revealed that the lugworm *Arenicola marina* and the sandmason *Lanice conchilega* could not be sampled in this way since the majority of these individuals live deeper in the sediments than 15cm. Ragnarsson (1996) suggested that there was almost a 1:1 relationship between *A. marina* individuals and their casts on the Ythan Estuary, Aberdeenshire, and by direct observations (following Carey, 1982) that at least 90% of *L. conchilega* tube-heads contained live worms. Therefore, for the grid surveys the relative abundances of *A. marina* and *L. conchilega* were estimated by counting the numbers of casts and tube-heads (respectively) within a 1m^2 area around each plot. Consequently, for these two species, the grain was extended. The difference in grain used for these two species must be remembered when comparing their distributions with the other fauna since the numbers in the larger sampling unit would have been less sensitive to the presence of smaller-scale (i.e., <625cm^2) heterogeneity.

Three sediment samples, each 2.4cm internal diameter and 3cm depth, were taken from within each box-core sample and pooled.

The faunal samples were processed and sediment variables analysed in the same way as described for the transect survey.

The sampling for the 1m, 8m and 40m surveys were carried out during 27-28th, 16-17th and 1-2nd of July 1996 respectively.

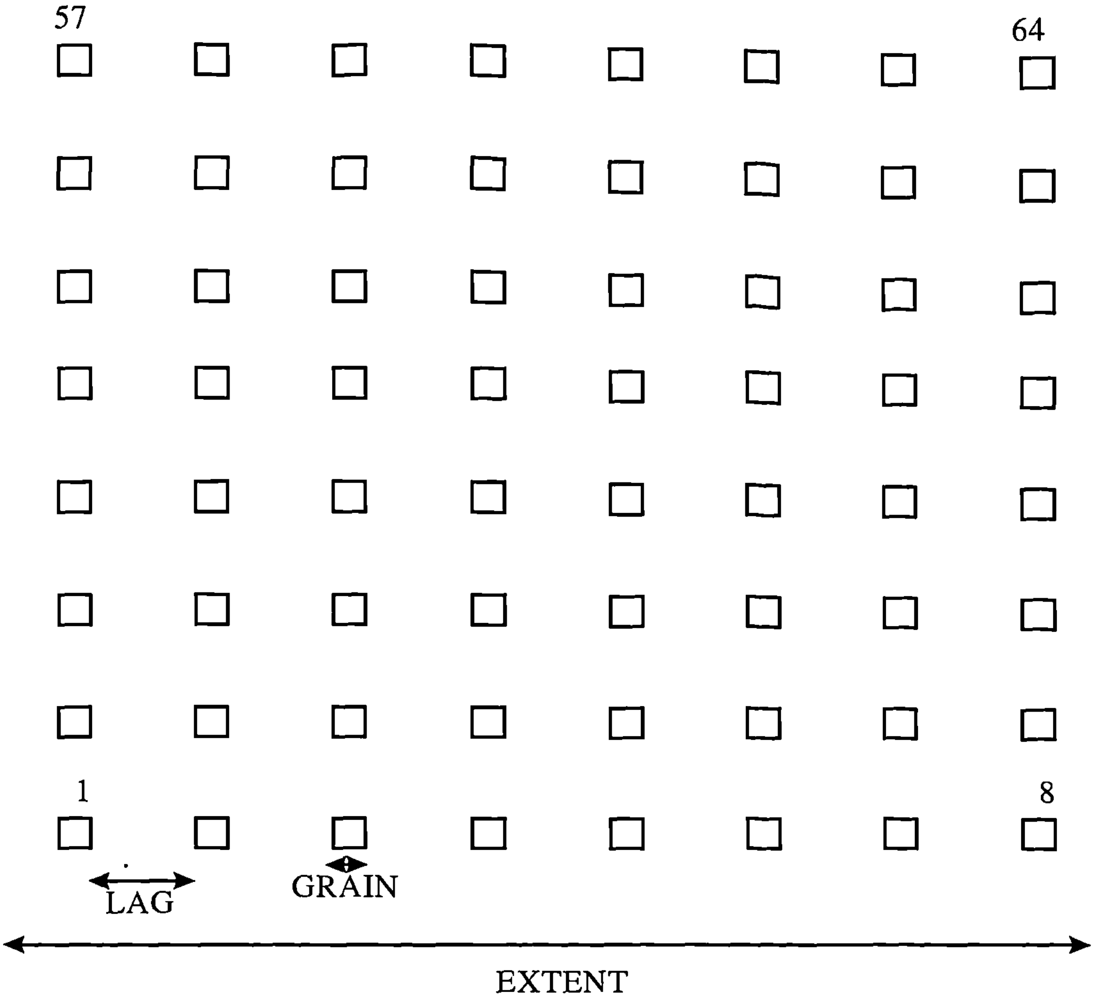


Figure 2.2 : Sample layout of the 1m and 8m grid surveys showing positions of plot numbers 1, 8, 57 and 64. For the 1m survey, the lag was 1m and for the 8m survey, 8m. The 40m survey had a similar design except a 9×7 grid was formed instead of an 8×8, with a 40m lag. One box-core sample (25×25cm, 15cm depth) was taken at each plot together with 3 sediment cores (2.4cm internal diameter, 3cm depth) which were pooled. The numbers of *A. marina* and *L. conchilega* were estimated by the numbers of casts and tube-heads respectively in a 1m^2 area around each plot.

Data analyses - Dispersion indices were calculated for each taxon with a mean abundance of at least 2 individuals per plot. This cut-off abundance was decided to limit the analyses to those taxa which were sufficiently abundant to allow a reasonable investigation of their spatial patterns. The dispersion indices calculated were the variance to mean (v:m) ratio, I; Morisita's index, I_d; and the standardised Morisita's index of dispersion, I_p. These calculations were performed on the abundance data using the NEGBINOM program (Krebs, 1989). This program gives each of these index values and indicates whether the v:m ratio is significantly different from 1:1. Departures from randomness of I_d were addressed for significance ($p<0.05$) when:

$I_d\ (\sum x - 1) + n - \sum x$ where: n = number of sampling units

$\sum x$ = total number of individuals

lies outside the appropriate significance levels of χ^2 for n-1 degrees of freedom (Elliot, 1977; Krebs, 1989). The standardised Morisita index of dispersion (I_p) ranges from -1.0 to +1.0 and has 95% confidence limits at 0.5 and -0.5 and, therefore, values outside this range have aggregated and regular distributions respectively (Krebs, 1989).

Correlation analysis of species abundances and sediment variables with *P. elegans* abundances at each scale was performed using Spearman Rank Correlation on Minitab version 12.1. This correlation method, which was performed after the data had been ranked, was chosen since it has no requirement of normality of the data (Fowler and Cohen, 1990). This was essential in the case of the sediment variables and appropriate for many of the species abundance data. The α level, 0.05, was adjusted using the Bonferroni correction where probabilities were compared to α' where $\alpha' = \alpha/k$ (where k = the number of independent tests, Sokal, 1986; Legendre and Legendre, 1997).

Mapping was carried out only on those taxa with spatial distributions which were significantly non-random (aggregated). Contour maps were produced using the Golden Software Inc. package SURFER 32 version 6.04 using kriging as the interpolation technique. Kriging is a geostatistical gridding method which produces visually appealing contour plots by expressing trends in the data, for example, high points tend to be connected as a ridge rather than isolated by bull's-eye type contours (Keckler, 1997). This method was chosen since it is a very flexible method which is suitable for most types of data (Keckler, 1997; or see review by Burrough, 1987) and has been shown to perform well on spatially autocorrelated data (Simard *et al.*, 1992).

Maps produced by kriging and other suitable interpolation methods were essentially similar.

Spatial autocorrelation analysis was carried out using the Spatial Autocorrelation Analysis Program (SAAP) version 4.3 (Wartenberg, 1989). This package produces correlograms of autocorrelation coefficient values against each distance class. Moran's '*i*' and Geary's '*c*' autocorrelation coefficients (Cliff and Ord, 1973) were calculated in the present study since these are the most commonly used and have been recommended for use in ecological applications (Sokal, 1979; Hubert *et al.*, 1981; Legendre and Fortin, 1989). The SAAP program gives *i* values in the range 1 to -1 and *c* values in the range 0-2; while low values of *i* correspond to negative autocorrelation and high values correspond to positive autocorrelation, the opposite applies for values of *c*. Each coefficient is sensitive to slightly different behaviours of the data (Jumars *et al.*, 1977). For example, *i* bears a close resemblance to a Pearson product moment correlation coefficient and is therefore most sensitive to extreme values in the data set while *c*, which is a distance-type function, is most sensitive to the proximity of similar or dissimilar values, regardless of their departure from the mean (Jumars *et al.*, 1977).

Following Oden (1984) the overall significance of each spatial autocorrelogram was assessed by checking that the most significant spatial autocorrelation coefficient found in a correlogram was significant at a Bonferroni-corrected significance level α', where $\alpha'=\alpha/k$, k being the number of autocorrelation coefficients (i.e., the number of distance classes) in the correlogram (Sokal, 1986). Spatial autocorrelation analysis allowed the nature of patterns and estimates of patch sizes to be made in this study. The spatial characteristics of patches indicated by autocorrelation analysis were only accepted if the contour plots were consistent with these patterns.

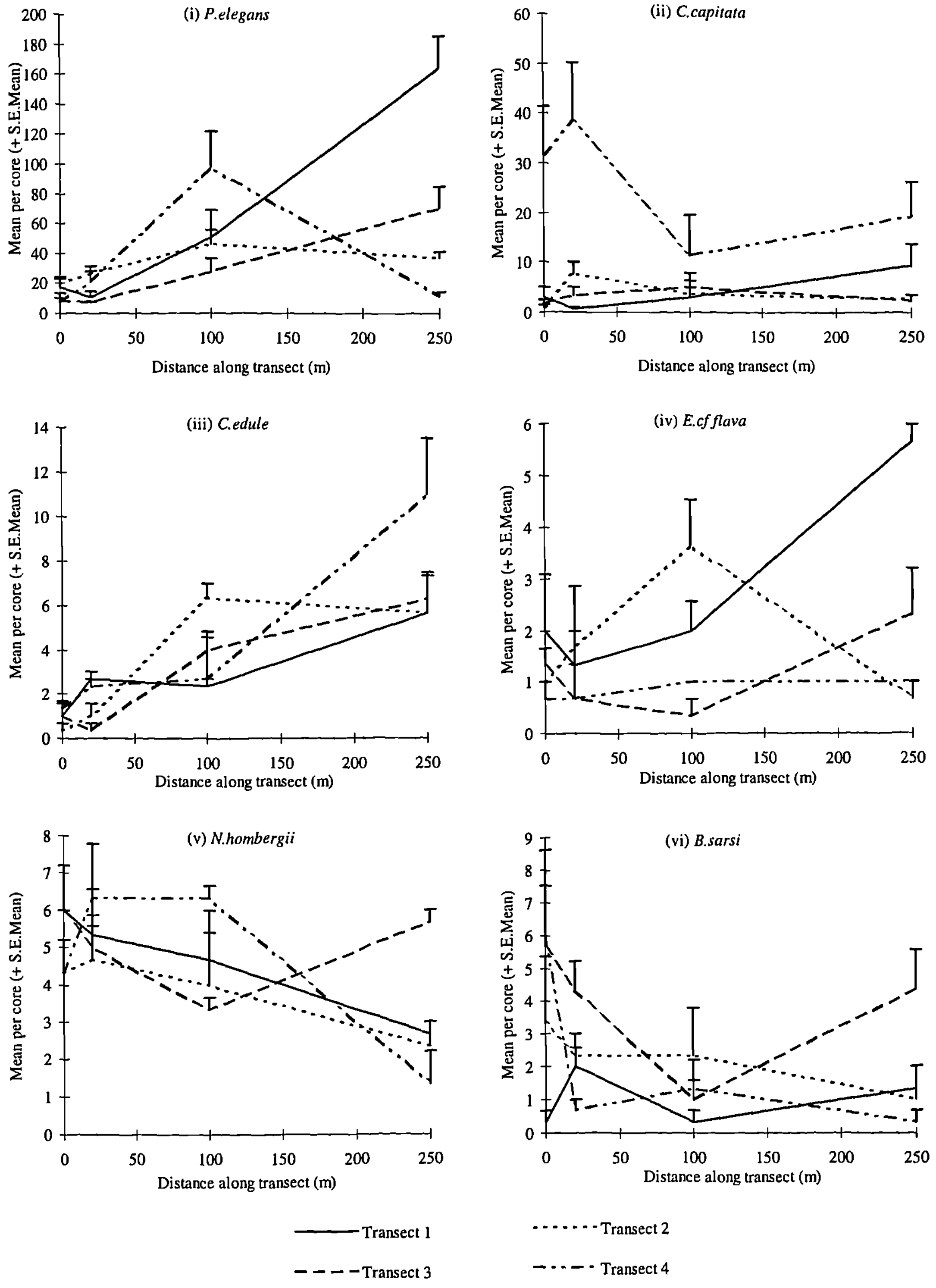
RESULTS

Scales of Spatial Variability - Transect Survey

From the 48 faunal samples taken for this survey, 3062 individuals were collected from a total of 48 taxa. By far the most abundant (2508 individuals) and diverse group was the polychaetes, 26 species from 13 families. The second most abundant group was the molluscs (262 individuals) with 8 species from 4 families. 257 individuals were collected from the crustaceans; 12 species from 7 families.

Most of the species sampled were too rare for numerical analyses, i.e., means of <2 individuals per core for all transects. This was partly due to the fact that the survey was carried out during March when macrofaunal species abundances are around their annual lowest. Only 5 species other than *P. elegans* were considered sufficiently abundant for numerical analyses. These were the amphipod *Bathyporeia sarsi,* the mollusc *Cerastoderma edule,* and the polychaetes *Eteone* cf *flava, Nephtys hombergii* and *Capitella capitata.* The abundances of these are presented diagrammatically in Figures 2.3(i-vi). The standard errors are relatively large suggesting there to be appreciable within-plot variation, i.e., micro- to small-scale patchiness.

The results of the One-way ANOVA tests with Tukey multiple comparison test and Kruskal-Wallis tests are presented in Table 2.1. These results suggest that for the majority of the species, variability along the transects was non-significant. This was partly because of both the large within-plot replicate variability and the low mean abundances (except for *P. elegans*). For *P. elegans*, for example, spatial variability was only found at a scale of 230m on transect 1, i.e., Tukey test revealed that the only significant difference detected at the 5% level was between plot 2 (20m along the transect) and plot 4 (250m) despite the large differences in mean abundances observed for all transects in Figure 2.3(i).

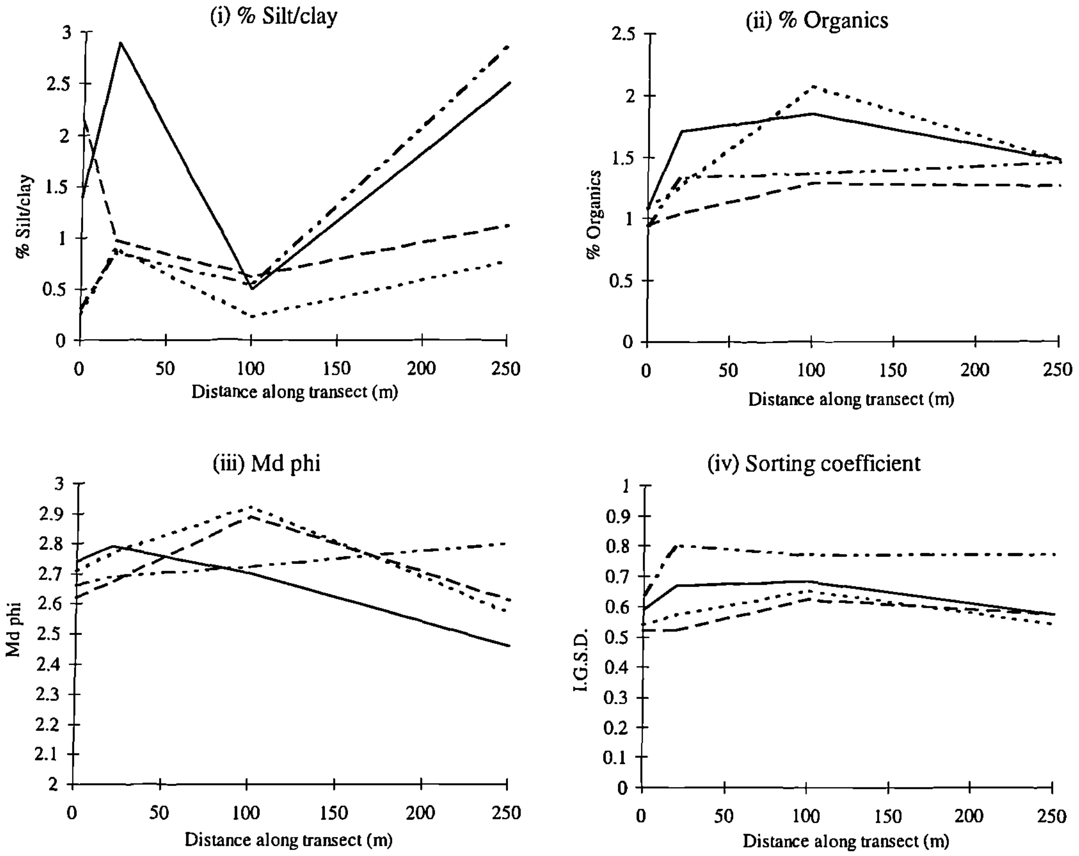


Figures 2.3(i-vi) : Abundances of the six species sufficiently abundant for statistical analyses from the transect survey. Mean abundances per core (+ S.E.Mean, n=3) are given for each plot from each of the 4 transects.

Species	Transect	20m	80m	100m	150m	230m	250m
P. elegans	1					Yes	
C. edule	1						Yes
	2		Yes	Yes			Yes
	3		Yes			Yes	Yes
	4					Yes	Yes
C. capitata	n/s						
N. hombergii	3			Yes			
E. cf *flava*	1			Yes			
B. sarsi	n/s						

Table 2.1 : Scales of variability found to be statistically significant using One-way ANOVA with a Tukey multiple comparison test at 5% level of significance for *P. elegans*, *C. capitata* and *C. edule* on log(x+1)-transformed data and Kruskal-Wallis on the raw abundance data for *E.* cf *flava*, *M. balthica* and *B. sarsi* with *post hoc* Tukey test. 'Yes' indicates statistical significance and n/s represents not significant at any scale for all transects.

The results of the sediment organic content and granulometric analyses are presented in Figures 2.4(i-iv) showing the % silt/clay, % organics, Md phi and the sorting coefficient values for each plot along transects 1-4. Due to different sampling protocols and to the random positioning of sediment cores within plots rather than within faunal cores, correlation analysis between sediment properties and faunal abundances cannot be unequivocally carried out. These results, however, do suggest that there were no distinct patches or definite gradient in the environmental variables measured within the study area. Although the values did vary along and between transects it is not possible to assess whether these are significant differences without replication. The sediments of the study site have silt/clay contents of 0.50-2.89%; organic carbon contents of 0.95-2.08%; Md phi of 2.57-2.89 (fine sand) and sorting coefficients of between 0.52-0.80 (moderately sorted to moderately well-sorted).



Figures 2.4(i-iv) : Sediment results from transect survey. Values of (i) % silt/clay, (ii) % organics, (iii) Md phi and (iv) Inclusive Graphic Standard Deviation (I.G.S.D.) sorting coefficient are given for each distance along transect (in metres) for all 4 transects.

Pattern Analysis - Grid Surveys

A total of 31, 31 and 33 taxa were collected from the 1m, 8m and 40m surveys respectively. A full species list, together with abundances per plot for each survey, are given in Appendices 1.1, 1.2 and 1.3 for the 1m, 8m and 40m surveys respectively. Species are listed in the Appendices in the order according to Howson and Picton (1997). From these 3 surveys, 9, 10 and 11 taxa respectively were considered sufficiently abundant for pattern analysis, i.e., a mean abundance of at least 2 individuals per core. Since these surveys were carried out during the summer, the abundances of the majority of the species were greater than found from the transect survey. Tables 2.2-2.4 show the dispersion indices; v:m, I_d and I_p, for each of these taxa from each grid survey with the distributions they imply. There was a very good agreement between the 3 indices used. Therefore, one can be confident that the distributions inferred from these indices are correct.

The results from the 1m survey suggest that at this scale, 7 of the 9 species showed an aggregated distribution. These were *P. elegans*, *A. marina*, *L. conchilega*, *E.* cf *flava*, *M. balthica*, *B. sarsi* and *G. duebeni.* The distributions of *N. hombergii* and *C. edule* were not significantly different from random. Of the 10 species sufficiently abundant for analysis from the 8m survey, 8 were aggregated, i.e., *P. elegans*, *S. martinensis*, *L. conchilega*, *C. capitata*, *E.* cf *flava*, *M. balthica*, *G. duebeni*, and *C. edule*. *N. hombergii* and *A. marina* were found to be randomly distributed. All 11 species analysed from the 40m survey were found to have significantly aggregated distributions.

Pygospio elegans had by far the greatest v:m ratio in each of the grid surveys, i.e., 31.69, 68.46 and 64.58 for the 1m, 8m and 40m surveys respectively. This suggests that this species showed a high spatial variability even at relatively small scales (1m survey), forming patches within which their densities were far greater than those in surrounding non-patch areas.

	v : m	pattern	I_d	pattern	I_p	pattern
P. elegans	31.69	***A	1.944	*A	0.507	*A
A. marina	1.58	**A	1.156	*A	0.501	*A
L. conchilega	8.79	***A	2.846	*A	0.514	*A
N. hombergii	1.08	Random	0.018	Random	0.109	Random
E. cf *flava*	2.14	***A	1.664	*A	0.504	*A
M. balthica	5.09	***A	1.431	*A	0.503	*A
C. edule	0.91	Random	0.986	Random	-0.143	Random
B. sarsi	5.95	***A	4.093	*A	0.523	*A
G. duebeni	4.27	***A	2.505	*A	0.511	*A

Table 2.2 : Indices of dispersion for each of the taxa in the 1m grid survey. The results from the variance to mean ratio, Morisita's index (I_d) and standardised Morisita's index (I_p) are given together with the type of dispersion/pattern they suggest (A=Aggregated) and the significance level. * Denotes significance at $p<0.05$; ** at $p<0.01$; and *** at $p<0.001$.

	v : m	pattern	I_d	pattern	I_p	pattern
P. elegans	68.46	***A	2.164	*A	0.509	*A
S. martinensis	7.81	***A	2.289	*A	0.510	*A
A. marina	1.26	Random	1.073	Random	0.349	Random
L. conchilega	9.76	***A	2.889	*A	0.514	*A
C. capitata	53.24	***A	8.217	*A	0.557	*A
N. hombergii	1.12	Random	1.027	Random	0.152	Random
E. cf *flava*	1.65	***A	1.179	*A	0.501	*A
M. balthica	15.22	***A	2.605	*A	0.512	*A
C. edule	25.13	***A	1.424	*A	0.503	*A
G. duebeni	11.89	***A	9.681	*A	0.567	*A

Table 2.3 : Indices of dispersion for each of the taxa in the 8m grid survey. The results from the variance to mean ratio, Morisita's index (I_d) and standardised Morisita's index (I_p) are given together with the type of dispersion/pattern they suggest (A=Aggregated) and the significance level. * Denotes significance at $p<0.05$ and *** at $p<0.001$.

	v : m	pattern	I_d	pattern	I_p	pattern
P. elegans	64.58	***A	2.049	*A	0.510	*A
S. martinensis	5.34	***A	3.265	*A	0.517	*A
A. marina	1.74	***A	1.159	*A	0.501	*A
L. conchilega	33.55	***A	4.336	*A	0.527	*A
C. capitata	3.24	***A	1.893	*A	0.506	*A
N. hombergii	1.39	*A	1.124	*A	0.500	*A
E. cf *flava*	2.67	***A	1.551	*A	0.503	*A
M. balthica	32.18	***A	2.311	*A	0.510	*A
C. edule	5.72	***A	1.260	*A	0.502	*A
B. sarsi	15.71	***A	6.301	*A	0.542	*A
G. duebeni	12.46	***A	3.682	*A	0.521	*A

Table 2.4 : Indices of dispersion for each of the taxa in the 40m grid survey. The results from the variance to mean ratio, Morisita's index (I_d) and standardised Morisita's index (I_p) are given together with the type of dispersion/pattern they suggest (A=Aggregated) and the significance level. * Denotes significance at $p<0.05$ and *** at $p<0.001$.

Table 2.5 shows the results of Spearman Rank Correlation analyses of *P. elegans* with other species present and the 4 sediment variables measured. Only those species with a mean abundance of at least 4 individuals per core (or per m^2 for *A. marina* and *L. conchilega*) were used for correlation analyses with *P. elegans*. This was to limit the number of correlations to prevent relatively low p values being non-significant after a Bonferroni correction. Therefore, correlation analysis was performed on *P. elegans* abundances with the abundances of *M. balthica*, *C. edule*, *A. marina*, and *L. conchilega,* together with those of *C. capitata* (8m survey only). The sediment variables were % organic carbon, % silt/clay content, Md ϕ and sorting coefficient.

	1m		**8m**		**40m**	
	r_s	p	r_s	p	r_s	p
M. balthica	0.244	0.052	**0.674**	**<0.001**	**0.707**	**<0.001**
C. edule	0.023	0.857	0.305	0.014	0.212	0.096
A. marina	-0.302	0.015	**-0.513**	**<0.001**	-0.045	0.729
L. conchilega	-0.013	0.917	0.113	0.373	0.032	0.806
C. capitata	-	-	-0.263	0.036	-	-
% Organics	0.027	0.830	**0.434**	**<0.001**	**0.401**	**0.001**
% Silt/clay	0.038	0.768	**0.650**	**<0.001**	**0.829**	**<0.001**
Md ϕ	-0.063	0.619	**0.616**	**<0.001**	0.258	0.041
Sort. coeff.	0.127	0.317	**0.579**	**<0.001**	**0.449**	**<0.001**

Table 2.5 : Results of Spearman Rank Correlation of *P. elegans* with the most abundant species and sediment variables from the 3 grid surveys. Correlation coefficients (r_s) and p values are given, those in bold represent those significant after Bonferroni corrections for multiple testing (α'=0.05/8 for 1m and 40m surveys; 0.05/9 for 8m survey) had been applied.

The results show that at the smaller scale, i.e., 1m survey, *P. elegans* distribution was not correlated with any species nor with any sediment variable. The results from the 8m survey suggest that at this scale, *P. elegans* was positively correlated with *M. balthica* and all the sediment variables, i.e., % organic carbon, % silt/clay, Md ϕ and sorting coefficient, and negatively correlated with *A. marina*. At the larger scale, i.e., 40m survey, *P. elegans* was only positively correlated with *M. balthica* and all the sediment variables, except Md ϕ. The significant correlations of *P. elegans* abundances with those of *A. marina* and the sediment variables must be treated with caution because of the differences in sampling protocols (see Methods).

Some of the correlations which were significant even after the Bonferroni correction, which Legendre and Legendre (1997) suggested was overly conservative and often led to rejecting too few hypotheses, appeared only weakly correlated when their scatter plots were examined. This was because the numbers of degrees of freedom (i.e., 64) were so high that even relatively low values of the coefficient, e.g., 0.401 for % organic carbon content from 40m survey, were significant. Fowler and Cohen (1990) suggested that this correlation coefficient should be used only when the number of sampling units is 30 or less. Therefore, caution is needed in the interpretation of these correlation results and thus it is important to examine the contour maps when interpreting them.

1m survey - spatial patterns

The contour maps presented in Figures 2.5(i-vii) display the distributions of the most abundant species from the 1m survey which had significantly non-random distributions, and Figures 2.6(i-v) present the significant correlograms from spatial autocorrelation analysis. The distance classes 1-6 in Figures 2.6(i-ix) represent those samples that are 0-1m, 1-1.5m, 1.5-2m, 2-2.5m, 2.5-3m and 3-3.5m apart respectively. These were chosen instead of larger intervals so that a more accurate estimate of patch size could be achieved.

Sokal (1979) described the inferences which can be made about the spatial distributions of biological populations from autocorrelation analysis and provided some useful examples. Low-order (short-distance) positive autocorrelation, where neighbouring samples usually assume similar values, may arise from gradients or patches exceeding the diameter of inter-sample distances. Significant positive autocorrelation (high Moran's *i* and low Geary's *c*) at distance class 1 therefore implies a patch size of between 1-1.5m^2 and at distance class 2, a patch size of 1.5-2m^2.

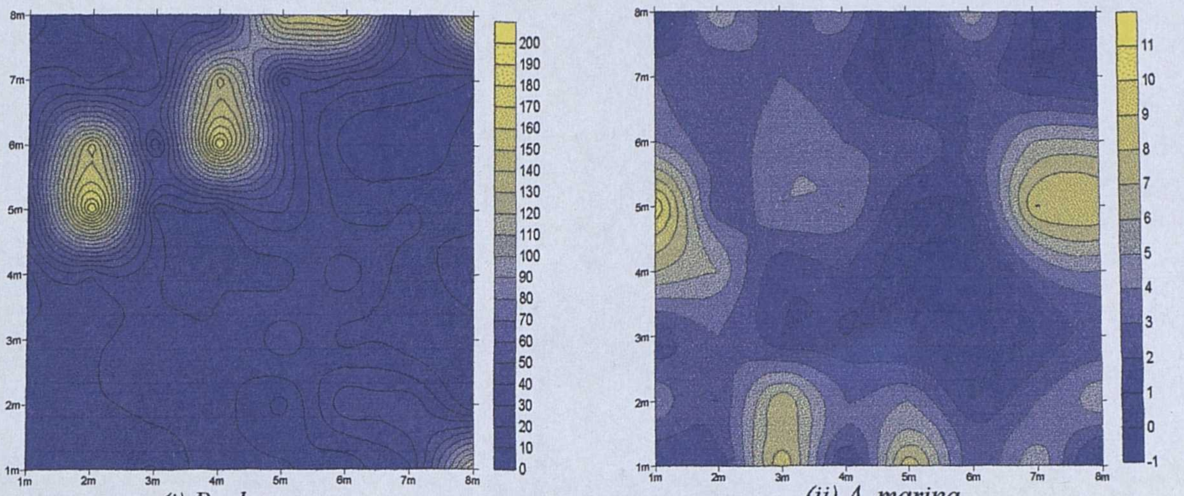
Generally, there were very good agreements between the two autocorrelation coefficients used: Geary's coefficient was nearly always significant when Moran's coefficient was significant and both gave similar estimates of patch sizes in most cases. Cliff and Ord (1973) proposed that *i* was generally better than *c*, although the margin of the advantage was slight. Therefore, patch sizes are given here as indicated by Moran's coefficient.

The density plots (Figures 2.5(i-vii)) suggest that all of the species with significantly non-random distributions formed areas of increased densities, or patches, of either less than 1m^2 (e.g., *M. balthica* and *E.* cf *flava*) or between 1-2m^2 (e.g., *P. elegans*, *A. marina*, *L. conchilega*, *G. duebeni* and *B. sarsi*) with very low abundances outside the patches. However, mapping only gives a guide to spatial patterns, they do not confirm them. The patterns indicated in Figures 2.5(i-vii) are supported by their correlograms. For example, patch sizes smaller than inter-sample distances (or lag, in this case 1m) are not revealed by spatial autocorrelation analysis and therefore *M. balthica* and *E.* cf *flava* had non-significant correlograms. For these species, smaller inter-sample distances would have been needed to determine their underlying spatial structure. The significant correlograms with positive autocorrelation at distance class 1 indicate that *P. elegans*, *A. marina*, *L. conchilega* and *G. duebeni* formed patches of 1-1.5m^2 while the positive autocorrelation at distance class 2 suggests that *B. sarsi* formed patches of 1.5-2m^2. For *P. elegans*, 2 patches were sampled wholly within the 8×8m grid, with 3 others on the edge. These corresponded to the positions of areas of smooth, raised sediment (pers. obs.) and therefore confirm that these areas did indeed contain significantly increased numbers of *P. elegans*. Furthermore, Figure 2.5(i) shows that although the patch sizes were approximately equal, the inter-patch distances varied suggesting that the *P. elegans* patches were randomly distributed at this scale.

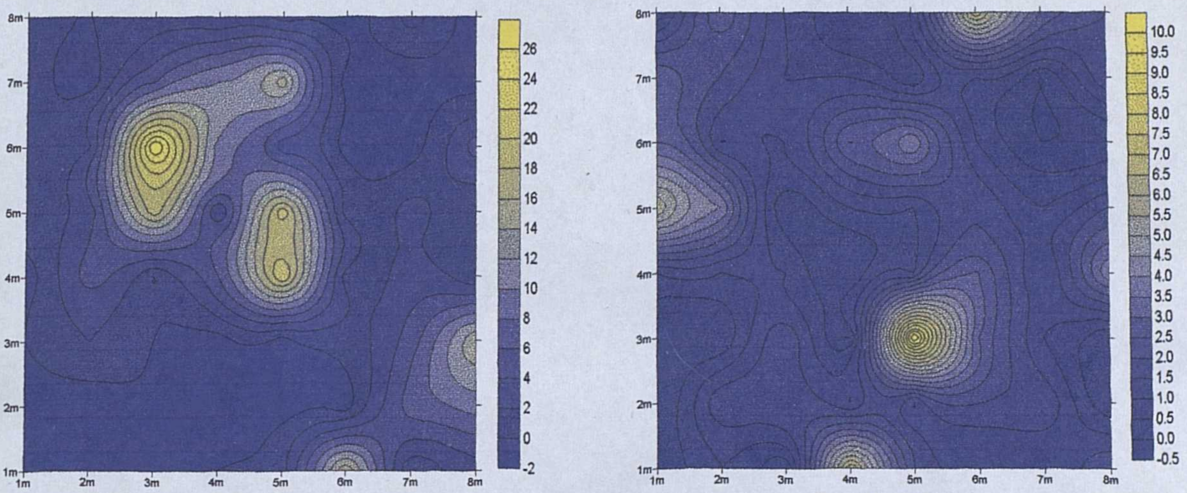
Nephtys hombergii's spatial distribution produced a significant correlogram (Figure 2.6v) even though its distribution was not significantly different from random (Table 2.2). The correlogram implies that *N. hombergii* formed patches between 1-1.5m^2 which were 1.5-2m apart, this is supported by its density plot, Figure 2.5(viii). Similarly, Thrush *et al.* (1989) found that some species which were randomly distributed according to their indices of dispersion did in fact have significant spatial structures.

Figures 2.5(ix-xii) display the spatial heterogeneity of % organic carbon, % silt/clay, Md ϕ and sorting coefficient. These sediment variables also appeared clumped: patches of increased organic carbon and silt/clay contents, together with areas of higher Md ϕs and sorting coefficients, were present. These patches appeared larger than those formed by most of the faunal species analysed. The significant correlograms presented in Figures 2.6(vi-ix) suggest spatial structures with patch sizes 1.5-2m^2 for % organic content, % silt/clay and sorting coefficient and >3.5m^2 for Md ϕ. Within these patches, sediments contained higher levels of these variables compared to surrounding sediments. According to their contour plots, these 4 sediment variables appeared to have been positively correlated with each other in their spatial distributions. A comparison of the spatial heterogeneity of these sediment variables with those of the fauna must be made with caution due to the mis-match of scales (see Methods). Although % organic content, % silt/clay and sorting coefficient formed patches similar in size (1.5-2m^2) to many of the species the contour plots suggest that they were not spatially correlated. This was formally tested for *P. elegans* (Table 2.5) but the density plots suggest that this appears to have been the case for all the other species.

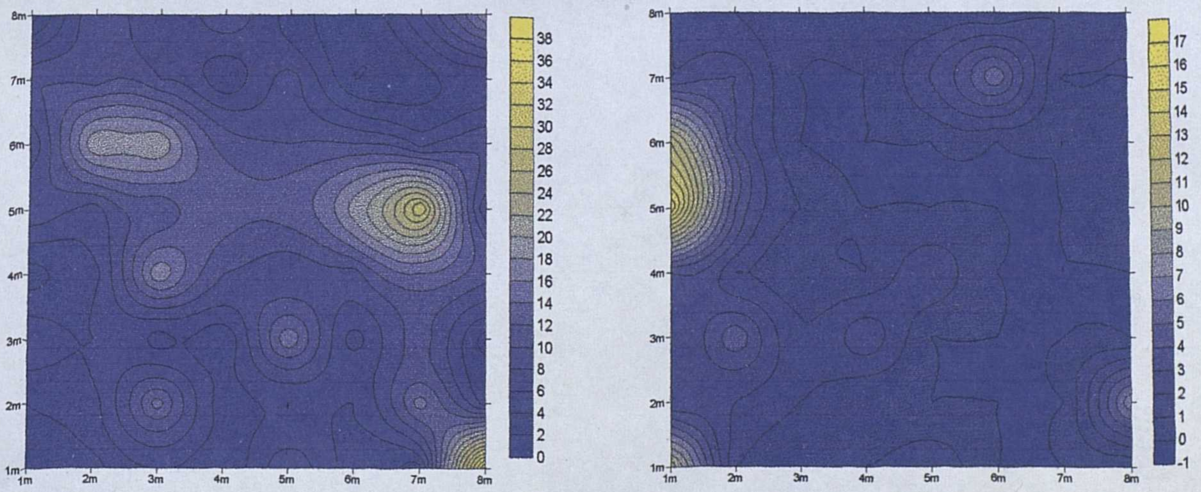
Figures 2.5(i-xi) support the results of the correlation analyses. For example, high density areas, or patches, of *P. elegans* did not occur in the same areas as those formed by other species, nor did they appear in the same areas as high levels of the 4 sediment variables.



(i) P. elegans *(ii) A. marina*

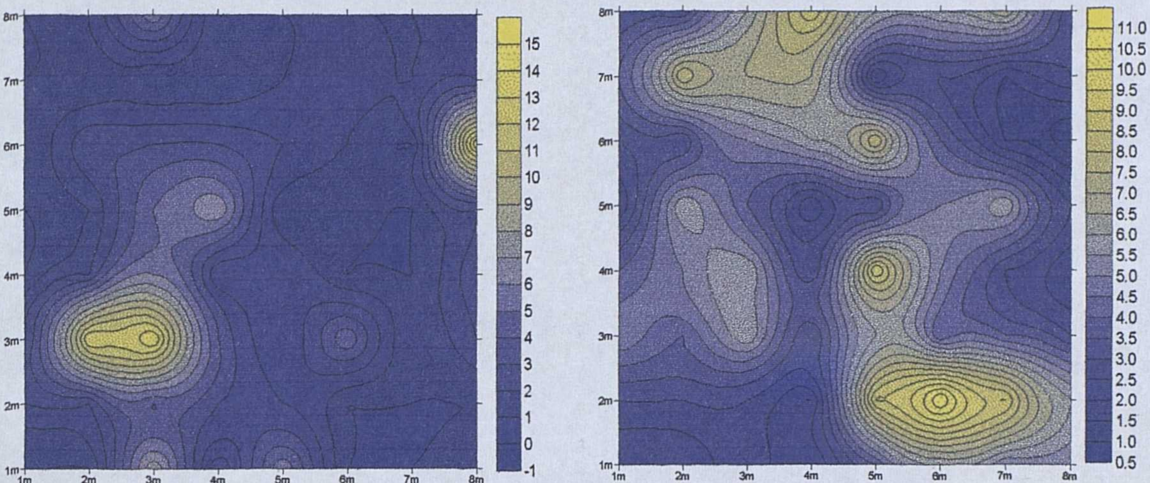


(iii) L. conchilega *(iv) E. cf flava*



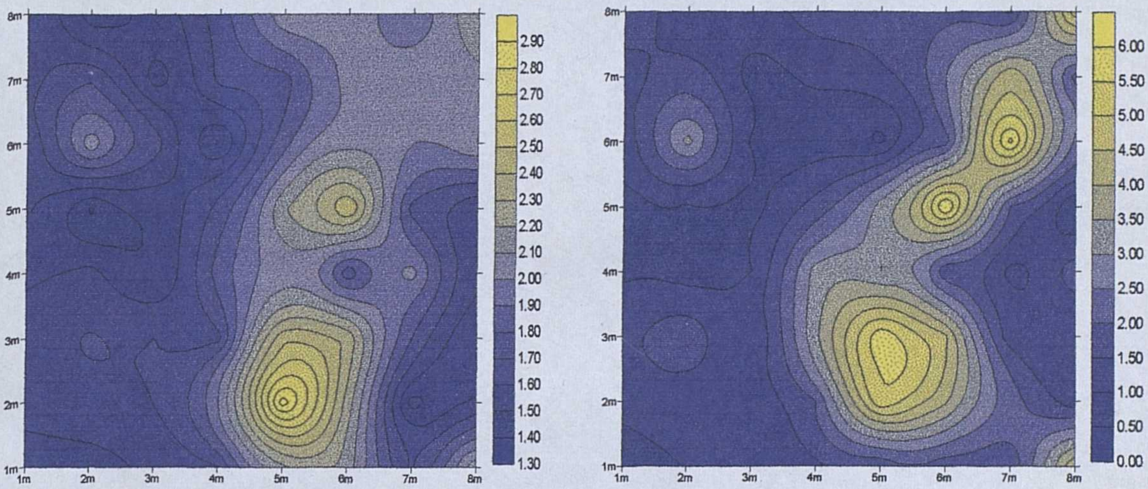
(v) M. balthica *(vi) B. sarsi*

Figures 2.5(i-vi) : Contour map of species abundances and sediment variables from 1m survey with non-random distribution using kriging.



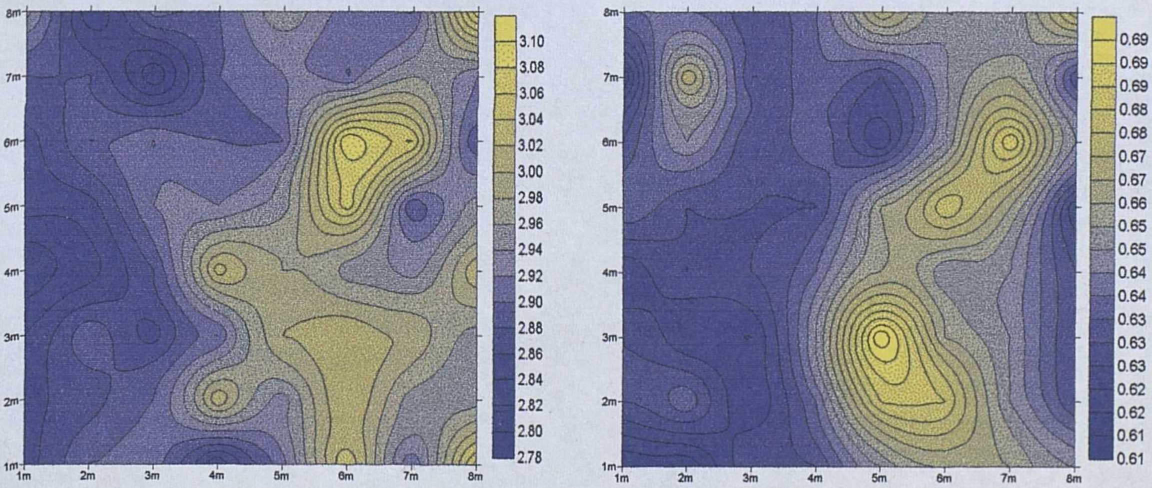
(vii) G. duebeni

(viii) N. hombergii



(ix) % Organic content

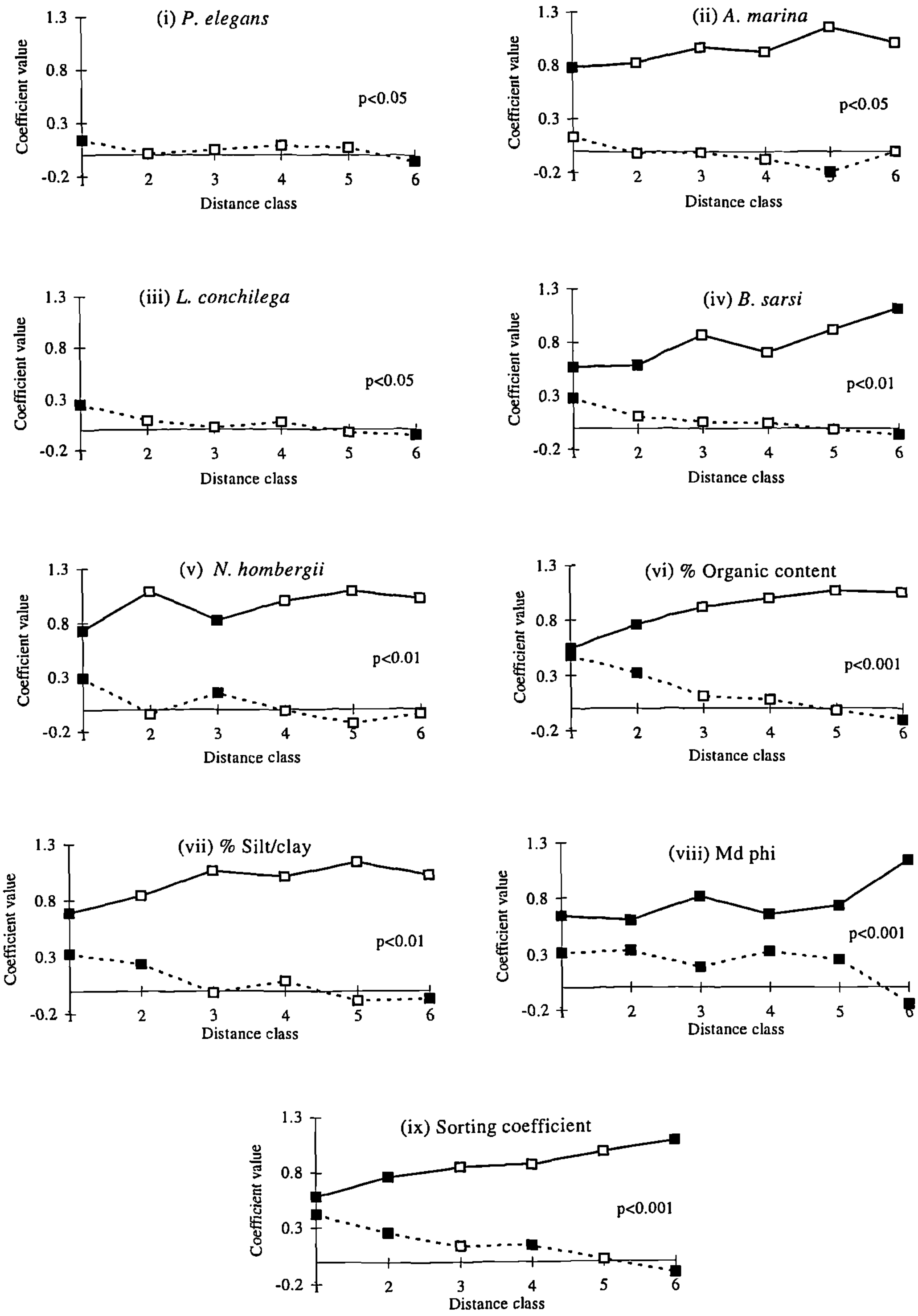
(x) % Silt/clay content



(xi) Md phi

(xii) Sorting coefficient

Figures 2.5(vii-xii) : Continued



Figures 2.6(i-ix) : Significant correlograms for the fauna and sediment variables from the 1m survey. Dashed lines represent Moran's coefficients while solid lines represent Geary's coefficients. P-values refer to whole correlogram of Moran's coefficient after a Bonferroni correction while individual points significant at 5% are shown as solid symbols.

8m survey - spatial patterns

Figures 2.7(i-viii) present the interpolated density maps of the non-randomly distributed species from the 8m survey while Figures 2.8(i-v) display the significant correlograms. The distance classes 1-6 for these correlograms represent inter-sample distances of 0-8m, 8-12m, 12-16m, 16-20m, 20-24m and 24-28m, respectively. The density maps suggest that 2 species appeared to form patches less than 8m^2 (*E.* cf *flava* and *G. duebeni*; both of which produced non-significant correlograms) while the other species either formed patches between 8-24m^2 (*C. capitata*, *S. martinensis* and *L. conchilega*) or patches of various sizes (*P. elegans*). The correlograms do not appear to support the density plots for all species. For example, while the density plot for *L. conchilega* (Figure 2.7(iii)) suggests a patch of approximately 20m^2 was present, the correlogram (Figure 2.8(ii)) implies a patch size of only 8-12m^2.

Areas of increased densities of some species, *C. edule* and *M. balthica* for example, were located at the edges of the 56×56m survey area and therefore it is not possible to give an indication of patch sizes from the density plots and one must be cautious when drawing conclusions from their correlograms.

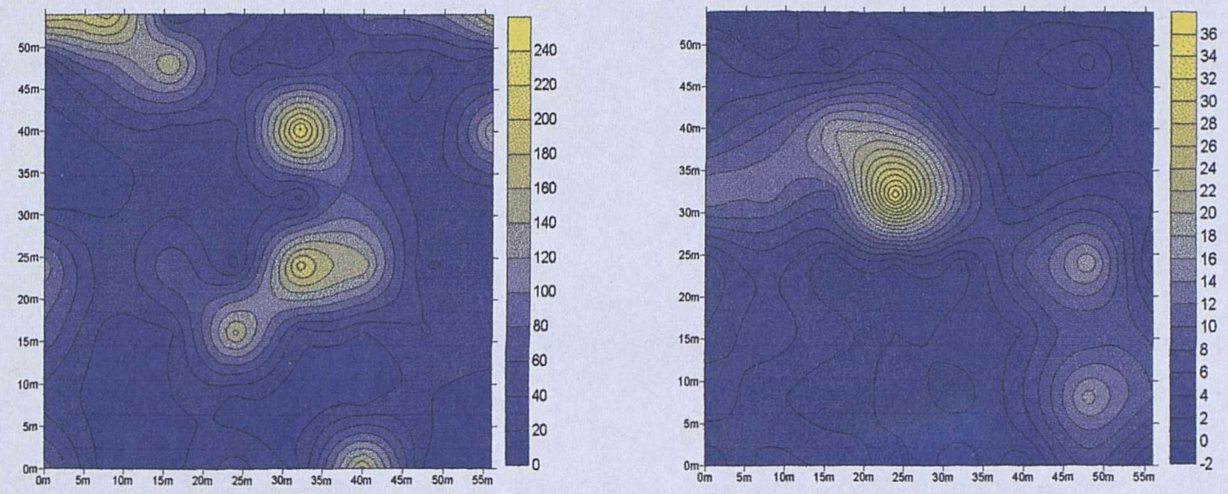
Figures 2.7(i-xii) support the results of the correlation analyses (Table 2.5). The non-significant correlations between *P. elegans* and most of the other species are clearly defended by the maps since high density patches of most species do not seem to have been spatially correlated within the survey area. Furthermore, the significant positive correlation between *P. elegans* and *M. balthica* is vindicated by their contour plots, although the locations of moderate *M. balthica* densities as well as high densities have to be observed to see this.

Figures 2.7(ix-xii) suggest that the 4 measured sediment variables were spatially correlated with each other to a certain extent. Increased levels of organic carbon and silt/clay, together with Md ϕ and sorting coefficient were mainly found at the top of the 56×56m grid, although high levels of organic carbon content and Md ϕ were also found in other small areas. The significant correlograms produced for the distribution of these variables (except % organic content) in Figures 2.8(vi-viii) indicate patch sizes of approximately 20-24m^2. However, since these were located at the edges of the survey area, one must be cautious. The significant positive correlations between *P. elegans* abundance and the levels % silt/clay, % organics and sorting coefficient are supported by the contour plots.

40m survey - spatial patterns

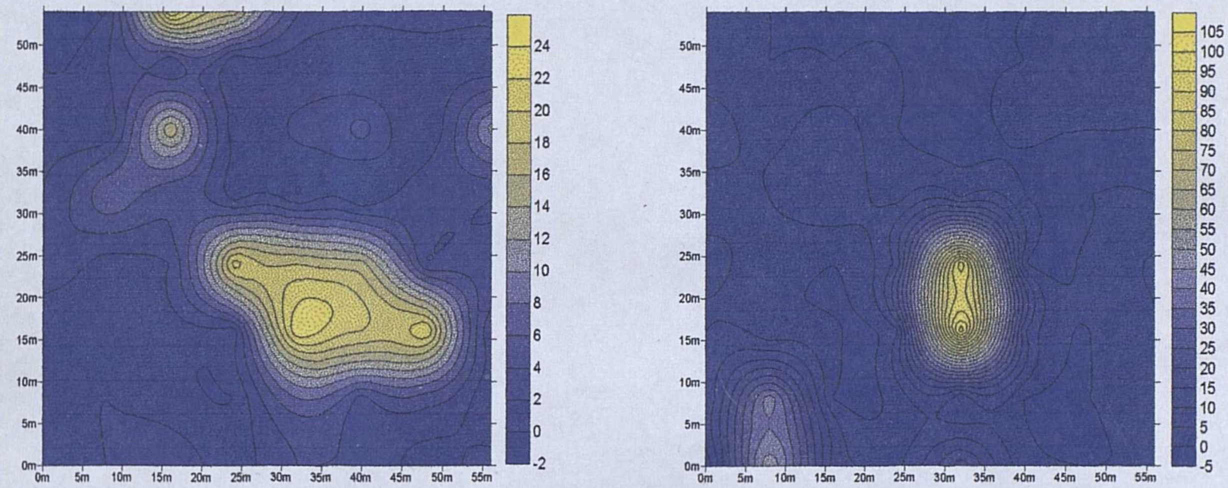
Figures 2.9(i-xi) present the contour maps of the non-randomly distributed species from the 40m survey and Figures 2.10(i-ix) display the significant correlograms. The distance classes 1-6 for these correlograms represent inter-sample distances 0-40m, 40-60m, 60-80m, 80-100m, 100-120m and 120-140m respectively. These Figures suggest that *P. elegans*, *E.* cf *flava*, *M. balthica* and *C. edule* formed patches between 40-60m^2. Some species, *S. martinensis*, *A. marina*, *L. conchilega* and *B. sarsi* for example, formed patches which were located at the edge of the survey area and so it is difficult to estimate their patch sizes. Although not formally tested, none of the species appeared to form patches which were spatially correlated with any other species. The significant positive correlation between *P. elegans* and *M. balthica* (Table 2.5) is not strongly supported by the contour plots, although their patch sizes were similar they were not spatially correlated.

Figure 2.9(xii-xv) show that the sediment variables appear to have had increased levels approximately across the middle region of the survey area. The correlograms indicated that these patches were approximately 80-100m^2. The significant positive correlations between *P. elegans* and % organic carbon, % silt/clay and sorting coefficient (Table 2.5) were better supported by the maps for the 40m survey than they were for the 8m survey with high levels of these variables occurring at approximately the same areas as the *P. elegans* patches. The contour plots support the significant positive correlations between *P. elegans* and % silt/clay, % organics and sorting coefficient and suggest that no other species was positively correlated with them.



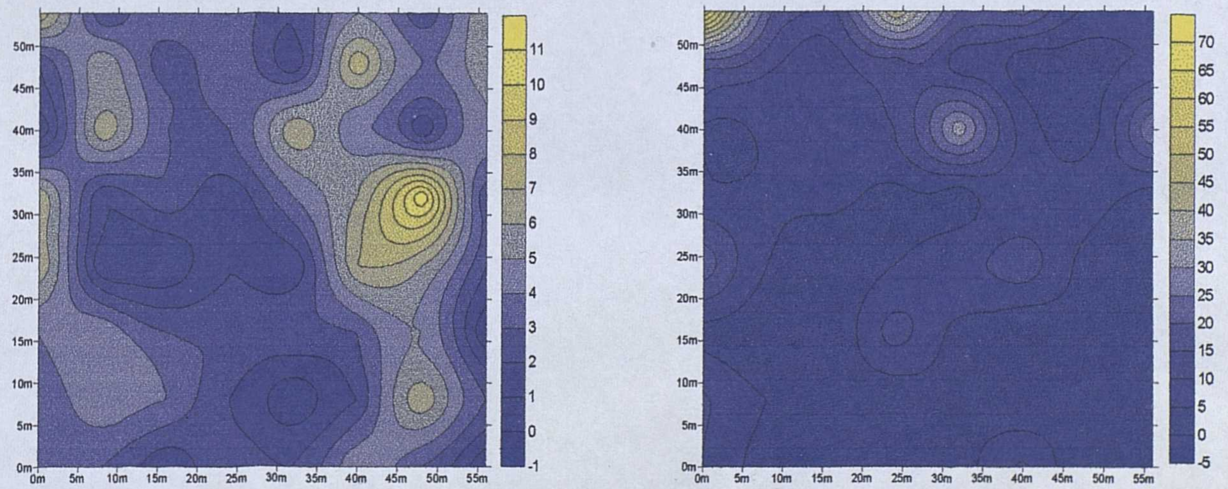
(i) P. elegans

(ii) S. martinensis



(iii) L. conchilega

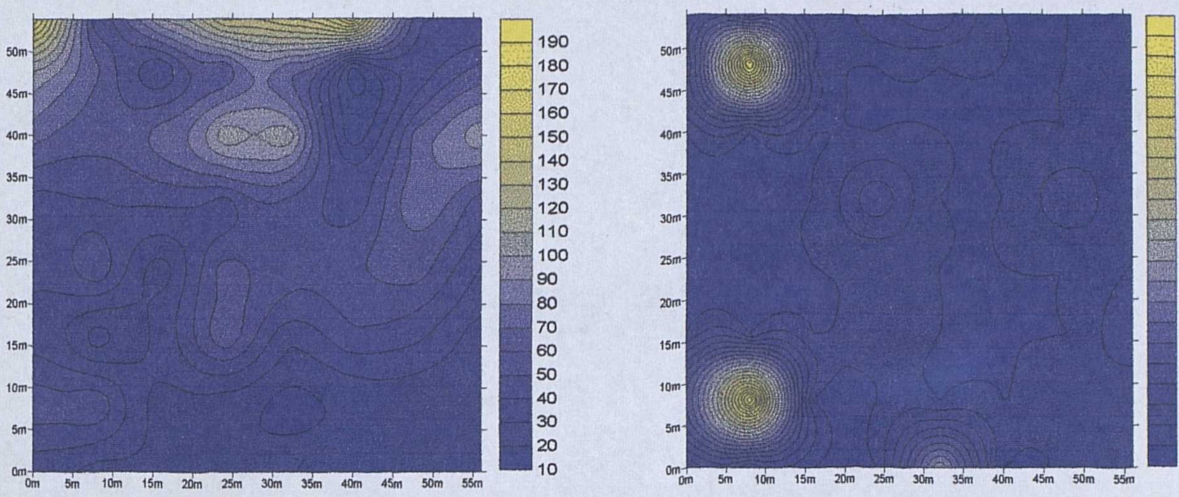
(iv) C. capitata



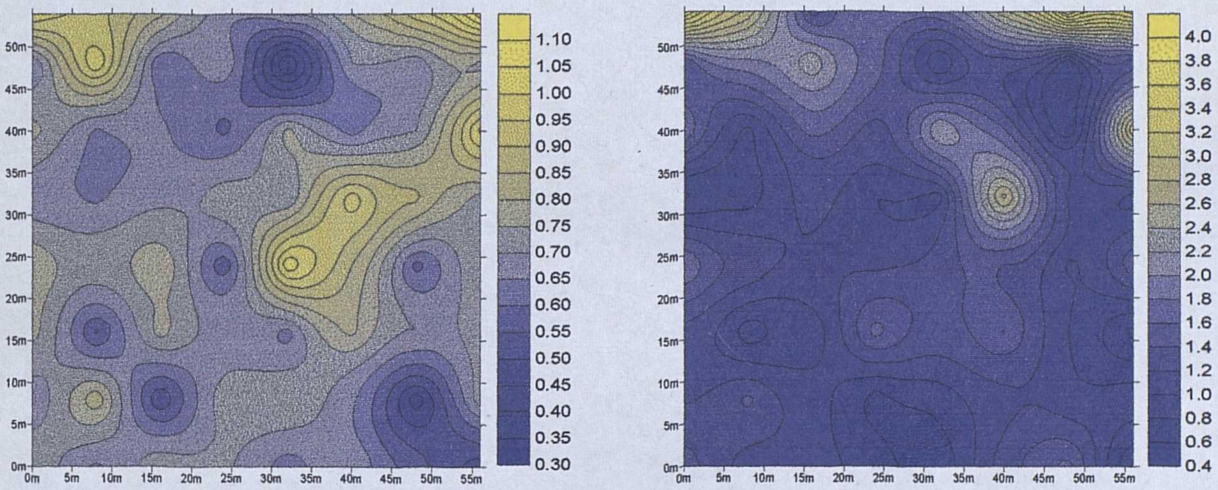
(v) E. cf flava

(vi) M. balthica

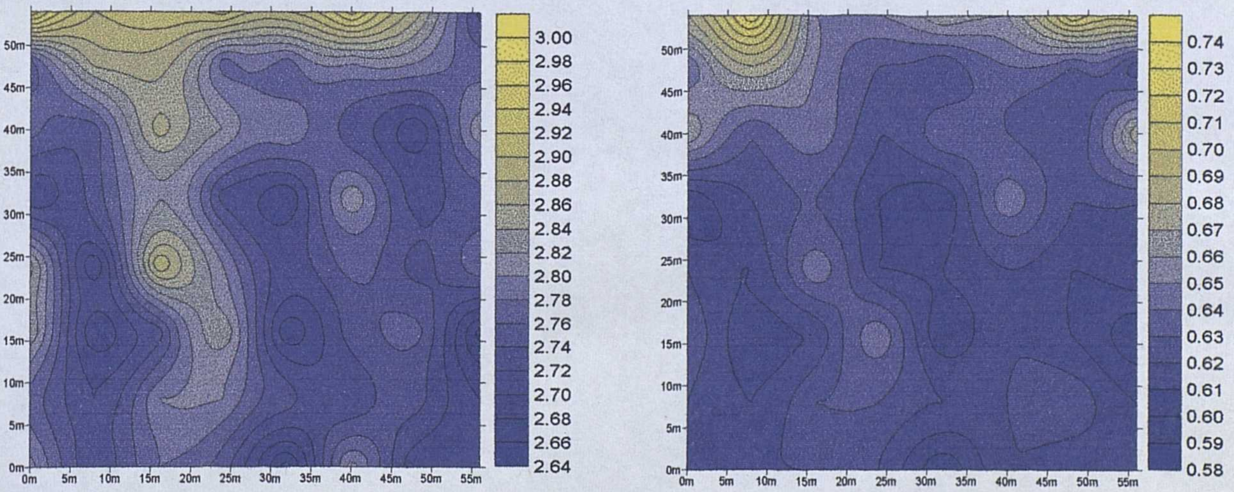
Figures 2.7 (i-vi) : Contour maps of species abundances and sediment variables from 8m survey with non-random distributions using kriging.



(vii) C. edule *(viii) G. duebeni*

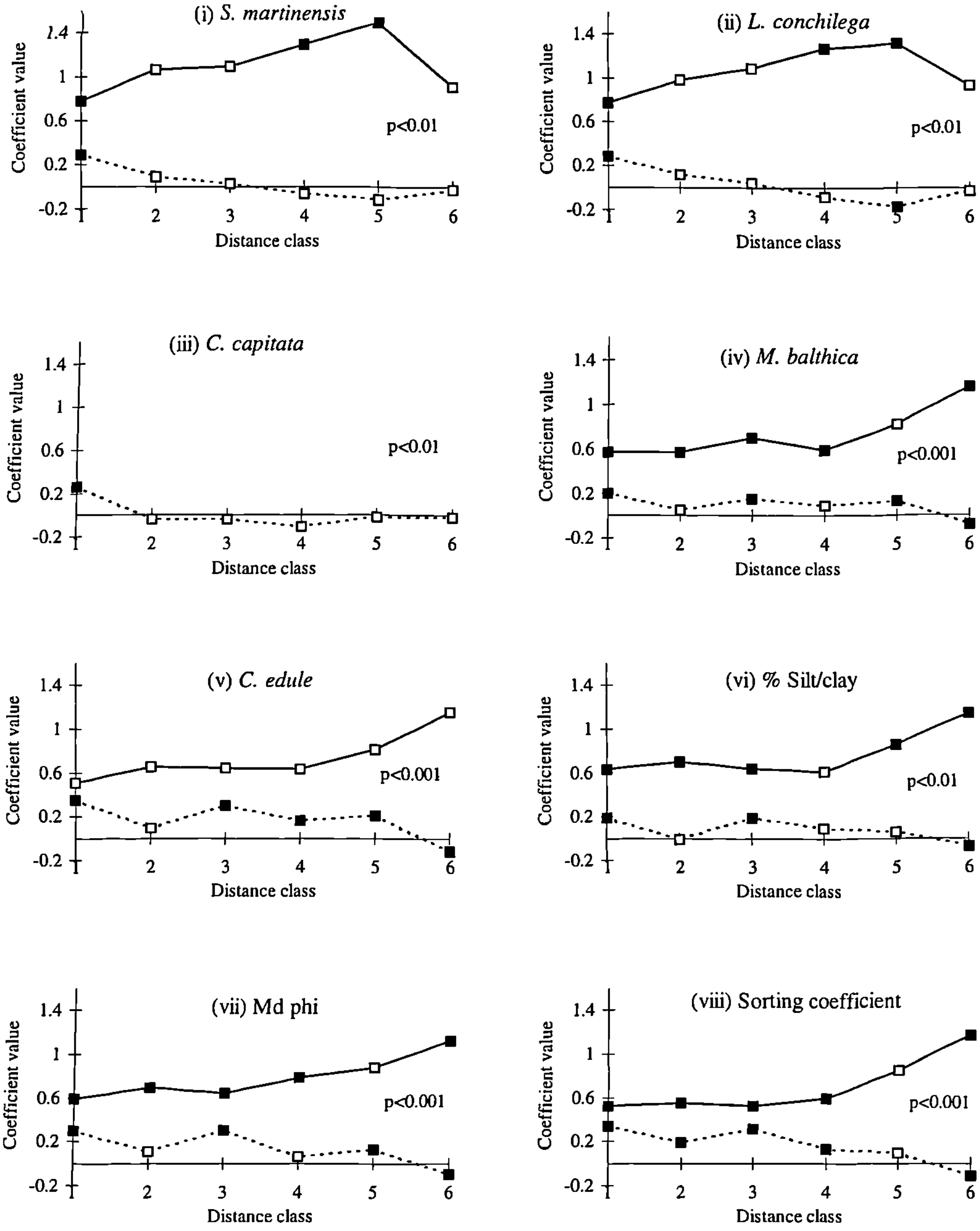


(ix) % Organic content (x) % Silt/clay content

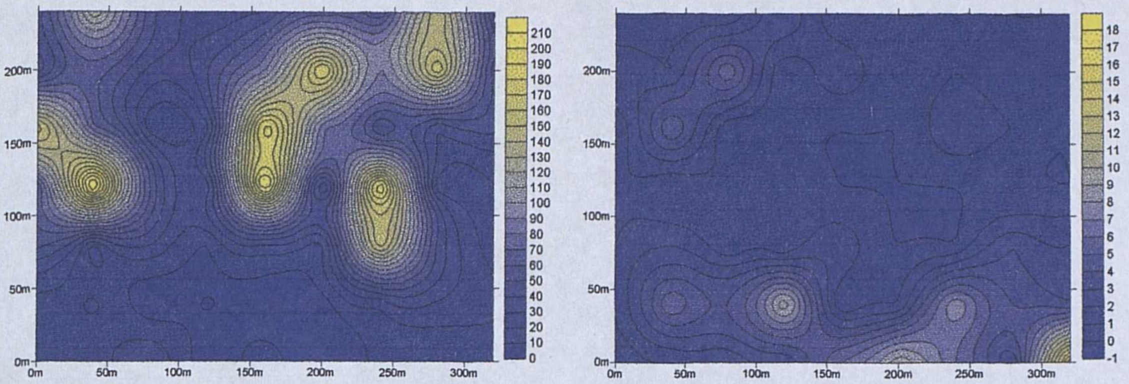


(xi) Md phi (xii) Sorting coefficient

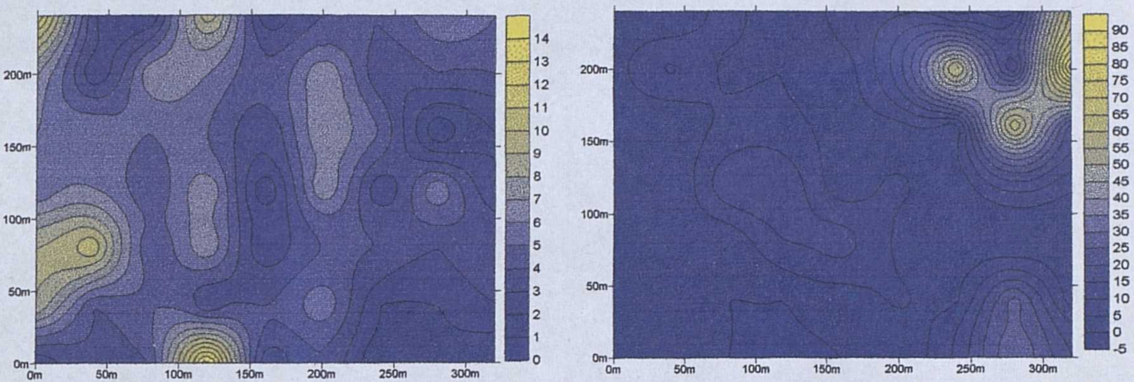
Figures 2.7 (vii-xii) : Continued



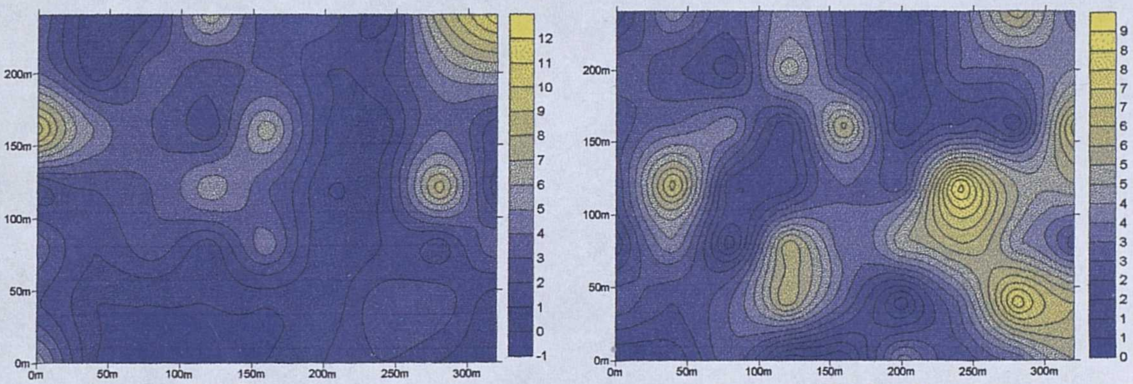
Figures 2.8(i-viii) : Significant correlograms for fauna and sediments of the 8m survey. Dashed lines represent Moran's coefficients while solid lines represent Geary's coefficients. P-values refer to whole correlogram correlogram of Moran's coefficient after a Bonferroni correction while individual points significant at 5% are shown as solid symbols.



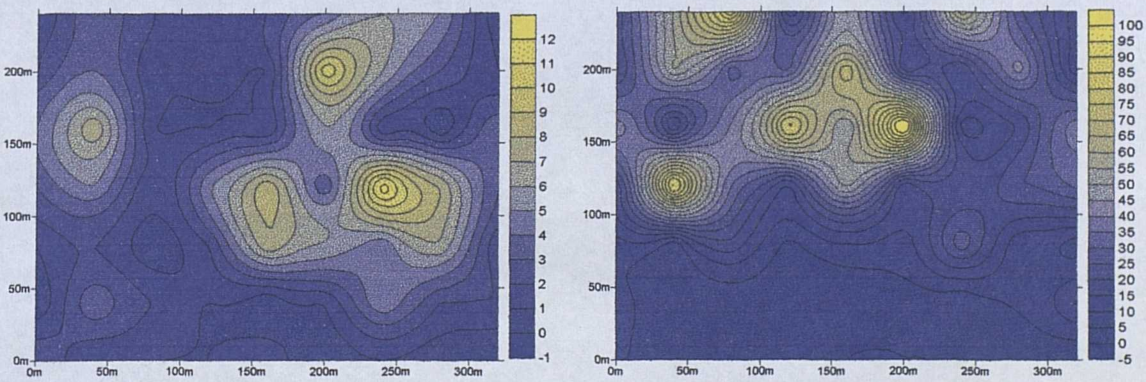
(i) P. elegans *(ii) S. martinensis*



(iii) A. marina *(iv) L. conchilega*

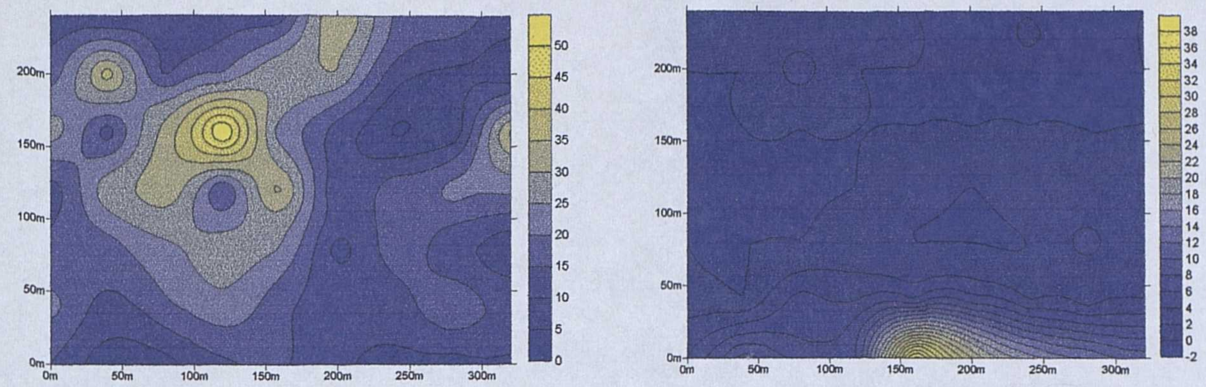


(v) C. capitata *(vi) N. hombergii*

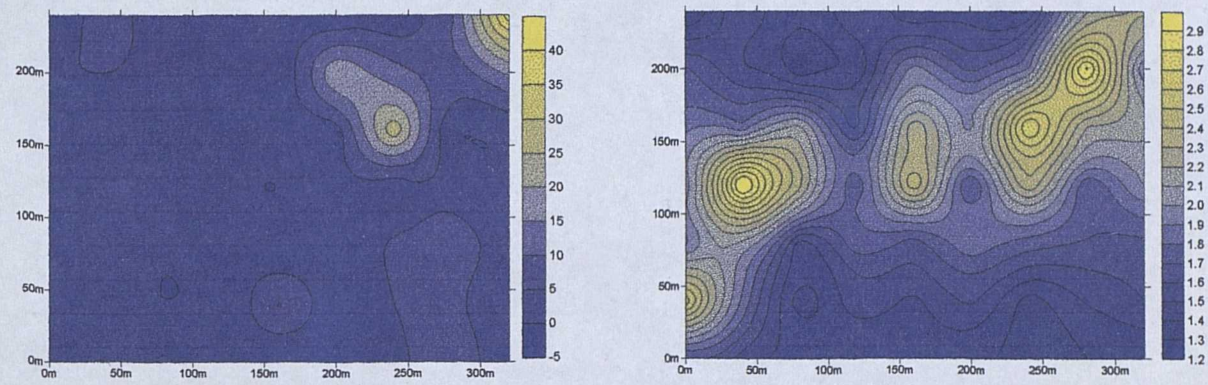


(vii) E. cf flava *(viii) M. balthica*

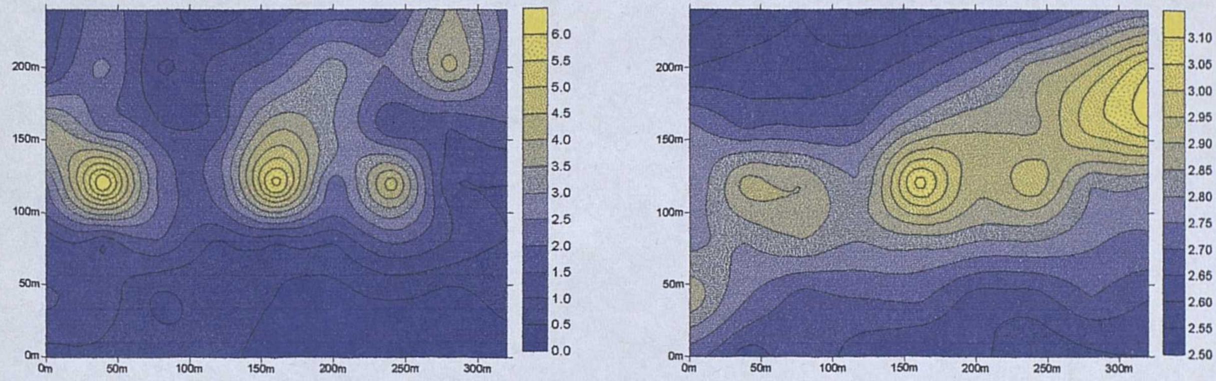
Figures 2.9 (i-viii) : Contour maps of species abundances and sediment variables from 40m survey with non-random distributions using kriging.



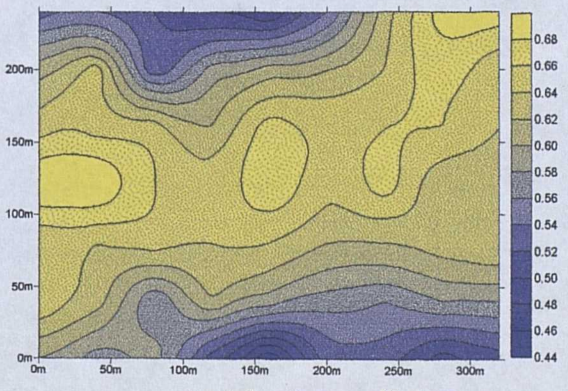
(ix) C. edule *(x) B. sarsi*



(xi) G. duebeni (xii) % Organic content

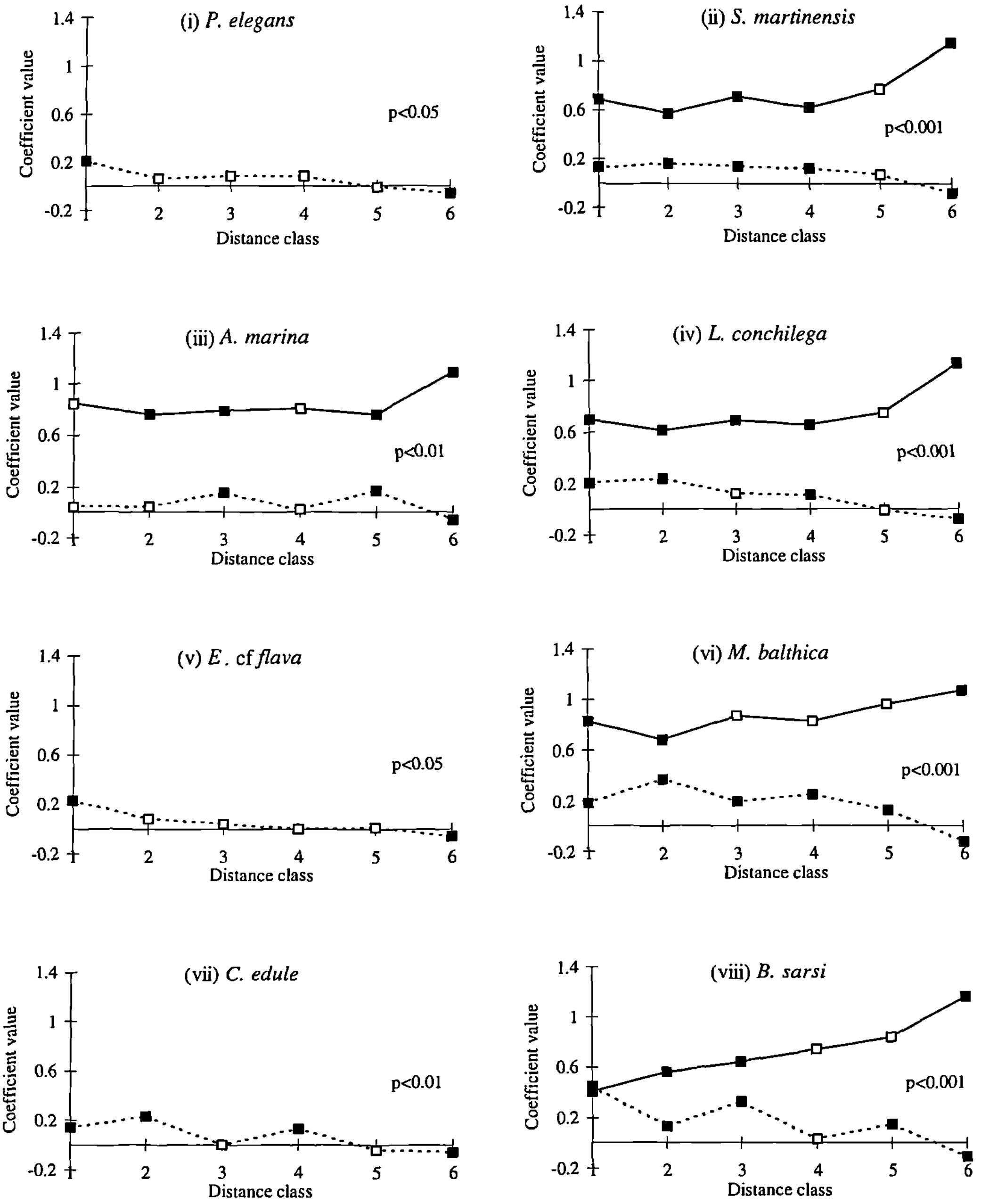


(xiii) % Silt/clay content (xiv) Md phi

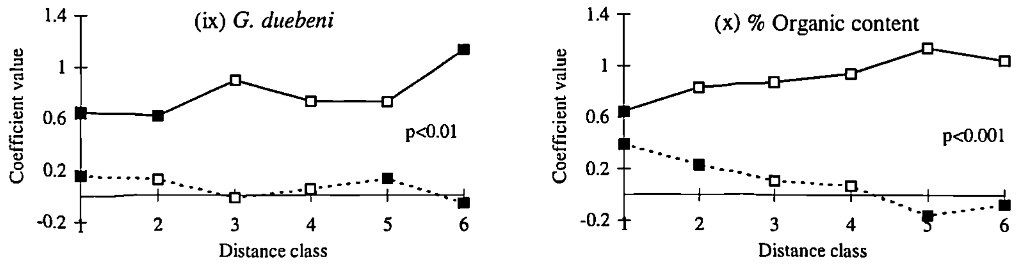


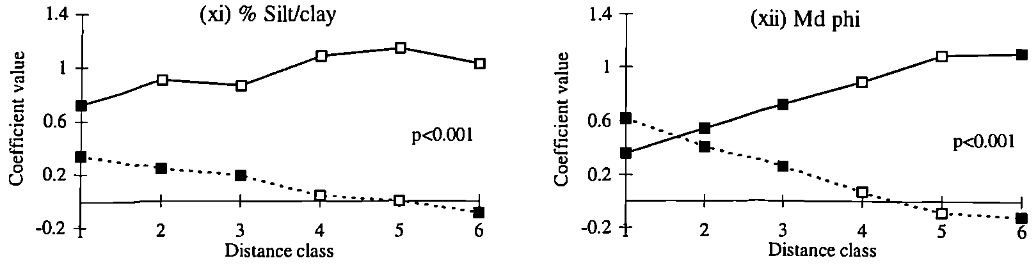
(xv) Sorting coefficient

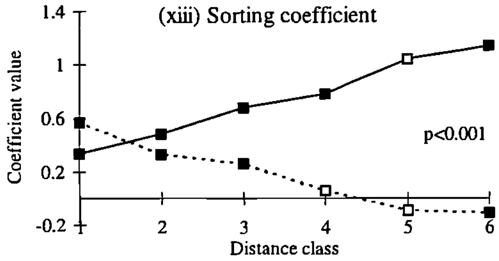
Figures 2.9 (ix-xv) : Continued.



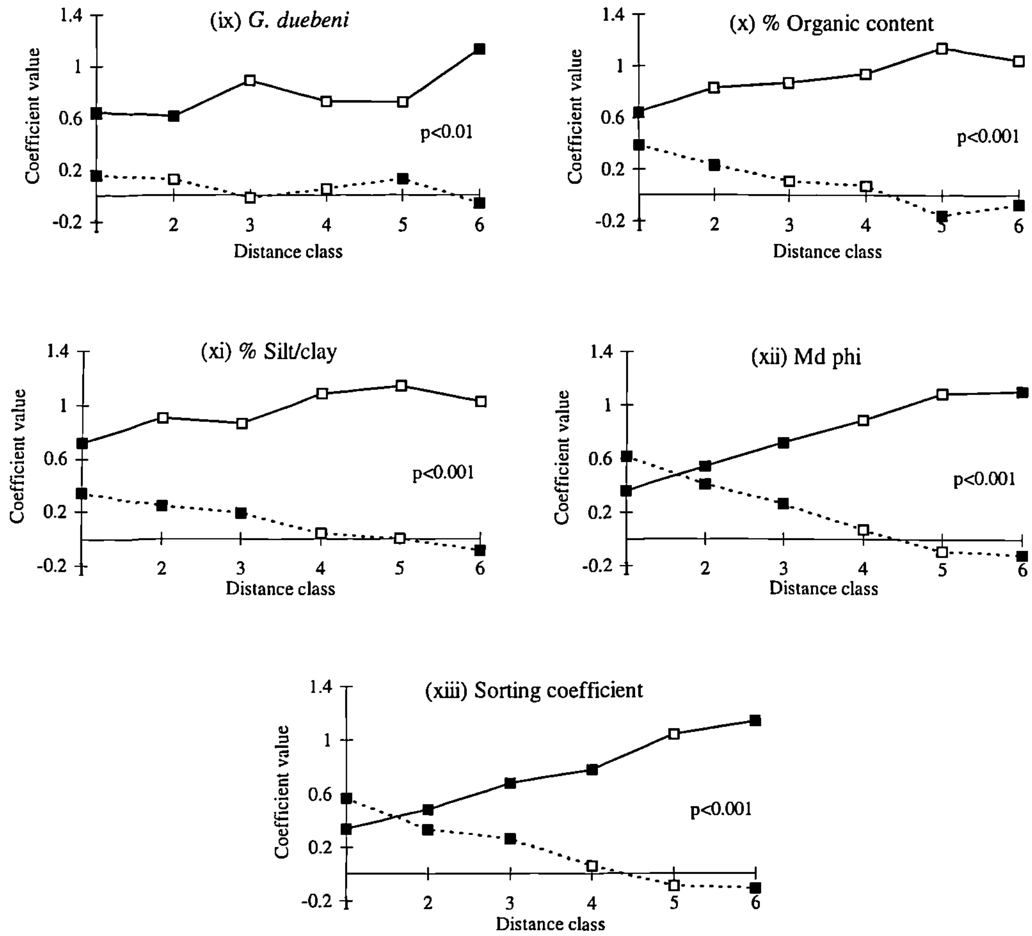
Figures 2.10(i-viii) : Significant correlograms for the fauna and sediments of the 40m survey. Dashed lines represent Moran's coefficients while solid lines represent Geary's coefficients. P-values refer to whole correlogram of Moran's coefficient after a Bonferroni correction while individual points significant at 5% are shown as solid symbols.







Figures 2.10(ix-xiii) : Continued.



Figures 2.10(ix-xiii) : Continued.

DISCUSSION

The main aims of this study were:

1) to investigate the spatial heterogeneity of the macrobenthic species and sediment variables at different spatial scales on an intertidal sandflat;
2) to determine whether the heterogeneity created by a dominant biogenic species affects the spatial patterns of other species.

The spatial patterns of macrobenthic species and sediments on Drum Sands, Firth of Forth.

This study used a variety of techniques to assess the distributions of the macrobenthic invertebrate species within the study area of Drum Sands. Firstly, a pilot survey was carried out from which spatial heterogeneity was investigated using analysis of variance. Although some species, e.g., *P. elegans*, *C. edule* and *E.* cf *flava*, had significantly different mean abundances between plots at one or more scales, this technique did not give a good insight into spatial patterns for several reasons. Firstly, the survey was carried out during March when the invertebrate abundances were generally low and secondly, although mean abundances of many taxa varied greatly at different scales, most were non-significant because of large within-plot replicate variability. This survey design is appropriate for pilot surveys giving an indication of mean abundances and variability on an intertidal sandflat but gives little information about their spatial patterns.

A much more detailed assessment of spatial patterns was given by the results of the grid surveys using dispersion indices, mapping and spatial autocorrelation analysis. Spatial patterns which were exhibited over scales of about 1-120m were defined in these surveys. Patterns which occurred over the less than tens of centimetre scale were lost in the small-scale heterogeneity and this was partly defined by the constraints of the sampling design. At this scale, the spatial patterns of *P. elegans* within high-density patches are discussed in Chapter 7.

Dispersion indices provided an assessment of the intensity of pattern but they gave no information about the form of any pattern of macrobenthic invertebrates on Drum Sands. Of the species sufficiently abundant for spatial analyses from the 1, 8 and 40m surveys; 7 out of 9; 8 out of 10 and 11 out of 11 species exhibited significantly non-random distributions respectively with very good agreements between the 3 dispersion indices (i.e., I, I_d and I_p) used. All of these were aggregated distributions, i.e., their variances were greater than their means. These dispersion indices gave a simple but useful indication as to the degree of spatial heterogeneity exhibited by many of the species within each survey. This is in agreement with many other studies of the marine benthos (e.g., Gage and Geekie, 1973; Volkaert, 1987; Meire *et al.*, 1989; Thrush *et al.*, 1989; Lamont *et al.*, 1995; Lawrie, 1996). These studies have revealed that the majority of macrobenthic populations in both intertidal and sublittoral areas are aggregated and that apparent randomness or uniformity at the scales defined in the present study are rare.

The lack of significance from a random distribution did not preclude a significant spatial pattern in all cases. For example, according to its dispersion indices, the distribution of *N. hombergii* (mean abundance of 5 individuals per core) in the 1m survey was random, yet spatial autocorrelation analysis indicated that it exhibited a significant spatial structure. Gage and Geekie (1973) proposed that spatial analysis based on variance estimates is influenced by the number of individuals and consequently low density populations are less likely to show significant differences from random. This may explain why *P. elegans* which was by far the most abundant species had relatively high variance to mean ratios. Consequently, dispersion indices do not give reliable indications of spatial intensity for rarer species. Therefore, previous studies relying solely upon dispersion indices may have under-estimated the presence of spatial heterogeneity for low-density species.

Mapping, together with spatial autocorrelation analysis, provided detailed and less equivocal assessments of the form of spatial patterns. These techniques suggested that the majority of the species within the study area indicated in Figure 1.2 formed patches of increased density at one or more scales. In the 1m survey, 4 of the 7 species with significantly non-random distributions displayed significant spatial patterns in addition to *N. hombergii*. These species, *P. elegans*, *A. marina*, *L. conchilega*, *B. sarsi* and *N. hombergii*, formed patches between 1-2m^2. The other species with non-random distributions, i.e., *M. balthica*, *G. duebeni* and *E.* cf *flava*, formed patches less than $1m^2$ and thus had non-significant correlograms at this scale. At a larger scale, the 8m survey also revealed patches of different sizes, e.g., less than $8m^2$ (*P. elegans*, *E.* cf *flava* and *G. duebeni*) and 8-$24m^2$ (*C. capitata*, *S. martinensis* and *L. conchilega*). The two bivalve species *M. balthica* and *C. edule* had significant spatial structures at this scale but the sizes of their patches could not be estimated because of their location at the edge of the survey area. At the largest scale investigated, 8 of the 11 species with aggregated distributions exhibited significant spatial patterns. Many of these formed patches between 40-$60m^2$, *P. elegans*, *E.* cf *flava*, *C. edule* and *M. balthica*, for example.

The sediments were also spatially structured within the study area. Again, mapping, together with spatial autocorrelation analysis revealed that at the smallest scale, patches of 1.5-$2m^2$ of increased % organic carbon content, % silt/clay and sorting coefficient were present while patches >$3.5m^2$ of increased median particle size (Md ϕ) were present. These variables formed larger patches in the 8m survey but their sizes could not be ascertained with any confidence because they were located at the edge of the survey area. The 40m survey indicated that these sediment variables formed patches approximately 80-$100m^2$ across the centre of the survey area.

High-density patches formed by tube-dwelling polychaetes on intertidal sandflats have been well documented (e.g., Sanders *et al.*, 1962; Daro and Polk, 1973; Dupont, 1975; Featherstone and Risk, 1977; Noji and Noji, 1991; Morgan, 1997). Patches of spionid polychaetes vary greatly in size from 0.04-$9m^2$ (*Marenzelleria viridis*; Zettler and Bick, 1996) to $150,000m^2$ (*Clymenella torquata*; Sanders *et al.*, 1962). However, comparisons of the spatial patterns identified in this study with those of tube-builders found at other intertidal sandflats are difficult since most studies have been carried out in either very different habitats and/or focused on defining smaller-scale patterns. The few studies explicitly investigating spatial distributions at this scale have found that soft-bottom macroinvertebrates generally exhibit significant spatial structuring on intertidal sandflats, forming patches of various sizes. For example, Thrush *et al.* (1989) investigated the spatial arrangements of polychaetes and bivalves in the intertidal sandflats of Manukau Harbour, New Zealand. Of the 36 populations studied, 30 were found to have significant spatial patterns, as assessed by variance to mean ratio and spatial autocorrelation analysis, forming patches of increased densities between 5 and 30m radius. McArdle and Blackwell (1989) found the bivalve *Chione stutchburyi* formed patches of increased density of 5-15m in a sandy lagoon in Ohiwa Harbour, New Zealand. Morrisey *et al.* (1992), using a nested sampling design, showed that the abundances of the infauna in the soft sediments of Botany Bay, Australia, were patchy at scales from 1 metre to several kilometres. None of the species in the study by Thrush *et al.* (1989) exhibited identical spatial patterns at all of the 6 sandflats which suggests that patterns and patch sizes are partly affected by their environment and that different studies are likely to give different spatial patterns for the same species. In addition, Hewitt *et al.* (1997) showed that spatial patterns varied temporally within the same site.

Heterogeneity results from a complex interaction of biotic and abiotic processes (Livingston, 1987; Caswell and Cohen, 1991). At the scale investigated in this study, metres to tens of metres, spatial heterogeneity of macrofauna may result from many processes including disturbance, larval settlement, competition and sediment heterogeneity. In most studies, the causes of the patterns are only hypothesized or inferred from the data available. For example, Thrush *et al.* (1989) suggested that feeding pits generated by rays may have been responsible for the generation of small-scale heterogeneity within larger homogeneous density patches at two of their sites, while McArdle and Blackwell (1989) proposed that the pattern of *C. stutchburyi* at their site may have resulted from an environmental gradient. Morgan (1997) suggested that a large, gregarious settlement of larvae must have been one of the prerequisites for the formation of very dense patches of *P. elegans* in the intertidal sandflats of the Baie de Somme, France.

Determining the process(es) responsible for an observed pattern at this scale (metres to hundreds of metres) is very difficult (McArdle *et al.*, 1997). Although controlled, manipulative experiments are possible at smaller scales (centimetres to a metre) their conclusions cannot be scaled-up to larger scales since different processes are likely to be responsible for giving rise to patterns. For example, Hewitt *et al.* (1996) showed that it was possible to predict the spatial patterns (<6m) of both the adults and juveniles of the two dominant bivalve species, *Macomona liliana* and *Austrovenus* *stutchburyi*, at Wirroa island, New Zealand, based on their size, feeding mode and mobility. However, studies carried out at the same location by Legendre *et al.* (1997) revealed that the larger-scale patterns (10m to several 100m) of these two species were largely created by physical variables and that biotic effects were undetectable. They proposed that the reason for the disparity between the results from their study and the one by Hewitt *et al.* (1996) was due to scale differences.

The study described here was not explicitly aimed at determining the processes responsible for any spatial patterns observed. The results from other studies, for example Hewitt *et al.* (1996) and Legendre *et al.* (1997), suggest that patchiness at the smaller scale investigated in this study (1-2m^2) may have been generated by biological processes while those at larger scales (tens of metres to a hundred metres) may have resulted from physical processes. Patches between 1-2m^2 exhibited by species in the present study on Drum Sands did not appear to be spatially correlated with each other which suggests that they may have been generated either by negative interspecific or positive intraspecific interactions. Hewitt *et al.* (1996) showed that it was possible to infer processes from small-scale (<6m) patterns with a good knowledge of the natural history of the species. Patches observed in the present study for relatively immobile species, *P. elegans* and *L. conchilega*, for example, were presumably created mainly by larval recruitment while those of more mobile species, *M. balthica* and *C. edule*, for example, may reflect the distance over which adults are capable of moving. The possibility of interspecific interactions, specifically the effects of *P. elegans* on the distribution of other species within the study area, is discussed further in the next section of this chapter and in Chapter 8.

This study revealed that the measured sediment variables were spatially structured at several scales and that this may have been partly responsible for the generation of patterns observed for some of the macrobenthic species. The patches of none of the species (except *P. elegans*) appeared to have been spatially correlated with high levels of any of the measured sediment variables at any scale in this study, although this was not formally investigated with correlation analyses. This would suggest that sediment heterogeneity was either not important for the generation of the spatial patterns of most of the species studied or that other variables not measured were important. This lack of apparent correlation must be treated with caution due to different sampling regimes for the sediments and fauna. There were significant positive correlations of *P. elegans* density with high levels of % organic content, % silt/clay, Md ϕ and sorting coefficient in the 8m and 40m surveys. Tube-building polychaetes have been shown to affect these sediment properties (Noji, 1994; Morgan, 1997) and, therefore, the sediments may not have been responsible for the generation of *P. elegans* patchiness but vice versa. This will be discussed further for *P. elegans* on Drum Sands in Chapter 8.

Drum Sands is a relatively high energy sandflat with frequent sediment movement (pers. obs.) and macroalgal mats are capable of forming during the summer (summer of 1996 for example). Therefore, the mosaic of species patches observed in this study may have been generated by disturbances. The role of disturbance in structuring macrobenthic populations on Drum Sands will be addressed in Chapters 4, 5 and 6.

This study revealed spatial patterns of many common intertidal macrobenthic species found in European sandflats at various scales using regular grid-sampling techniques. This sampling design is simple to carry out, is capable of covering a range of scales and spatial patterns can be easily detected and displayed. This study revealed the presence of patches of 1-2m^2 in many species.

The effect of a dominant biogenic species on the spatial patterns of other invertebrate species on an intertidal sandflat.

One of the most conspicuous biological features on an intertidal sandflat are the mounds or plateaus formed by high densities of tube-building polychaetes. On Drum Sands, *P. elegans* forms areas of smooth, raised sediment, approximately 1-1.5m^2, within an otherwise wave-rippled sandflat. These areas are characterised by increased densities of *P. elegans*. Many studies have reported different sediment characteristics within dense arrays of tube-building polychaetes (Dupont, 1975; Featherstone and Risk, 1977; Noji, 1994; Morgan, 1997; Chapter 8) and these have resulted in different faunal assemblages (Sanders *et al.*, 1962; Fager, 1964; Ragnarsson, 1996; Chapter 8). None of these studies, however, have assessed to what extent the spatial pattern exhibited by the tube-building polychaete has an effect upon the spatial pattern of other species.

Species with similar structure functions (correlograms) do not necessarily occupy the same spatial locations (Hewitt *et al.*, 1996). For example, while the correlograms of *P. elegans*, *L. conchilega*, *B. sarsi* and *N. hombergii* suggested that these species formed patches of increased densities approximately 1-1.5m^2, their density plots revealed that their patches were not spatially correlated. For *P. elegans*, this was examined more formally using correlation analyses which supported the observations that *P. elegans* abundances were not correlated with the abundances of *L. conchilega* or *M. balthica* (*B. sarsi* and *N. hombergii* were not considered sufficiently abundant for correlation analyses). This suggests that the spatial patterns of *P. elegans* on Drum Sands did not have a large positive effect on those of the other common species.

Pygospio elegans was only positively correlated with one species in this study, *M. balthica* (8m and 40m surveys). However, positive association does not necessarily imply a positive interaction, since negative interactions (e.g., predation) can take place between species coincident in space, or coincidence may occur due to some common ecological preference between two species. Controlled manipulative experiments, together with spatial autocorrelation analysis, are needed to test explicitly for the presence of an interaction between these two species.

Tube-building polychaetes are capable of affecting species distributions via many direct and/or indirect interactions, e.g., hydrodynamic effects (Eckman *et al.*, 1981; Eckman, 1983), provision of refuges (Woodin, 1978, 1981; Lukenbach, 1986) and increased food availability (Eckman, 1983; Noji, 1994) which suggest that the positive association between *P. elegans* and *M. balthica* in this study may have been non-coincidental. A change in spatial pattern of *M. balthica* or reduced survival, growth or recruitment may, therefore, be expected in the absence of *P. elegans*. The processes by which *P. elegans* affect other fauna are discussed further in Chapter 8 in which the faunal communities and sediment variables of *P. elegans* patches are compared with non-patch sediments using not a non-parametric correlation approach as in this study but a more suitable, parametric method of statistical analysis, i.e., t-tests.

The study described here has provided important information about the spatial patterns exhibited by the abundant invertebrate species on Drum Sands. The results have provided invaluable information from which hypotheses can be tested about the generation of spatial patterns on intertidal sandflats, in particular, the small-scale patches formed by *P. elegans* and the role they play in structuring the community.

CHAPTER 3

THE POPULATION STRUCTURE AND REPRODUCTIVE BIOLOGY OF *PYGOSPIO ELEGANS* ON DRUM SANDS

INTRODUCTION

Natural and anthropogenic disturbances have been shown to be important factors influencing the structure of marine soft-bottom communities (Levin, 1981; 1984a; Zajac and Whitlatch, 1982a; 1982b; Dobbs and Vozarik, 1983). The effect of a disturbance on the marine benthos is partly determined by the scale and intensity of the disturbance. A disturbance such as a natural storm, for example, can result in the large-scale defaunation of the sediment (Dobbs and Vozarik, 1983). Increased wave and current action resulting from storms erode the sediment surface causing high species mortality and/or the redistribution of infauna (Rees *et al.*, 1977) or severe reductions in salinity and dissolved oxygen concentrations cause the mortality of many species (Boesch *et al.*, 1976; Santos and Simon, 1980a). Such a disturbance often results in a heterogeneous environment (Levin, 1984a).

A number of species have developed opportunistic life histories enabling them to exploit disturbed habitats (Grassle and Grassle, 1974). In general, opportunists are characterised as having a low reproductive age, high fecundity, strong dispersal ability and a short life span (Pianka, 1994). These characteristics enable opportunists to rapidly colonise an area under favourable conditions, although they tend to be unable to compete with non-opportunists. Many polychaete species such as *Capitella capitata* (Warren, 1976) and the spionids *Pygospio elegans* (Muus, 1967; Anger, 1977), *Polydora cornuta* (formerly *P. ligni*)(Zajac, 1991) and *Streblospio benedicti* (Levin and Creed, 1986) have been shown to rapidly increase in numbers following a disturbance (Grassle and Grassle, 1974; Pearson and Rosenberg, 1978). These polychaetes, with the exception of *P. elegans*, have been particularly well studied in relation to their opportunistic nature.

Pygospio elegans has been shown to be polytelic (Gudmundsson, 1985; Anger *et al.*, 1986) with a flexible reproductive strategy. This species normally reproduces sexually and, depending on the degree of adelphophagy (whereby the developing larvae consume 'nurse eggs'), planktotrophic or benthic larvae may be produced (Thorson, 1946; Smidt, 1951; Mileikovsky, 1971; Rasmussen, 1973; Anger, 1984; Levin *et al.*, 1991). The latter larval type was termed as 'non-pelagic lecithotrophic' larvae by Vance (1973). The existence of more than one mode of reproduction within a single species, or 'poecilogony' (Giard, 1904, cited by Hoagland and Robertson, 1988) is especially common in Spionidae where the presence of both brood protection and adelphagia allows considerable flexibility in the duration of the planktonic larval phase and in the mode of nutrition (Levin, 1984b). The existence of two different larval types within a species has important demographic implications (Levin, 1987).

After release, the eggs are retained in capsules attached to both the female and to the inside of her tube. As many as 19-34 capsules have been found in the deepest part of the female tube (Rasmussen, 1973). The numbers of eggs per capsule have been shown to vary greatly, but in general, far fewer eggs are laid down in capsules producing benthic larvae. Non-brooded larvae hatch from 3 setigers (Anger *et al.*, 1986) to 6 setigers (Hannerz, 1956) while brooded ones hatch later at 12-16 setigers (Hannerz, 1956; Rasmussen, 1973.

At the 12 to 14 setiger stage the larvae are ready to metamorphose (Hannerz, 1956). However, metamorphosis to the juvenile stage does not occur until a suitable sediment type is encountered, the particle size distribution and organic content of the sediments being important factors (Smidt, 1951; Hannerz, 1956). Newly settled individuals grow rapidly and reach maturity within a few months (Smidt, 1951), thus populations of *P. elegans* can reach very high densities in a relatively short period of time.

Asexual reproduction by fragmentation has also been reported for *P. elegans* (Rasmussen, 1953; Wilson, 1985) and has been found to be more important for the maintenance of some local populations than sexual reproduction (Hobson and Green, 1968).

According to Anger *et al.* (1986) the normal life span of *P. elegans* is between one and two years and it is likely that a female worm is able to produce two generations per lifetime (Hannerz, 1956; Rasmussen, 1973). The species is dioecious and the ratio of males to females has been shown to vary from month to month (Rasmussen, 1973). In addition, male worms have been shown to change sex in relation to season (Rasmussen, 1973), an increase in temperature causes the male sexual characteristics to degenerate. The male, therefore, appears to be a sexually immature female during the summer months which alters the male to female sex ratio.

The aim of this study was to provide information on the population structure and reproductive biology of *P. elegans,* both of which are important factors affecting the spatial distribution of a population. Knowing the timing of reproductive activity and the method of reproduction, for example, are necessary prerequisites in an examination into how the population is likely to respond to both physical and biological changes on Drum Sands. Furthermore, the ability of a population to undergo asexual fragmentation and/or production of benthic larvae has important implications for small-scale distribution. This is particularly pertinent for a species such as *P. elegans* whose method and timing of reproduction has been shown to vary between locations (Smidt, 1951; Gudmundsson, 1985).

The *P. elegans* population on Drum Sands, Firth of Forth, Scotland, was studied in terms of its size distribution, annual proportions of adults and juveniles, sex ratio of adults and reproductive activity of adult females from March 1997 to February 1998. The following two aims were specifically addressed in this study:

1) to investigate the population structure and reproductive mode of development of *P. elegans* on Drum Sands, Firth of Forth;

2) to discuss what implications these have for the population maintenance and the generation of spatial patterns of *P. elegans* on Drum Sands.

METHODS

Survey design - It has been shown (see Chapter 2) that *P. elegans* forms patches of increased density, approximately 1m^2 in area, within the 400×250m study area on Drum Sands. These patches could be seen as areas of smooth, raised sediment as opposed to the wave-rippled sediments of non-patch areas. Eighty *P. elegans* patches were marked by a cane, 2m away from the patch, and numbered. Some of these numbered patches were used in later studies described in Chapters 6 and 8.

On each sampling date, 3 *P. elegans* patches were chosen at random for sampling. Patches were sampled monthly between March and August 1997 and every other month thereafter until February 1998. Thirty-two contiguous cores (3×3cm, 8cm depth) forming a transect were taken across each patch. Preliminary sampling on Drum Sands had shown that no individuals occurred lower than 8cm below the sediment surface. These cores were also used to investigate micro-scale spatial patterns of *P. elegans* (see Chapter 7). For the purpose of the present study the data from the 32 cores were pooled. Therefore, an equivalent of 1 core (3×96cm) was taken from three patches each month. The cores of sediment were then preserved in 10% saline formaldehyde solution, neutralised with Borax containing 0.01% Rose Bengal stain. The samples were later sieved on 500μm and 212μm mesh sieves. The smaller mesh size retained newly settled *P. elegans* (Gudmundsson, pers. comm.). The numbers of *P. elegans* and other fauna were counted, the former being kept in 70% alcohol for size and sex determination.

Size measurements and sex determination of *P. elegans* were carried out on only half of each sample (i.e., 16 out of the 32 cores were randomly selected). This was a necessary procedure due to the number of samples and the time involved in determining the sizes of individuals. It was considered that this procedure would not compromise the results obtained due to the large number of individuals. Size determination of *P. elegans* individuals was carried out by measuring the width of the 5th setiger using a dissecting microscope (×40 magnification) fitted with an eyepiece micrometer. Fifth setiger width measurements have been used as a standard body size measurement technique for many spionid polychaetes (e.g., Yokoyama, 1990; Zajac, 1991; Ragnarsson, 1996; Morgan, 1997) and is the method used in all later studies (Chapters 4, 5, 6 and 8). Body length measurements were not possible for all individuals since many were damaged during sampling and processing. However, lengths of all intact worms were measured to the nearest millimeter allowing regression analysis of 5th setiger width and body length to be carried out.

Sex could be determined for sexually mature individuals only. Adult males possess a pair of branchiae on the 2nd setiger which distinguishes them from females (Rasmussen, 1973). The branchiae, or nuchal appendages, have been shown to be important in copulation (Schlotzer-Schrehardt, 1987; 1991). This method of sex determination is both a convenient and a reliable one (Rasmussen, 1973; Gudmundsson, pers. comm.).

Each month, the number of adult female tubes containing embryos and/or larvae were recorded. This method of assessing the reproductive status of *P. elegans* has been successfully used in other studies (e.g., Morgan, 1997). Embryos and larvae present were compared to the drawings given in Thorson (1946), Hannerz (1956) and Rasmussen (1973). Those female tubes containing larvae were retained and preserved in 70% ethyl alcohol. Fifty larvae per month were randomly selected from these tubes, their general appearance were noted and their lengths measured using a dissecting microscope fitted with an eyepiece micrometer.

Data analyses - Regression analysis was carried out, using Minitab version 10.0, between the 5th setiger widths and lengths of all complete *P. elegans* individuals. The size distributions of the larvae removed from the female tubes were tested for differences between months using the Kolmogorov-Smirnov (K-S) test. Since the K-S test only tests for differences between pairs of distributions, this test had to be repeated many times. These tests were not independent from each other and so a Bonferroni correction was applied where $\alpha'=0.05/15$, where 15 was the number of tests performed. The Kolmogorov-Smirnov tests were carried out by hand using the formula for large sample sizes given by Smirnov (1948). Growth rate analysis was carried out for *P. elegans* using the ICLARM software package ELEFAN (Pauly and David, 1981; Gayanilo *et al.*, 1989).

RESULTS

The species abundances in each core for this survey are given in Appendix 2. This appendix gives the numbers of adult *P. elegans* per core for each replicate, together with the numbers of *P. elegans* tubes containing embryos or larvae, the numbers of *P. elegans* new recruits and the numbers of other species. After *P. elegans*, species are listed in the order according to Howson and Picton (1997). This data is also used in the investigation of the micro-scale patterns of *P. elegans* in Chapter 7.

Size distribution of *Pygospio elegans* - The use of 500μm and 212μm sieves throughout the study allowed a more accurate assessment of the population size structure of *P. elegans* than would be obtained by the use of a 500μm sieve alone (Gudmundsson, 1985; Yokoyama, 1990; Morgan, 1997). The use of the smaller mesh size allowed the assessment of the numbers of new recruits as near as possible (given the monthly sampling regime) to their time of settlement rather than after a period of growth. This allowed the timing of settlement to be more accurately determined and gave a more realistic population size distribution (Bachelet, 1990). However, a small error might have arisen in this study due to the relatively long time intervals between sampling intervals. Livingston (1987) provided direct evidence that monthly sampling might obscure the weekly variations in recruitment.

Regression analysis of 1398 *P. elegans* (36.47% of the total sample) indicated that there was a highly significant regression between the width of the 5th setiger and the body length of *P. elegans* ($p<0.01$, Regression Analysis) (Figure 3.1), although the low p value probably resulted from the large sample size. The high r^2 value (0.854, Figure 3.1) however serves to validate the use of the 5th setiger width as a measure of size for *P. elegans*. The following equation can be used to estimate body length:

$$\log_{10}\text{length(mm)} = (1.69 \times \log_{10}\text{width(mm)}) + 1.56 \qquad \text{(Equation 1)}$$

Length and width values were $\log_{10}$-transformed in order to normalise the error term from the model. In the regression analysis there were several outliers, which, although included in this model, were shown to have a negligible effect on the equation since the same regression equation was obtained when the analysis was carried out with the outliers removed. The production of gametes takes place at the expense of somatic growth (Yokoyama, 1990) suggesting that the variability may have been partly caused by individuals undergoing sexual reproduction.

Total setiger number, suggested by Anger *et al.* (1986) to be a better guide to body size for spionids, can be estimated using the equation given by Morgan (1997);

Total setiger number = 9.85 + (93.6 × 5th setiger width (mm)) (Equation 2)

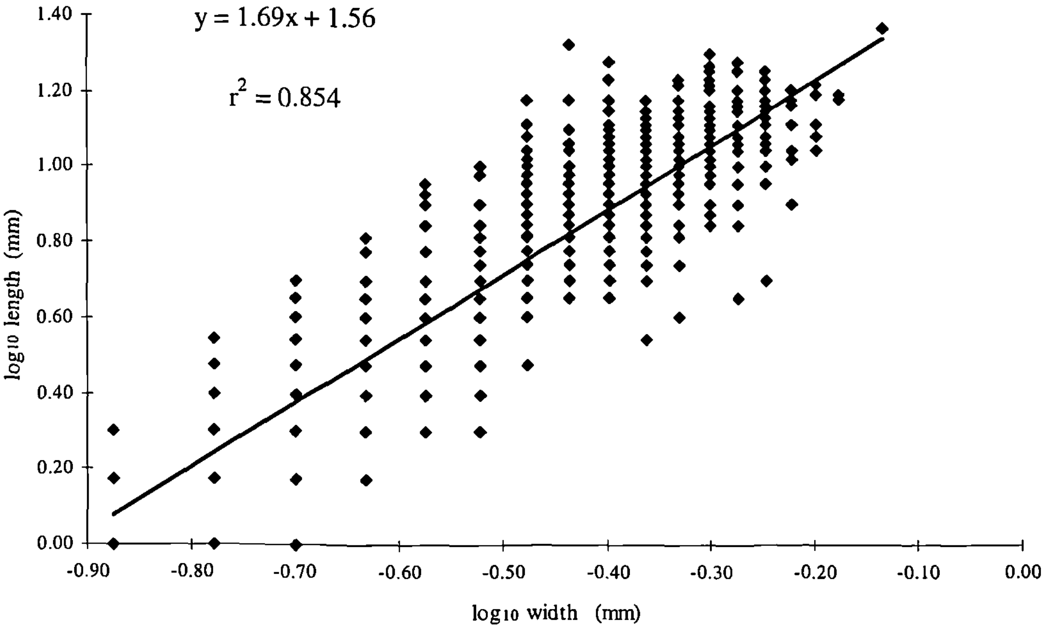


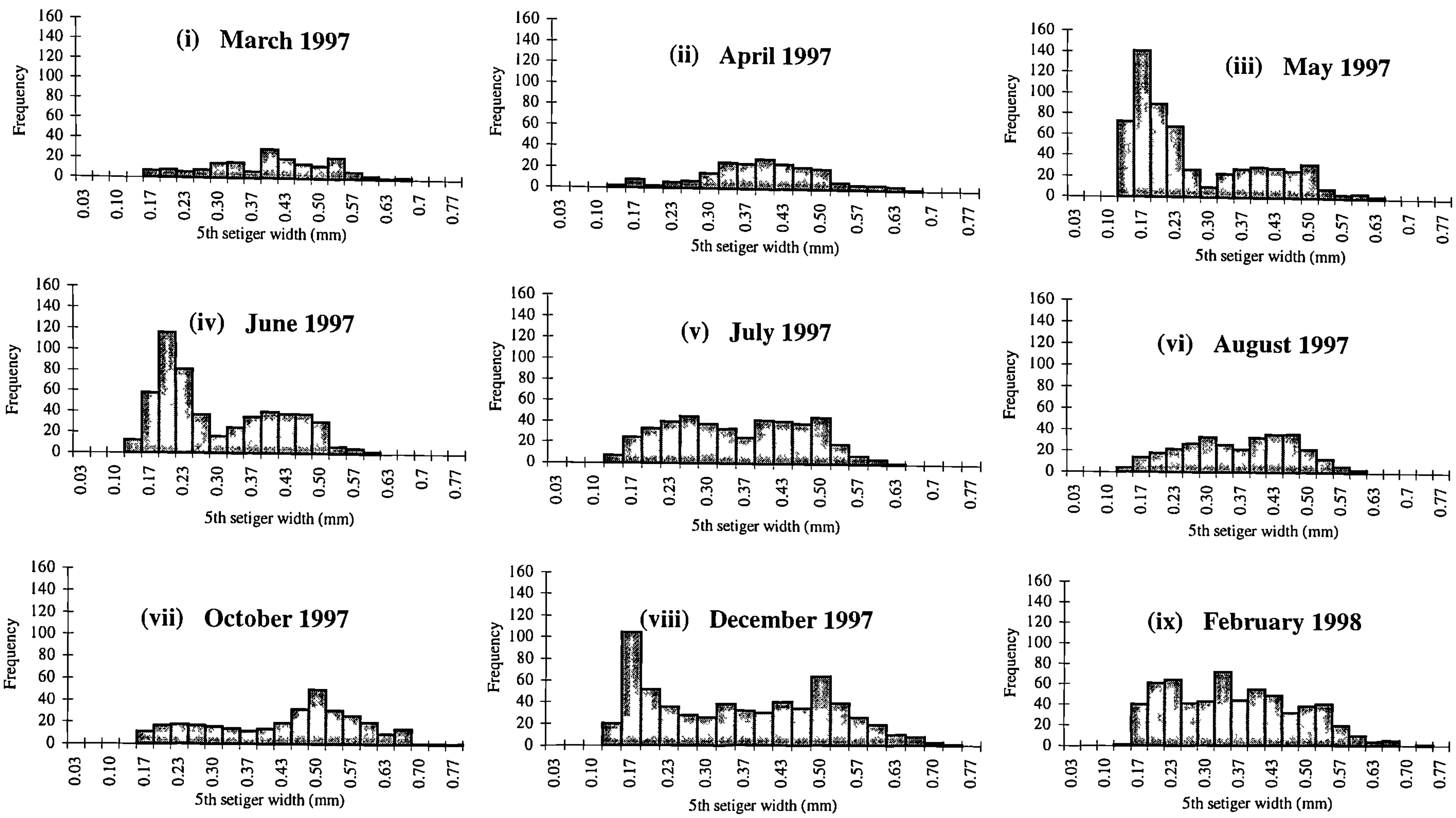
Figure 3.1 : Regression line of 5th setiger width against length for *P. elegans*, n=1398.

The smallest post-planktonic individuals found had 5th setiger widths of 0.13mm (or 22 setigers according to Equation 2 and 18-22 setigers by direct counting of a sample of these individuals, n=25). This agrees with the findings of Hempel (1957) and Rasmussen (1973) who suggested that *P. elegans* may settle from the plankton anywhere between 11-20 setigers.

This study suggested that adult *P. elegans* sexually mature when they reach a 5th setiger width of approximately 0.37mm. This corresponded to the smallest size that branchiae were found on the 2nd setiger of *P. elegans* throughout the sampling period. Since this method only determined the size at which males mature, the assumption made here is that both males and females mature at the same size. This size corresponds to 44 setigers using Equation 2. Several individuals with a 5th setiger width of 0.37mm were randomly selected and their number of segments were found to be approximately 40. This agrees with the results of Gudmundsson (1985) and Morgan (1997) who suggested, based on the size which gametes first appear, that *P. elegans* become sexually mature when they reach 40 setigers. This agreement supports the contention that the relatively simple method of sex determination used in this study is a reliable one.

Figures 3.2(i-ix) displays the *P. elegans* population size distribution throughout the sampling period. New recruits (individuals with a 5th setiger width of 0.13-0.17mm) were present throughout the study period. However, intense recruitment was confined to two relatively short periods, one during April/May and the second during November/December. Only two cohorts could be clearly defined at any one time during the sampling period. This was because newly settled individuals reached the size of the adult population before the next cohort appeared. In March 1997 (Figure 3.2(i)), when the abundance of *P. elegans* was relatively low, the population structure followed an asymmetric distribution, skewed towards adults. In April, the population structure followed a bell-shaped distribution, although the majority of the individuals fell into the adult size categories. In May, there was a sudden increase in new recruits which resulted in a rapid increase in total abundance and a bimodal appearance of the population size distribution. One month later, in June, the population size structure was much the same except the modal size class for the smallest individuals had slightly increased. In July and August (Figures 3.2(v) and (vi) respectively), the structure of the population was still slightly bimodal and it was still possible to distinguish the April/May cohort from the parental population. During October, the April/May cohort became indistinguishable from the parental population. The population structure was distinctly bimodal in December due to another sudden increase in new recruits. Since the modal size class of this cohort approximately corresponded to that of the cohort observed in May (i.e., 0.17mm 5th setiger width) when sampling was monthly, it is likely that these new recruits had settled no more than one month before the sampling date for December (sampling at this time was on alternate months). This caused the marked increase in total abundance between October and December. In February 1998 (Figure 3.2(ix)), abundance was relatively high and the population structure approximated a bell-shaped distribution, although slightly skewed towards juveniles (individuals with a 5th setiger width of 0.33mm or less).

Growth rate analysis using the ELEFAN program did not produce sensible results for the *P. elegans* data obtained in this study. There are several possible reasons for this. Firstly, the growth of only one cohort could be analysed, and secondly, for a dataset which only covered 11 months the time intervals between sampling dates were too long. Additionally, modes have to be clearly discernible for the ELEFAN technique to deliver sensible results. Therefore, the growth rate of *P. elegans* was estimated as the difference in mean size (5th setiger width) of the individuals of identified cohorts between successive samplings, similar to the method used by Mendez *et al.* (1997). It was possible to establish the normal curve for the April/May cohort from May until August, the mean growth rate for this period being 0.14mm 5th setiger width/month, i.e., individuals initially grew in length by 1.31mm/month (from Equation 1) or by 23 setigers/month (Equation 2). This suggests that the large number of individuals settling during April/May 1997 (0.13mm 5th setiger width) would have been capable of reaching sexual maturity (i.e., 0.37mm 5th setiger width) during September of that year and were, therefore, potentially capable of reproducing that year, resulting in the second peak of larval settlement during November/December. Therefore, these results indicate that the population at any one time potentially comprised of individuals from at least 3 generations.



Figures 3.2(i-ix): Size-frequency histograms of *P. elegans* from March 1997 to February 1998 (same vertical scale for all graphs).

Sex ratio of *Pygospio elegans* - Throughout the study period, females were always more abundant than males, resulting in a female-biased sex ratio (Figure 3.3). Numbers of each sex rose fairly steadily during spring to a mean density of 30.0±3.18 females and 25.0±5.2 males per core in May. However, during the summer the abundance of females increased sharply to 60±8.39 per core in July, whilst the abundance of males decreased to a mean density of 11±2.89 per core in August. This produced a sharp increase in the female:male ratio from 1.35±0.33 in May to 6.19±0.48 in October. The mean number of males increased rapidly during winter, to 41.7±2.73 per core, whilst the female density remained relatively constant. In February 1998, the female:male sex ratio was low (1.4:1±0.07), similar to that in March 1997, although the densities of each sex were higher.

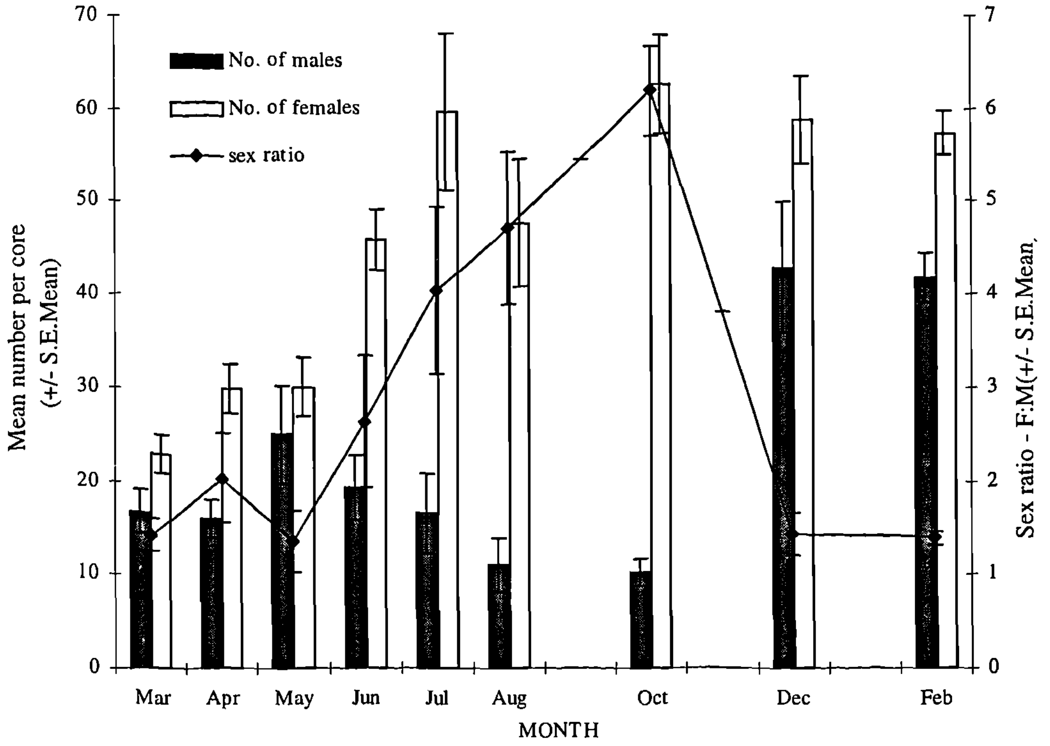


Figure 3.3 : Mean numbers of male and female *P. elegans* (bar graph) and sex ratio (line graph) from March 1997 to February 1998 (± S.E.Mean, n=3).

Reproductive activity of *Pygospio elegans* - Approximately 50% of the sexually mature females sampled between March and June 1997 contained embryos and/or larvae in their tubes (Figure 3.4). Reproductive activity decreased during the summer and by October very few female tubes contained embryos or larvae. However, reproductive activity increased again over the winter months and by February 1998, the majority (81.2±12.5%) of female tubes again contained embryos or larvae. These two increases in the proportions of mature females brooding larvae in their tubes potentially explain the timings of larval recruitment. The high numbers of female tubes containing larvae during the spring (Figure 3.4), approximately 50%, may have been responsible for the cohort observed settling during May (Figure 3.2(iii)). It is not possible to account for the December cohort in this way without sampling during November when a high percentage of tubes containing larvae would have been expected. The high percentage observed during February 1998 would presumably have been responsible for a spring recruitment during 1998.

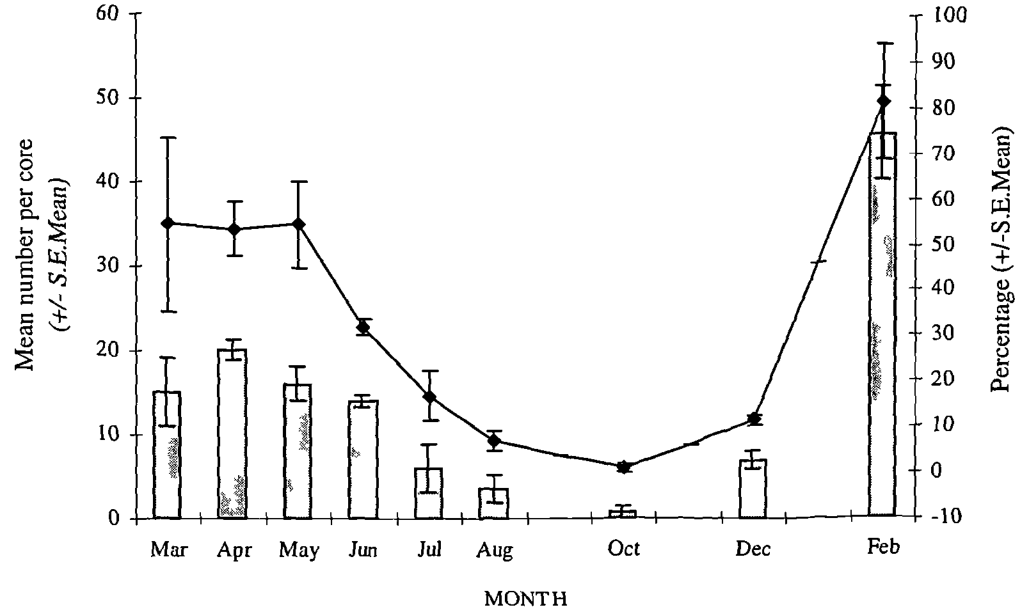


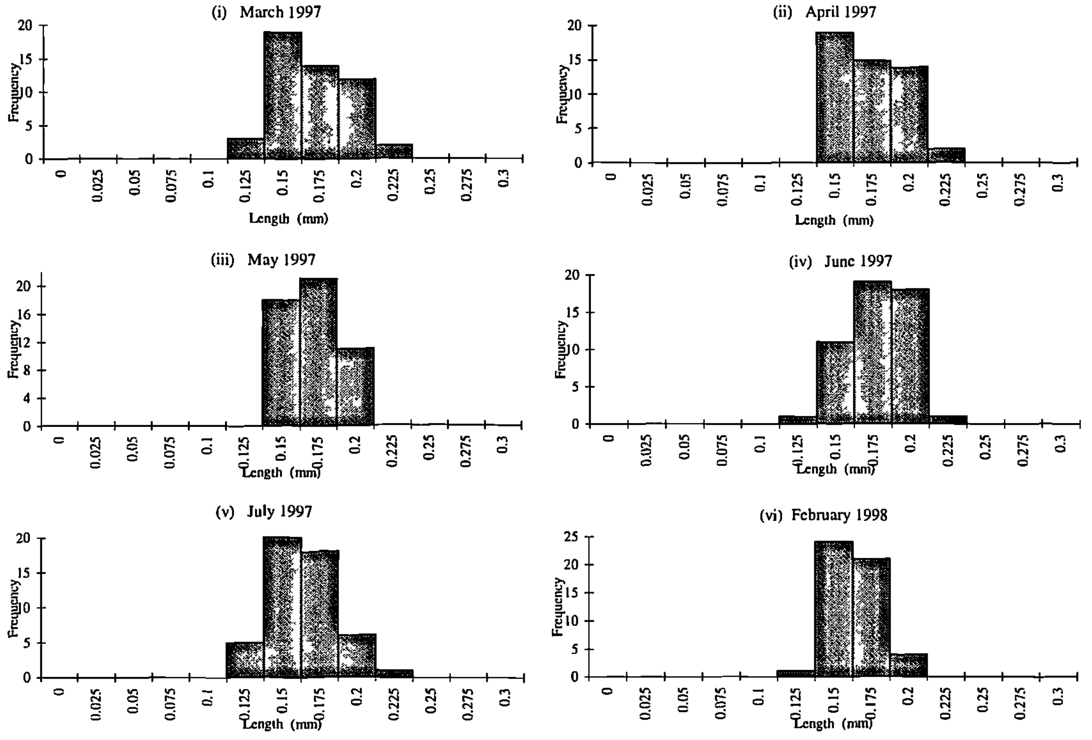
Figure 3.4 : Mean number per core (bar graph) and percentage (line graph) of female tubes containing embryos or larvae from March 1997 to February 1998 (± S.E.mean, n=3).

The larvae found within the female tubes were all of the 3-5 setiger stage and had long natatory bristles. These resembled the *P. elegans* planktonic larvae described by other authors, e.g., Smidt (1951). There is strong evidence to suggest that this larval type was the only type produced by *P. elegans* at Drum Sands within the study period. Measurements of larval body length (Figures 3.5(i-vi)) showed that the majority of the individuals ranged in size from 0.15 to 0.20mm between March to July 1997 and February 1998, with a mean length of 0.17mm, and there were no significant differences in their size distributions between these months (Kolmogorov-Smirnov test with a Bonferroni correction). Furthermore, the maximum lengths of the larvae did not increase during the summer months when some *P. elegans* populations have previously been shown to produce benthic larvae. The mean larval length (0.17mm) was far smaller than the average lengths of benthic larvae (0.65mm) observed emerging from egg capsules in the study by Hannerz (1956). Muus (1967) observed 20 setiger benthic larvae still inside egg capsules, although most tend to hatch at the 12-14 setiger stages (Hannerz, 1956). This is in contrast to the 3-5 setiger larvae continually observed in the parental tubes in this study. Further evidence for the production of planktonic larvae only was the complete absence of 'hunchback larvae' (Thorson, 1946; Rasmussen, 1973). These are 3 setiger larvae distended in shape due to the large amount of yolk ingested. These larvae are destined to hatch at a later stage of development to become benthic larvae.

It is possible that the larvae produced by the *P. elegans* population at Drum Sands would have remained in the plankton for a relatively long period of time since Hannerz (1956) found that the lengths of the larvae found in the plankton ranged between 0.33-0.42mm; the maximum length obtained in this study being noticeably shorter, 0.225mm. However, the results here support the findings of Anger *et al.* (1986) who suggested that the larvae reared by laboratory cultured *P. elegans* hatch anywhere within the size range 250-330μm. There is likely to be some size discrepancy between the results obtained by Hannerz and this study since the larvae measured in this study were taken from within the parental tubes rather than from the plankton, and larval body length, rather than actual length (including natatory bristles) was measured. The significant differences between the sizes perhaps suggest that the

P. elegans larvae at Drum Sands have a prolonged planktonic larval phase compared to those reported by Hannerz (1956).

Larval measurements for the August, September and December samples were not taken due to the small number of females brooding larvae. However, observations suggested that the larvae present were also of the 3 to 5 setiger stage and resembled those previously described.



Figures 3.5(i-vi) : Size-frequency histograms of *P. elegans* larvae from adult female tubes between March to July 1997 and February 1998 (n=50 for each month). No significant differences between size distributions for any month were observed (Kolmogorov-Smirnov test with Bonferroni correction)

DISCUSSION

The aim of this study was specifically to investigate the population structure and reproductive biology of *P. elegans* on Drum Sands, Firth of Forth, and to elucidate the significance of these factors for population maintenance and the generation of the spatial patterns exhibited by *P. elegans* on this sandflat.

Population structure and reproduction of *Pygospio elegans* at Drum Sands.

This study has indicated that *P. elegans* on Drum Sands has adopted a planktonic mode of reproduction. No evidence of asexual reproduction and/or the production of benthic larvae was found between March 1997 and February 1998 for this population. At peak periods of larval development, approximately 50% of the adult female tubes contained embryos and/or larvae during the spring of 1997, although the following year, during February 1998, this reached 80% of the adult female population. Larvae were released at the 3-5 setiger stage into the water column. Settlement occurred during two main recruitment phases: the first, and numerically the most significant occurred during April/May 1997 while the second occurred during November/December 1997. Larvae settled at a size of approximately 0.13-0.17mm 5th setiger width, or 20 setigers, and grew rapidly (around 23 setigers/month) reaching sexual maturation size within 3 months after settlement. The adult population always consisted of a greater proportion of females than males, especially during the summer when the female:male ratio reached 6.19±0.48. Sampling was carried out from high density patches only and it is assumed that the same reproductive strategy and population structure occurred in lower density areas, although sampling in these areas would have been necessary to confirm this.

Since *P. elegans* has been shown to exhibit very different reproductive strategies in different localities, it is not possible to predict the reproductive biology of a particular population. This point was addressed by Levin (1984b) who stated 'we should not assume that life history traits reported in the literature for a particular population will necessarily be accurate for different populations'. Consequently, assessing the timing and method of reproduction and the mode of larval development were prerequisites for the study of the processes affecting the spatial distribution of the *P. elegans* population at Drum Sands.

Pygospio elegans showed great seasonal changes in both the female to male ratio and sexual activity on Drum Sands. The proportion of female tubes containing embryos or larvae decreased during the summer, possibly as a result of limited sexual reproduction due to the decreased abundance of mature males. When the abundance of ripe males increased during the winter there was a marked increase in reproductive activity. This suggests that sexual reproduction was probably the primary method of propagation at Drum Sands, which is in agreement with previous studies elsewhere (Thorson, 1946; Smidt, 1951; Rasmussen, 1973; Anger, 1984). It is likely that the majority of the adult males at Drum Sands began to show sex reversal in May after the main breeding season as a result of a slight increase in water temperature. Sex reversal continues during the summer, resulting in a high female : male ratio (Rasmussen, 1973). In late autumn the immature individuals develop into sexually mature males and females according to their original sex, probably due to a decrease in water temperature (Rasmussen, 1973). This corresponded to the sudden increase in the number of males sampled in the population at Drum Sands and the consequent decrease in the female : male sex ratio. This was also observed in the study by Wilson (1985) who found that during November the males, which were indistinguishable from the females during the summer, developed secondary sexual structures and became ripe. Since sexual reproduction was the primary method of propogation with the population at Drum Sands, the availability of males, and the spatial distribution of males relative to the females, were likely to be major factors governing the reproductive output of the population as a whole.

Anger (1984) suggested that *P. elegans* was unique among spionids in being able to reproduce at the low temperatures encountered during the winters at high latitudes. The presence of juvenile worms, i.e., those <0.37mm 5th setiger width, during the entire period of this study and the presence of females brooding larvae in egg capsules in most months indicated that this species was capable of reproducing throughout the whole year. However, recruitment was mostly limited to two main periods. Continual larval recruitment with 1 or 2 acute increases has been reported in other spionid polychaetes e.g., *Paraprionospio* sp. (form A)(Yokoyama, 1990); *Polydora ciliata* (Hannerz, 1956; Dorsett, 1961) as well as in *P. elegans* (Anger, 1984; Gudmundsson, 1985; Morgan, 1997). These observations support the fact that the acute *P. elegans* recruitment phases on Drum Sands were seasonal events rather than responses to non-seasonally related events.

The timing and duration of recruitment phases have been shown to vary for different *P. elegans* populations. The adult population studied by Gudmundsson (1985) at Cullercoats, North Sea coast of England, were 100% sexually mature during December and eggs were laid into egg capsules from December to March with hatching occurring from February to April. A second population studied at the nearby Blyth Estuary showed a similar reproductive timing, although lagging 1 month behind the Cullercoats population (Gudmundsson, 1985). Rasmussen (1973) studied *P. elegans* populations at Horsen's Fjord and Isefjord. The former population reached sexual maturity during September, egg-laying occurred between September and March with larval hatching from November to April. At Isefjord, a shorter reproductive season was reported with egg-laying not taking place until January and eventuating in April with larvae hatching between February and May. Muus (1967) found that the female *P. elegans* population in the brackish Kysing Fjord had eggs/larvae in their tubes during only April and May, while Hempel (1957) found that a North Sea population off the German coast had a more prolonged spawning season, from February to September.

The differences observed between Kysing Fjord (Muus, 1967) and North Sea populations (Hempel, 1957) were suggested to have been due to differences in salinity between the two locations (Muus, 1967). This is supported by the more-or-less continual recruitment at Drum Sands where the salinity is typically marine with only a small freshwater input from the River Almond. Additionally, from her observations, Anger (1984) suggested that reproduction may occur throughout the year in the Baltic and North Seas, with spring and autumn being the most likely seasons in which production of offspring mainly takes place. Brey (1991) suggested that a mild winter led to a prolonged recruitment phase and Muus (1967) stated that higher densities of *P. elegans* in the Kysing Fjord occurred as a result of the mild winters of 1956/57. Therefore, it appears that temperature and salinities are the two main factors determining the periods of larval recruitment for *P. elegans*.

Previous studies have produced similar results concerning the growth rate of *P. elegans*. Smidt (1951) proposed that new recruits grew rapidly and reached sexual maturity within a few months and Gudmundsson (1985) suggested that the *P. elegans* population at Cullercoats reached sexual maturity and bred at the end of their first year. These results were supported by Anger *et al.* (1986). They found that for *P. elegans* grown in the laboratory, the minimum time from metamorphosis to the first hatching of offspring larvae (3 setiger stage) was 81 days and suggested that each individual could produce 2 generations per year. These findings were supported by the growth rate calculated from the mean sizes of the cohort settling during April/May at Drum Sands which suggested that these individuals reached sexual maturity during September, a period of less than 90 days.

New recruits in this study were classed as being 18-22 setigers. This is slightly larger than the size quoted by other authors e.g., 11 setigers (Rasmussen, 1973) and 12-14 setigers (Hannerz, 1956), although it approximately corresponds to the size given by Hempel (1957), i.e., 17-20 setigers. Since sampling was carried out monthly in the present study, significant growth after settlement may have occurred before sampling in May. This may explain why the new recruits reported at Drum Sands were larger than observed in other areas. Although metamorphosis is not clearly defined in most spionid polychaetes (Anger *et al.*, 1986), most authors agree that it occurs when the individuals are approximately 14-17 setigers (Hannerz, 1956; Hempel, 1957), i.e., at or shortly after settlement. Therefore, the new recruits sampled during May 1997 in the present study were probably post-metamorphic, young juveniles.

Rasmussen (1953), Gudmundsson (1985) and Wilson (1985) observed asexual reproduction in *P. elegans* and Hobson and Green (1968) proposed that this species reproduced almost exclusively by this method of propagation in Barnstable Harbor, Massachusetts. Asexual reproduction in *P. elegans* occurs by fragmentation into numerous pieces at any part of the worm's body (Rasmussen, 1953). The fragments then remain in the parental tube for about eight days until each piece has developed into a new individual. It is unlikely that this occurred at Drum Sands as a maximum of only 2.03% of the population sampled showed signs of regeneration following fragmentation at any one time. It is more likely that this apparent fragmentation of *P. elegans* individuals observed at Drum Sands resulted from predation (Muus, 1967) rather than as a reproductive strategy. This is supported by the fact that those seen regenerating in this study were in the process of growing new anterior regions only. If asexual reproduction had been occurring, individuals growing new posterior regions, as well as individuals present in all stages of regeneration, would have been observed.

Implications of planktotrophic larval development for the population maintenance and spatial distribution of *P. elegans* on Drum Sands.

In view of the relatively high densities and the spatial pattern (Chapter 2) exhibited by *P. elegans* at Drum Sands, it was expected that the species reproduced with the production of benthic larvae and/or asexual proliferation, at least at certain times of the year. This would have helped to explain the high local densities and its patchy distribution. However, this study has revealed that the population here, in contrast to what was initially thought, reproduced entirely by the production of planktotrophic, pelagic larvae.

Studies on *P. elegans* and other spionids have suggested that differences in reproductive mode are not due to adaptations to suit its environment, as shown for other polychaetes, but to non-poecilogonous behaviour and genetic divergence between populations (Anger, 1984; Levin and Creed, 1986; Hoagland and Robertson, 1988; Chia *et al.*, 1996). For example, Anger (1984) conducted laboratory studies of seasonal reproduction in *P. elegans* and found that temperature and salinity changes did not trigger shifts to or from planktotrophy, lecithotrophy or asexual reproduction. Furthermore, Levin (1984a) stated that studies on many species have never shown a single female to produce more than one larval type, and many apparently poecilogonous polychaetes have actually been sibling species. This implies therefore, that the *P. elegans* population at Drum Sands has explicitly evolved this method of reproduction and is possibly not capable of producing other larval types or reproducing asexually. The spatial pattern exhibited by *P. elegans* at Drum Sands (Chapter 2) has therefore been established by processes acting on planktotrophic larvae and/or on post-metamorphic individuals. Some of these processes will be addressed in Chapters 4-8.

The sole reliance on a planktonic mode of recruitment has implications for not only the smaller scale (metres) heterogeneity of this species on Drum Sands (Chapter 2) but also for the larger-scale maintenance of high population densities on Drum Sands in view of very high losses of planktonic larvae (Thorson, 1950; Mileikovsky, 1971; Vance, 1973; Bachelet, 1990). Morgan (1997) suggested that for the *P. elegans* population in the Baie De Somme, population maintenance was facilitated by the larval retentative properties of the bay. Active migration in the water column, which could enable a species to take advantage of directional water flows, has not been shown for polychaete larvae and therefore passive retentive mechanisms must be responsible for population maintenance in some areas (Morgan, 1997). The differences in passive larval retention between bays and the open coast was investigated by Gaines and Bertness (1992). They found that during periods of long flushing times, recruitment of barnacles within Naragansett Bay, Rhode Island, was significantly higher than recruitment to nearby coastal sites, while during periods of short flushing times, this difference was not observed. Tidally-induced retainment of spionid larvae have been shown in many bays and estuaries (see Morgan, 1997). Therefore, it is possible for passively dispersing larvae to be retained within their bay or estuary of origin by the hydrodynamic characteristics of the area and thus the possibility of population maintenance by a dispersive mode of reproduction is increased.

There is evidence to suggest that the planktonic larvae of the *P. elegans* population on Drum Sands may be retained within the area to a certain extent. Dyke (1987) proposed that within the Firth of Forth, tidal residuals are small and that total residuals are more due to wind than the tide. Craig (1972) indicated that the residence time for seawater within the area was about 8 months. This suggests that the flushing time within the Firth of Forth is relatively long and, therefore, larval retention is likely to be high. Furthermore, Covill (1972, 1975) found that bays or indented coastlines along the southern Firth of Forth produced eddy currents which tended to distort the general tidal flow pattern of the Firth of Forth and that this effect was exacerbated by freshwater flows from rivers (Covill, 1972). The indented shape of Drum Sands, together with the added effect of the River Almond, suggests that eddy currents probably exist around Drum Sands which may help retain *P. elegans* larvae. Furthermore, since the largest *P. elegans* populations within the Forth are found within the less saline Forth Estuary (SEPA, pers. comm.), planktonic larvae produced by them are likely to pass Drum Sands since this water passes along the south shore of the Forth (Dyke, 1987). This could be another potential input of larvae for the Drum Sands population. However, the mode of reproduction of *P. elegans* within the less saline Forth Estuary has not been studied.

The importance of pelagic larvae for shaping community structure has been discussed by Lewin (1986). He suggested that previous models of marine benthic community structuring, *sensu* Paine and Connell, have overlooked the importance of the larval fluxes since these models were based on experiments carried out where larval influxes were saturating. In areas where larval settlement is saturating, evidence suggests that communities are shaped by post-settlement processes such as predation and competition. In areas where larval recruitment is not saturated however, larval-supply fluctuations become more important in shaping demographic processes (Lewin, 1986; Bachelet, 1990). Therefore, it is possible that the *P. elegans* population at Drum Sands is structured by fluxes in larval settlement and the processes which effect it, rather than processes acting on the adult population. Consequently, the effect of larval recruitment on population density changes is specifically addressed in this study in response to a number processes including macroalgal mat establishment (Chapters 4 and 5), small-scale disturbances (Chapter 6) and the generation of micro-scale spatial heterogeneity due to adult-juvenile interactions (Chapter 7). However, further studies have to be carried out in order to assess whether *P. elegans* larval recruitment is indeed saturated or not on this sandflat.

Since the life history of a species governs that species' dispersal dynamics and recruitment in a particular environment, Levin (1984a) suggested that it determined the scale of disturbance a species was potentially capable of exploiting. She noted that polychaetes with small adult size, brood protection, small brood size and reduced larval phases (e.g., *Capitella* spp., *Streblospio benedicti*) were adapted to small-scale disturbances such as those caused by ray foraging and human pit-digging, while polychaetes with larger brood sizes and longer-lived larvae, whose planktonic abundance are highly seasonal, were adapted to large-scale disturbances such as those caused by a severe storm. This study has demonstrated that the *P. elegans* population on Drum Sands possesses the latter reproductive strategy. Levin (1984a) suggested that species adapted to large-scale disturbances were able to successfully colonise and dominate in areas where the timing of the disturbance coincided with periods of peak larval availability. The two peak periods of larval settlement at Drum Sands occurred during May and December coinciding with the most probable timings of macroalgal mat formation, and sediment movement by storms, respectively. If *P. elegans* larvae settle and metamorphose more successfully than other species in areas where these types of disturbances occur, then weed mat development and sediment movement are perhaps positive structuring forces in population maintenance. The effects of both artificially-implanted and natural weed mats on adult densities and larval recruitment, and colonisation of disturbed areas are discussed in Chapters 4, 5 and 6 respectively.

With the absence of both asexual reproduction and the production of benthic larvae, maintenance of *P. elegans's* spatial heterogeneity described in Chapter 2 must have involved either increased larval recruitment or adult migration to established high-density patches, or increased juvenile survival within them. Larval recruitment to patch and non-patch azoic and ambient sediments are compared in Chapters 6 and 8 respectively. In Chapter 6, the extent to which adult migration may have been influential in patch maintenance is also discussed.

This study has indicated that *P. elegans* on Drum Sands exclusively relied upon sexual reproduction for population maintenance. Schlotzer-Schrehardt (1987; 1991) suggested that *P. elegans* was the only reported spionid species in which direct spermatophore transfer is used during sexual reproduction. While other species indirectly transfer their free-floating spermatophores, a special pattern of reproductive behaviour including active seeking of the females tubes by the males is needed for spermatophore transfer. This has implications for both the population's reproductive potential and the micro-scale patterns of *P. elegans*. The latter will be addressed in Chapter 7.

This study has shown that, using relatively simple methods of sex determination, sexual activity and size measurements, a good understanding of the reproductive mode of development and population structure can be gained for a common intertidal polychaete. The results have shown that an understanding of both the mode and timing of reproduction can help elucidate which processes potentially structure a population and hence is an important prerequisite in an investigation into the factors affecting a species spatial (and perhaps temporal) distribution.

CHAPTER 4

THE EFFECTS OF MACROALGAL COVER ON THE SPATIAL DISTRIBUTION OF MACROBENTHIC INVERTEBRATES : AN EXPERIMENTAL STUDY

INTRODUCTION

Excessive growth of green macroalgae in response to nutrient inputs is a common phenomenon in marine estuaries and sheltered bays. In temperate regions, the growth of mat-forming algae occurs mainly in the spring and is capable of persisting at high maintained densities throughout the summer before disappearing in the late autumn (Hull, 1987). The effects of such growth of macroalgae on the benthic environment have been well documented (Perkins and Abbott, 1972; Fahy *et al.*, 1975; Wharfe, 1977; Nicholls *et al.*, 1981; Soulsby *et al.*, 1982, 1985; Reise, 1983a, 1985; Tubbs and Tubbs, 1983; Thrush, 1986a; Hull, 1987, 1988; Olafsson, 1988; Sundback *et al.*, 1990; Everett, 1991, 1994; Raffaelli *et al.*, 1991; Bonsdorff, 1992; Raffaelli *et al.*, 1999). Generally, macroalgal mats, usually of the genera *Enteromorpha, Cladophora, Chaetomorpha* or *Ulva* cause the underlying sediments to become more reducing, often leading to anoxia and the accumulation of toxic hydrogen sulphide (Wharfe, 1977; Reise, 1985). These chemical and physico-chemical changes within the sediments cause a general decline in species richness (Reise, 1985; Raffaelli *et al.*, 1991) and an increase in opportunistic species (Thrush, 1986a) similar to the changes occurring in areas of high organic loading (Pearson and Rosenberg, 1978). The resulting changes in infaunal invertebrates have an indirect effect on the numbers of predators, notably wading birds (Fahy *et al.*, 1975; Nicholls *et al.*, 1981; Soulsby *et al.*, 1982; Tubbs and Tubbs, 1983) and fish (Perkins and Abbott, 1972) that these areas are able to support.

The causes of increased growth of macroalgae on the sediment surface of many estuaries and sheltered bays have attracted considerable concern, mainly as a consequence of the detrimental effects of algae on the health, amenity, economy and general ecology of affected areas. However, understanding the causes of macroalgal blooms is complicated as they are the result of the interaction of many factors. An increase in the availability of nutrients such as nitrogen or phosphorus or changes in the hydrography of the area are thought to be the most influential factors (Raffaelli *et al.*, 1999). Even when these suitable conditions are present, macroalgal mat formation on more exposed intertidal sandflats has been shown to be facilitated by the invertebrate species present. Reise (1983a, 1985), for example, has shown that the thalli of green algae can become anchored by the feeding funnels of the lugworm *Arenicola marina*. Once a feeding funnel is clogged by algae, the lugworm builds a new funnel which again may serve to anchor more algae. He suggested that weed mats would not have been able to become established on the sandflats of the island of Sylt, North Sea, if it were not for the presence of the lugworm. Similarly, the importance of tube-building polychaetes and shell fragments in the establishment of macroalgal mats have been noted by Woodin (1977), Everett (1991) and Schories and Reise (1993).

Generalisations concerning the effects of weed mats upon soft-sediment invertebrate assemblages are very difficult and their effects still remain unclear (Everett, 1994). Differences in the nature of the environment, the genera of the algal species, whether the algae is attached or floating and differences in the weed biomass all have different effects upon the fauna (Raffaelli *et al.*, 1999). This makes direct comparisons between studies very difficult. Previous studies investigating the effects of weed mats on the sediments and associated fauna have been either descriptive surveys (e.g., Perkins and Abbott, 1972; Fahy *et al.*, 1975) or controlled, manipulated experiments (e.g., Woodin, 1977; Reise, 1983a; Hull, 1987, 1988; Everett, 1994; Cha, in prep.). Surveys have involved comparing the invertebrate communities of areas where algal mats are present to those where they are absent, usually in another part of the same estuary or sandflat (e.g., Nicholls *et al.*, 1981). However, Lowthian *et al.* (1985) suggested that the presence of algal mats may be influenced by factors other than nutrient availability and that these factors may affect the infaunal communities independent to the effects of the weed. Consequently, because of their large-scale separation, weed-affected and weed-free areas which have been used in observational studies may have been completely different environments and, therefore, not comparable.

Controlled, experimental manipulations are much more objective and less equivocal ways of investigating the effects of weed mats on the sediments and their fauna. Unfortunately, of the few experiments previously carried out, Everett (1991) suggested that the interpretation of the results is often difficult due to the lack of experimental controls (Olafsson, 1988) or lack of replication (Reise, 1983a). Such experiments have been carried out either by implanting weed into the sediments of areas where weed mats are not present (e.g., Thrush 1986a; Hull, 1987) or by removing algae from the sediments within algal-affected areas (e.g., Reise, 1985; Everett, 1991). These two approaches have been shown to produce similar results (Raffaelli *et al.*, 1999). The algal-removal method, however, makes two assumptions. Firstly, it assumes that the physical removal of weed has no effect on the sediment and its fauna, and secondly, that the effect of the weed upon hydrodynamics is very localised, i.e., algal-free plots are not affected by the surrounding weed. The latter may be an unreasonable assumption for weed species which form long strands such as *Enteromorpha* spp.. However, an experimental approach overcomes the inherent problem of surveys (i.e., the large-scale separation of weed-affected and weed-free areas) and allows variables known to affect the sediment and its invertebate fauna, e.g., weed species, biomass, weed-mat size and the timing of weed establishment, to be controlled. Furthermore, treatments can be fully interspersed (Krebs, 1989).

During the summer of 1996, part of the present study area within Drum Sands (Figure 4.1) was covered with weed mats. The weed (mainly *Vaucheria subsimplex*, with some *Enteromorpha prolifera*) occurred in patches, covering approximately 30-40% of the total sediments and 100% within patches. Unfortunately, Drum Sands is not regularly monitored and therefore it is not known whether this was an annual occurrence.

In order to investigate the faunal effects of these weed mats within this area of Drum Sands, a controlled weed-implantation experiment was conducted during the summer of 1997. It has been shown (see Chapter 3) that the life-history and the reproductive mode of development exhibited by *P. elegans* on Drum Sands made this species particularly suited to increase in numbers following a large-scale disturbance, particularly during early summer and mid-winter. Algal-mat formation is potentially an important large-scale disturbance at Drum Sands and, therefore, it was interesting to test the hypothesis that weed mats play an important role in structuring species distributions on Drum Sands, *P. elegans* in particular. The patchy nature of weed mat formation suggested that it could have been a potentially important structuring force in the production of the mosaic of communities revealed in Chapter 2. Therefore, this study specifically aimed at investigating the ecological effects of macroalgal mats on intertidal sandflats and whether such mats potentially played a role in *P. elegans* patch formation on Drum Sands.

METHODS

Study site - The exact position of the field experiment within the study area is shown in Figure 4.1. The sediments there were moderately sorted with median particle size of 2.6ϕ (Chapter 2) and with no obvious environmental gradient (pers. obs.). The sediment surface in the selected area was well oxidised and had no macroalgal cover during the summer of 1996. This was an important consideration for the maintenance of controls. For example, weed mat establishment within this area during the experiment would have resulted in a lack of proper controls.

Experimental design - Six experimental blocks were set out in a line perpendicular to the direction of the flood tide (Figure 4.2). The use of 6 replicates allowed non-parametric statistical analyses, if necessary, while greater replication was limited by the practical work involved. Within each block, three plots (each of $1m^2$) were marked out (Figure 4.2). These plots were 0.5m apart from each other and at least 1.5m away from those of neighbouring blocks. Since *P. elegans* patches were just above $1m^2$ in area, this design ensured that replicates would be independent since their separation was larger than the average *P. elegans* patch size. The plots were randomly assigned as unmanipulated control, net plot or weed treatment plot (see later) within each block. The size of the plots were as large as practically possible: maximising the number of replicates was considered to be more important than increasing the size of the plots. The spatial arrangement of experimental plots, therefore, corresponded to a randomised block design. This design is excellent for field experiments in which the distributions of the organisms are unknown since it automatically produces an interspersion of treatments and reduces the effect of chance events on the results of the experiment (Krebs, 1989). Furthermore, Zar (1984) suggested that the blocking enables more of the variability among the data to be accounted for, with the desirable outcome of a smaller mean square and greater statistical power.

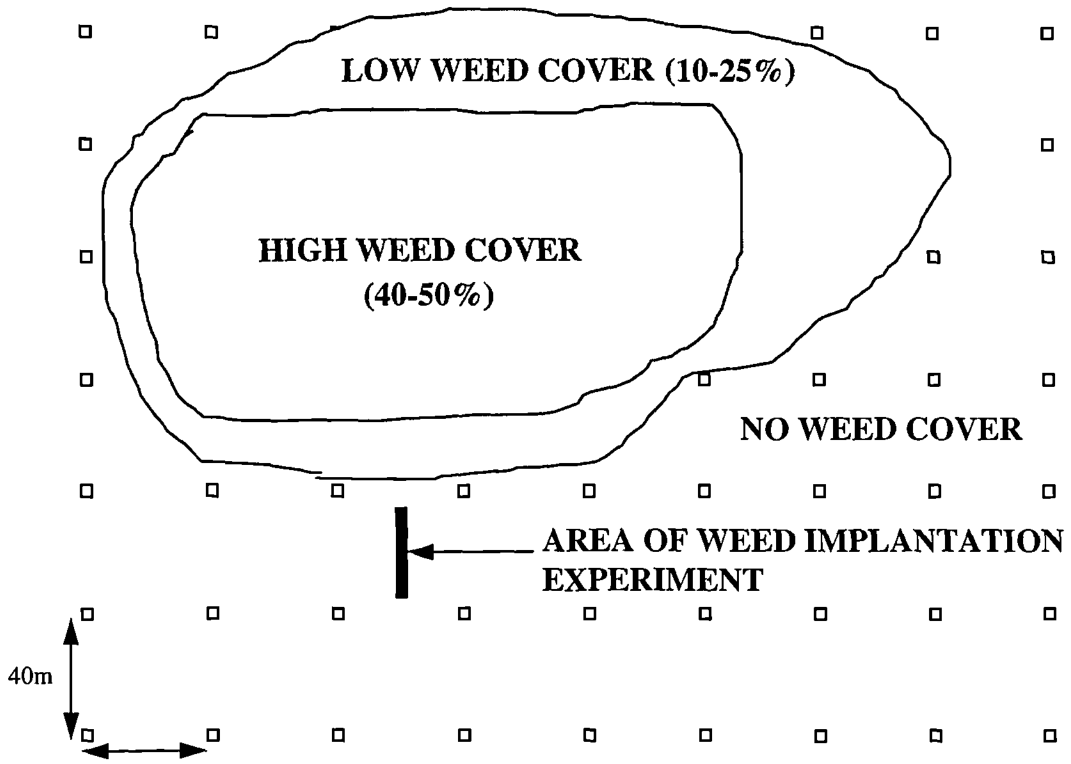


Figure 4.1 : Diagram showing the location of the experimental blocks and the extent of natural weed mat establishment during the summer 1996. 40m intervals shows sample sites from 40m survey (see Chapter 2).

Algae for the experiment were collected from Dalgety Bay, on the north coast of the Firth of Forth, approximately 3 miles (straight line distance) from Drum Sands. The algae (*Enteromorpha prolifera*) were washed thoroughly in seawater on collection to remove associated fauna. The algae were later examined for fauna, very few invertebrates remained and only *Hydrobia ulvae* remained in sufficiently high numbers (more than 1 individual per 1kg wet biomass of weed) to necessitate omitting this species from later analysis. Since *H. ulvae* were not very abundant, it was assumed that any between treatment differences observed were not due to differences in *H. ulvae* densities.

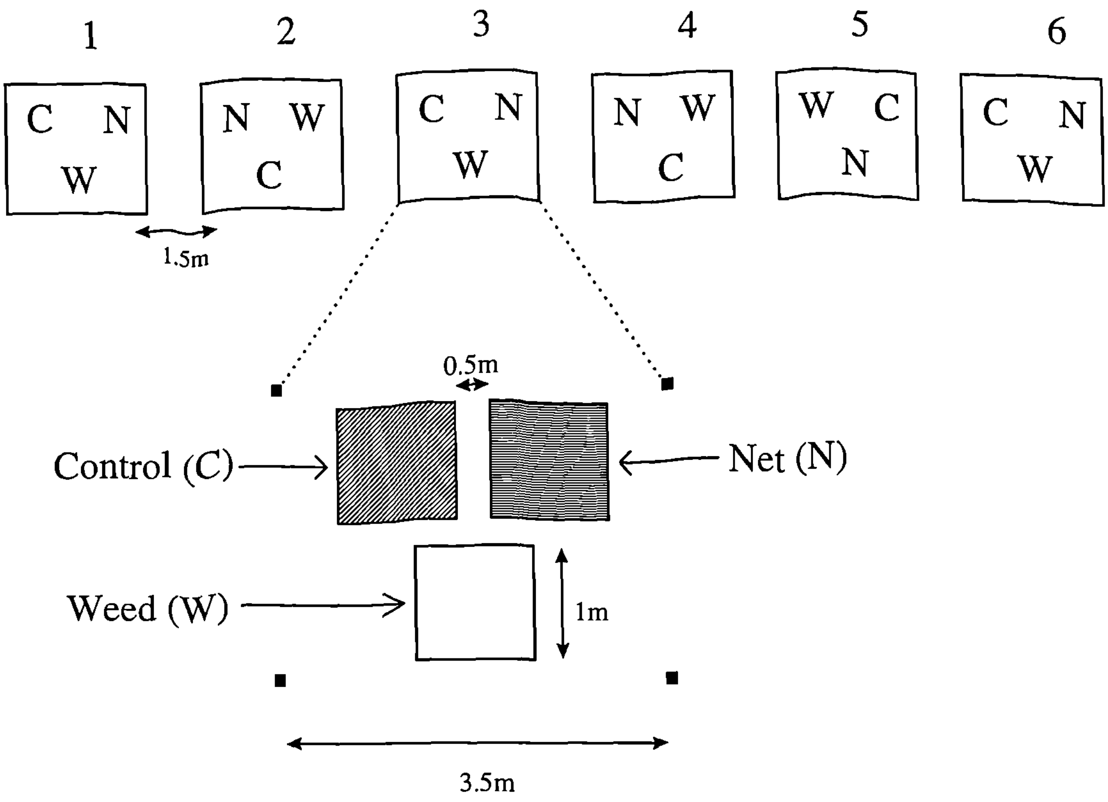


Figure 4.2 : Experimental layout of weed implantation experiment showing positions of the three treatments; unmanipulated control (C), net plot (N) and weed treatment plot (W) within blocks 1-6. Block 3 has been expanded to show layout of plots in more detail.

On June 1st, 1997, sediment and faunal samples were taken, together with redox potential measurements from each plot to represent the initial values at the start of the experiment. The fauna was sampled by taking 3 cores (each 6x6cm in area, 10cm depth), located within each plot by random numbers, sieved on a 500μm mesh sieve and preserved using 10% neutralised, saline formaldehyde solution with 0.01% Rose Bengal. The three cores were pooled to prevent pseudoreplication (Hurlbert, 1984). The preserved samples were later washed with freshwater, sorted with the aid of a magnifying lens, and the organisms identified to the lowest possible taxonomic level. *P. elegans* individuals were then stored in 70% ethyl alcohol for size measurements.

The sediment samples were taken by 3 randomly located cores (2.4cm internal diameter, 3cm depth). The 3 cores were pooled to avoid pseudoreplication. The samples were later frozen at -20°C for storage. Later in the experiment, weed was removed from the sediment surface before these cores were inserted to ensure that differences in organic content were not due to above surface weed. Water and organic contents and particle size distributions were analysed in the same way as described in Chapter 2.

Redox potential values were taken to characterise the physico-chemical conditions within the sediments. The redox measurements were taken at 5 depths; 1, 2, 4, 6 and 8cm. The redox potentials were taken after 60 seconds of the probe being inserted or before if the reading had stabilised (Pearson and Stanley, 1979). The redox meter, supplied by Russel Ltd., model RL100, had previously been calibrated with Zobell's solution to 228mV (Zobell, 1946). One redox profile was taken within each plot, the redox probe being washed with distilled water between each plot.

Hull (1987) found that the effects of macroalgal mats on benthic species was biomass dependent. Since no information was available on the algal biomass of the weed mats establishing on Drum Sands (i.e., no weed samples were taken for biomass determination during 1996), the 'medium' weed density used by Hull was considered appropriate, i.e., 1kg FW/m^2. Three kilograms fresh weight of algae were added to each weed plot and covered with plastic mesh (5cm mesh size). The weed biomass initially used was much more than 1kg/FWm^2 since preliminary experiments had shown that a significant proportion (30-40%) is lost soon after implantation on Drum Sands. The algae were then threaded up through the mesh so they could drift in the water. Net plots were included in the experiment to determine whether there were any artefacts associated with the mesh. These consisted of 1m^2 of plastic mesh without the addition of algae. The weed plots soon accumulated 5-6 cm of sediment within just 3 days. The weed plots were examined after 2 weeks and more weed added in areas where the weed had not properly established.

After 6 weeks, the plots were sampled for faunal and sediment analyses and redox measurements were taken as described above. These measurements were aimed at investigating the short-term effects of macroalgal cover, i.e. the effects of the weed at the established density. Redox measurements were also taken after 12 weeks. At the start of October (after 20 weeks) the weed started to disappear and faunal and sediment sampling, together with redox potential measurements, were repeated. At the end of the experiment, only 6% of each plot had been sampled and the precise core positions had been noted so that nowhere was repeatedly sampled.

The weed biomass was determined twice during the experiment, after 6 weeks (maintained density) and 20 weeks (during decay). This was done by inserting a 6×6cm corer randomly positioned into each weed treatment plot. The weed lying on the top of the sediment surface was collected and preserved in 10% saline formaldehyde solution. The weed was later washed in water to remove any fauna or sand grains then dried at 80°C for 24 hours and weighed (Everett, 1991). At low tide, the sediment was consistently more than 90% covered by the algae until it started disappearing in early October. The net plots noticeably collected some sediment and the nets became partially covered. Since the sediment is mobile at Drum Sands, it is likely that this could have been natural sediment movement and not due to the presence of the plastic mesh. Very small amounts of unanchored weed were present within the net plots after two weeks which were almost certainly drift fragments which had been deposited by the receding tide. These remained only loosely attached to the plastic mesh rather than establishing themselves within the sediments.

The 5th setiger widths of the *P. elegans* were measured directly using the same technique as in Chapter 3. Size measurements were carried out on the individuals from the weed treatment and the control plots only since there were no significant differences in their numbers between the weed treatment and net plots (see Results). Therefore, it was concluded that there were no artefacts associated with the plastic mesh and any differences in the size-frequency distributions between the weed treatments and the control plots were due to the weed alone. All individuals within these plots which were complete to at least their 10th setiger were measured.

Data analyses - Only those species with a mean abundance of more than one individual per core for any one treatment were included for analyses. The data were checked for normality using the Anderson-Darling test and for homogeneity of variance using the Bartlett test. Data not meeting these criteria were transformed using an appropriate transformation (see Zar, 1984) and again checked for normality and homoscedasticity. One-way ANOVAs were then carried out together with a Tukey test if significant. Weed effects were assessed by comparisons of weed treatment plots with net plots. Although these could have been performed by Two-sample t-tests, ANOVA tests together with a Tukey test were used so that the presence of artefacts associated with the experiment could be determined, i.e., by comparisons of the unmanipulated controls with net plots.

Pygospio elegans size-frequency distributions were compared between weed treatment and control plots using the Kolmogorov-Smirnov (K-S) test and the chi-squared (χ^2) goodness of fit test. Both tests were used since although the former is more appropriate for continuous data (Zar, 1984) the latter permits the identification of those sizes contributing most to any significant differences. Size classes were grouped so that no expected values were below 5 for the χ^2 test, as recommended by Elliot (1977). All statistical analyses were performed using Minitab version 10.0 except the Kolmogorov-Smirnov test which was carried out by hand using the formula for large sample sizes given by Smirnov (1948).

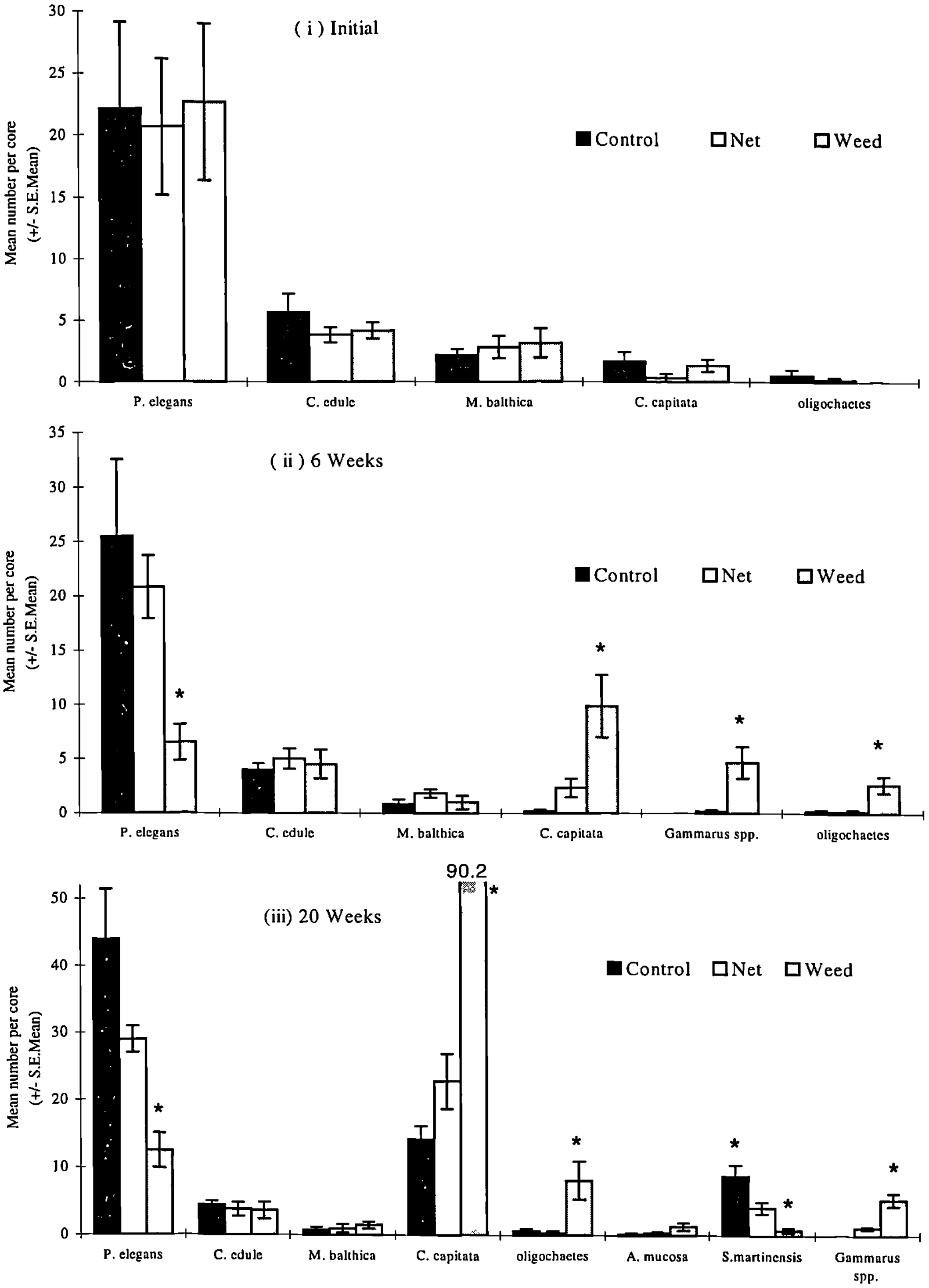
RESULTS

Species abundances - The mean numbers per core of each species on each sampling occasion, together with standard errors of the mean, are shown in Figures 4.3(i-iii). Only 5 taxa were sufficiently abundant at the start of the experiment for statistical analyses, these were the polychaetes *P. elegans* and *C. capitata*, the bivalve molluscs *C. edule* and *M. balthica* and oligochaetes. Prior to setting up the experiment, there were no significant differences in numbers for any taxa between any plot type (One-way ANOVA). After 6 weeks, 6 taxa were statistically analysed since *Gammarus* spp. had increased in density within the weed treatments. Four of these showed a significant weed treatment effect, i.e., a Tukey multiple comparison test revealed significant differences between weed treatment and net plots. *C. capitata,* oligochaetes and *Gammarus* spp. all showed significantly increased densities in the weed treatment plots compared to the net plots while the abundance of *P. elegans* significantly decreased. The two bivalve species, *C. edule* and *M. balthica*, showed no treatment effect. Tukey multiple comparison tests suggested that for no species were the net plots significantly different from the unmanipulated controls, suggesting there were no artefacts associated with the method of weed attachment after 6 weeks. The data for all these taxa were log(x+1)-transformed before statistical testing.

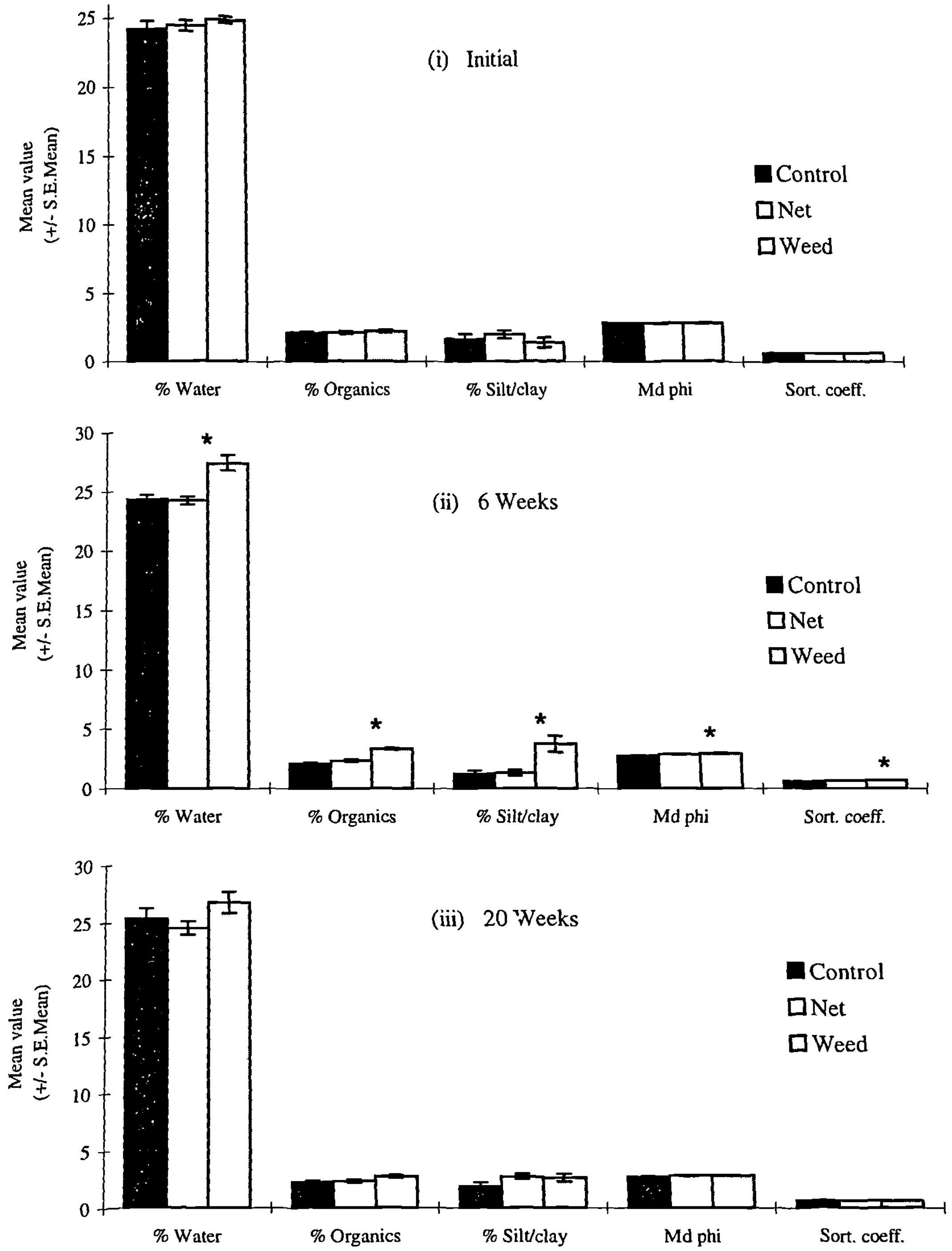
After 20 weeks, 8 taxa were analysed since the polychaetes *Anaitides mucosa* and *Spio martinensis* were sufficiently abundant for statistical analysis in at least one of the plot types. Of these, 5 taxa showed significant density changes in the weed treatment. The abundance data for *M. balthica*, *S. martinensis*, *A. mucosa*, *Gammarus* spp. and oligochaetes were log(x+1)-transformed before statistical analysis. *C. capitata*, oligochaetes and *Gammarus* spp. again showed significant increases in abundance with the weed treatments while *P. elegans* was lower in abundance in the weed treatment plots. *S. martinensis*, in addition to a significant weed effect, had a significant net plot effect, i.e., densities in the net treatments were significantly lower than in the unmanipulated controls while there was no significant difference between the weed and net plots. Therefore, although *S. martinensis* densities were significantly lower in the weed treatments than the controls, it appears that this was caused by the netting rather than the weed itself. This suggests that there was a slight artefact in the method of weed attachment in the longer term, although only one species was significantly affected. *C. edule*, *M. balthica* and *A. mucosa* showed non-significant changes in abundance between any of the plot types.

Sediment water, organic and silt/clay contents and granulometry - The mean values for water content, organic content, silt/clay fraction, median phi and sorting coefficient for the sediments at the start of the experiment, after 6 weeks and after 20 weeks are given in Figures 4.4(i-iii). At the start of the experiment there were no significant treatment differences for any of the sediment variables measured. Six weeks after the start of the experiment, the weed significantly increased the levels of all of the measured sediment variables (One-way ANOVA and Tukey test). The net plot was not found to be significantly different from the unmanipulated control for any of the variables measured suggesting that there were no significant artefacts associated with the plastic mesh for any of the measured sediment variables. This implies that the sediment accumulation observed within the net plots was probably natural and not due to the presence of the plastic mesh.

After 20 weeks, there were no longer any significant differences in water content, organic content, silt/clay fraction, median phi and sorting coefficient between the weed treatment and net plots. This suggests that the effects of the weed on the sediment variables were short-lived, i.e., as soon as the weed started to disappear the sediments began to return to ambient conditions.



Figures 4.3(i-iii) : Mean abundances per core for initial, 6 week and 20 week results (± S.E.Mean, n=6). * Denotes a statistical difference from net plot values using One-way ANOVA with Tukey multiple comparison test at 5% level of significance.



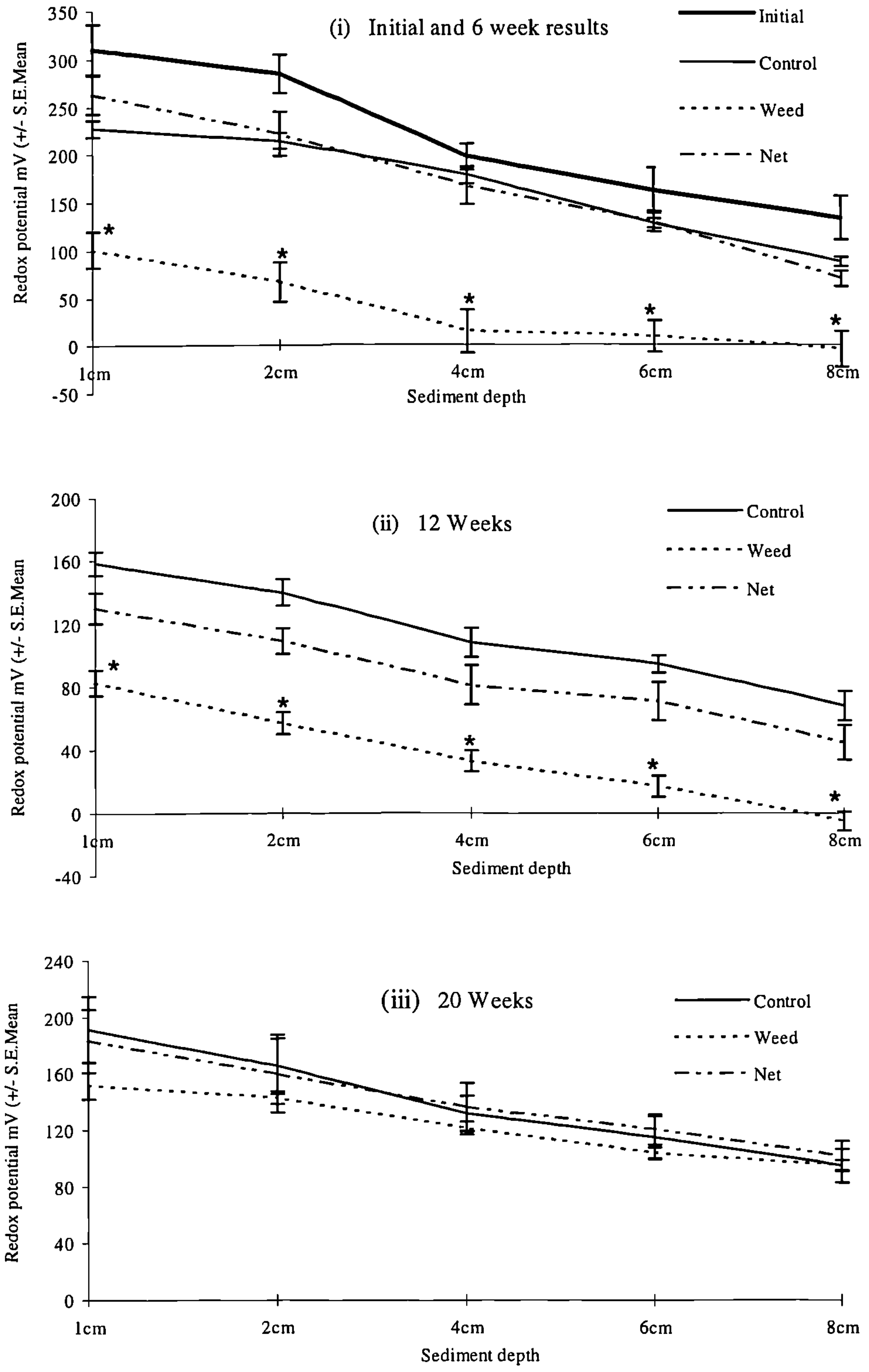
Figures 4.4(i-iii) : Sediment water, organic and silt/clay contents and granulometry results for initial values, and after 6 and 20 weeks (± S.E.Mean, n=6). * Denotes a

statistical difference from net plot values using One-way ANOVA with Tukey multiple comparison test at 5% level of significance.

Redox potentials - Redox potential has been shown to be well correlated with sediment sulphide, oxygen, and organic matter concentrations (Pearson and Stanley, 1979). The redox potential values at the start of the experiment were very similar for all three plot types and thus the initial values for the control plots only are shown in Figure 4.5(i). The redox potentials significantly decreased at all sediment depths measured in the weed treatments after 6 weeks, Figure 4.5(i), (One-way ANOVA with Tukey test). Although the mean redox potential for the weed treatment was never negative (except for 8cm depth with a mean of -2.3mV) the sediments at this time were black just below the sediment surface. In contrast, the sediments did not appear black until a depth of 7-8 cm within the net and control plots.

After 12 weeks, the effect of the weed on sediment redox potential (Figure 4.5(ii)) was similar to that after 6 weeks. The sediments within the weed treatment plots had significantly lower potentials for each depth relative to the net plots. The values for the net plots were lower, but never significantly lower, than the unmanipulated controls at every depth. This suggests that there was a slight decrease in the oxygen exchange between the sediments and the overlying water, perhaps due to the partial covering of the sediments by the plastic mesh. The net plot and unmanipulated control values after 12 weeks were both noticeably lower than those after 6 weeks suggesting that as the summer progressed the sediments at Drum Sands naturally became more reducing. This was also apparent between the initial and the 6 week control values, Figure 4.5(i).

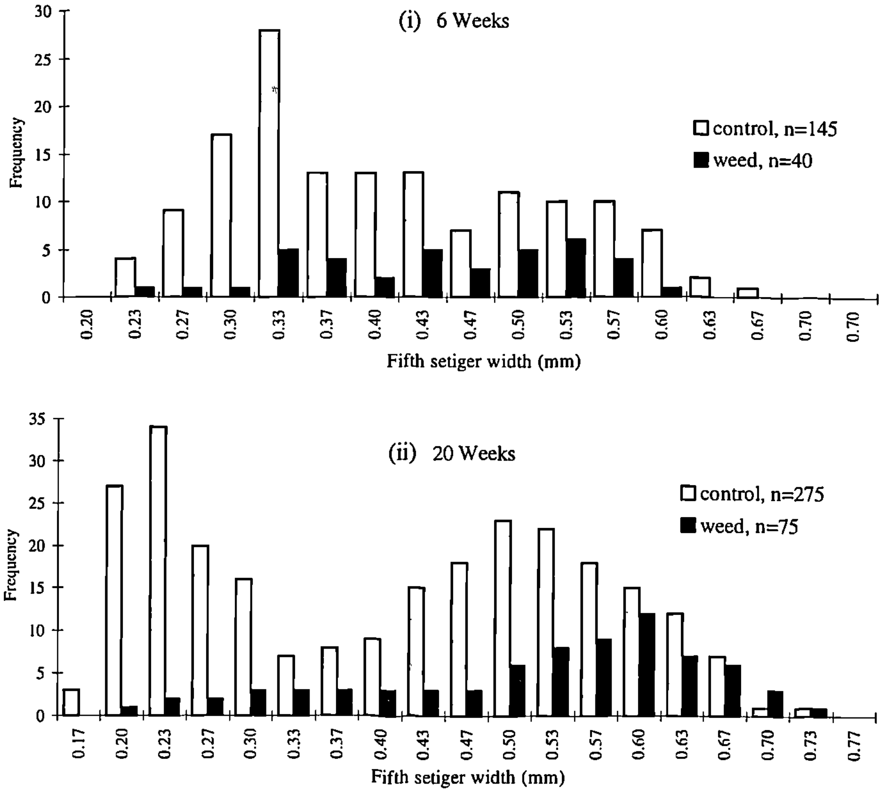
After 20 weeks, when the majority of the weed had disappeared, the sediments of the weed treatment plots were no longer significantly more reducing than those of the net or control plots (Figure 4.5(iii)). This is similar to the other sediment variables measured in that the effects of the weed were short-lived once the weed started to disappear.



Figures 4.5(i-iii) : Redox potential values initially and after 6, 12 and 20 weeks (± S.E.Mean, n=6). * Denotes a statistical difference from net plot values using One-way ANOVA with Tukey multiple comparison test at the 5% level of significance.

***Pygospio elegans* size distribution** - The *P. elegans* size-frequency distributions from the unmanipulated control and weed treatment plots after 6 weeks and 20 weeks are shown in Figures 4.6(i-ii) and the χ^2 goodness of fit and Kolmogorov-Smirnov tests results are presented in Table 4.1.

The results suggest that after 6 weeks of weed cover, although there was no significant difference between the size distributions of *P. elegans* in the weed treatment plots compared to the unmanipulated control plots, the significant decrease in abundance in the weed treatment (Figure 4.3(ii)) was mainly due to both the smallest individuals, ≤0.33mm 5th setiger width (38.8% of total variation), and those individuals with 5th setiger widths between 0.50 and 0.53mm (46.6%). However, caution must be taken because of the low abundances in the weed treatment plots.



Figures 4.6(i-ii) : Size-frequency results of *P. elegans* from control and weed treatment plots after 6 and 20 weeks. Total number of individuals measured for each treatment is given in legend.

After 20 weeks there was a significant difference in the size distribution of *P. elegans* between the two plot types. The significant reduction in numbers shown in Figure 4.3(iii) was mainly due to the smallest individuals, ≤0.33mm 5th setiger width (Figure 4.6(ii)).

	χ^2 goodness of fit						K-S
5th setiger width (mm)	≤ 0.33	0.37-0.40	0.43-0.47	0.50-0.53	≥ 0.57	**p value**	**p value**
6 weeks	38.8%	1.0%	13.4%	46.6%	0.1%	0.103	>0.05
20 weeks	37.9%	0.5%	3.7%	0.1%	57.8%	**0.001**	**<0.01**

Table 4.1 : Results of the χ^2 goodness of fit tests for the 6 weeks and 20 weeks results showing the % of the total χ^2 each size class is responsible for, and the p value. The p values for the K-S tests are also shown.

Algal biomass - The *Enteromorpha prolifera* used in this experiment successfully established within the weed treatment plots. Furthermore, weed growth did not occur in either the net plots or the unmanipulated controls. After 2 weeks, weed needed to be added to only 2 of the 6 weed treatment plots, the weed at the corners of these plots had not established. The implanted weed disappeared during October, approximately 20 weeks after the experiment was initiated. Throughout the 20 week period the weed always covered >90% of the sediment surface within the weed treatments.

The mean biomass of the *E. prolifera* estimated after 6 weeks (maintained density) and 20 weeks (during decay) was 139g DW/m^2 and 66g DW/m^2 respectively. This density is a realistic value when compared with the densities naturally occurring on intertidal mud- and sandflats (see Chapter 5). Table 4.2 shows the weed densities used in published controlled, algal-manipulation experiments. The mean weed biomass in this study after 6 weeks was generally low compared to those previously used, approximately equivalent to the *Enteromorpha* spp. biomass in the algal plots of the removal experiment by Cha (in prep.). At the start of this experiment, 3kg FW (equivalent to 600g DW/m^2) of *E. prolifera* were added to each weed treatment plot. This suggests that approximately only 23% of the initial weed added remained after 6 weeks within these plots, highlighting the difficulties in implanting weed in more exposed sandflats. The weed biomass within the weed treatments remained fairly constant until it started disappearing during October rather than a continual decline during the summer (pers. obs.).

Algal species	Mean algal biomass (gDW/m^2)	Implantation / Removal	Authors
Enteromorpha prolifera	66-139	I	This study
Ulva spp.	450-890	R	Everett (1991, 1994)
Enteromorpha spp.	*60, 200, and 600	I	Hull (1987) Raffaelli *et al.* (1991)
Rhodomela, Ceramium and *Polysiphonia* spp.	*180 and 360	I	Sundback *et al.* (1990)
Enteromorpha spp.	157	R	Cha (in prep.)

Table 4.2 : Mean algal biomasses used in controlled weed manipulation experiments. * Indicates that dry weight values have been obtained from wet weight measurements using a wet/dry ratio of 5 (Ramus and Venable, 1987).

DISCUSSION

The effects of weed mats on the sediments and invertebrate fauna of sheltered bays and sandflats have been studied by both descriptive surveys and controlled experimental manipulations. The objectives and underlying assumptions behind these two methods are very different and consequently often produce contrasting results. Therefore, this discussion will be limited to comparisons with, and conclusions relative to, other controlled algal-manipulation experiments. This will avoid this discussion becoming a hybrid between two fundamentally different approaches and, therefore, minimise inaccuracies. A comparative survey of the ecological effects of naturally occurring macroalgal mats on Drum Sands is given in Chapter 5.

This study aimed at specifically investigating the ecological effects of macroalgal mats on intertidal sandflats and whether mat formation had a potential role in *P. elegans* patch formation. These will be discussed separately.

The ecological effects of weed mats on intertidal sandflats.

The *E. prolifera* implanted within the weed plots in this study successfully established from the time of implantation until October, a period of 20 weeks. After an initial reduction the weed remained at a fairly constant biomass. Six weeks after implantation the weed caused marked changes in the macrobenthos, together with changes in all the measured sediment variables. While the numbers of *P. elegans* were significantly reduced, those of *C. capitata*, oligochaetes and gammarids increased under weed mats. Water, organic matter and silt/clay contents, medium phi and sorting coefficients significantly increased in the sediments under weed mats, these sediments also became significantly more reducing between 1-8cm depth. After 20 weeks, during weed decay, the effects of the weed on the fauna were similar to those after 6 weeks resulting in a community numerically dominated by *C. capitata*, while the sediment variables were no longer significantly different from controls.

Weed implantation experiments carried out previously have been conducted on more sheltered sandflats and the methods of weed attachment, wire hoops for example, have been less obtrusive (Reise, 1983a; Hull, 1987). These published studies, in contrast to this study, did not incorporate a control treatment to determine whether there were any artefacts associated with the method of weed attachment and it was assumed that the wire hoops did not confound the interpretation of the results. There seemed very little evidence from the results of the present experiment at Drum Sands to suggest that the plastic mesh had an effect upon either the physical or physico-chemical conditions of the sediments or upon the fauna.

The effects of weed cover on species abundances are sometimes both dramatic and complex and can play an important role in structuring benthic assemblages. Hull (1988) suggested that the observed changes result from the interaction of many factors. These include a reduced current velocity enhancing larval settlement, shelter from predation (although some epibenthic predators may be attracted to weed mats), a reduction in oxygen exchange between the sediment surface with the overlying water, accumulation of silt, anoxia and the production of toxic H_2S. Consequently, the effects of weed cover on the fauna (Bonsdorff, 1992) and the mechanisms by which these effects are brought about (Raffaelli *et al.*, 1991) are poorly understood. Many of the effects observed during controlled algal-manipulation experiments are similar to those resulting from organic enrichment (Pearson and Rosenberg, 1978), notably the large increases in *Capitella capitata* and *Malacoceros fuliginosus* (Hull, 1987, 1988; Cha, in prep.). Hull (1987) suggested that areas such as the Ythan Estuary, Scotland, where the community comprises many opportunistic species, are likely to cope with the anoxic environment which algal mats create and, therefore, the observed effects of macroalgae are likely to be small. This is in contrast to Drum Sands where reduced sediments were well below the sediment surface and opportunistic species such as *C. capitata* were present in very low numbers suggesting that the fauna there were likely to show a more dramatic response to the disturbance imposed by weed cover.

A review of the literature revealed that *C. capitata* tends to be the only benthic infaunal species to show a consistent response to weed cover in controlled manipulation experiments and in general, polychaetes exhibit a mixed response to macroalgal cover (Woodin, 1977). Warren (1976) found that *C. capitata* colonised by larval settlement giving increased densities during July and October. The timing of *C. capitata* larval availability therefore coincided with the period of *E. prolifera* cover in weed treatment plots in this experiment and presumably enabled this species to increase in numbers under the favourable conditions afforded by the weed mats on Drum Sands. Larval settlement of *C. capitata* was possibly facilitated in the weed plots by a reduction in water flow, and its success within these plots may have been due to its ability to tolerate the reducing conditions while being able to feed on the increased detritus (Price and Hylleberg, 1982).

Pygospio elegans showed a significant decline in abundance within the weed plots during the present experiment after 6 weeks and 20 weeks of *E. prolifera* cover. The responses of *P. elegans* abundance to weed cover has been shown to vary between experiments. For example, Bonsdorff (1992) found that drifting algal mats in the shallow sandy bottoms of the Baltic Sea decreased adult numbers of *P. elegans* to zero, while Cha (in prep.) found that *P. elegans* density was lower in *Enteromorpha*-removed plots compared to weed plots. However, the possibility of the disturbance created by the physical removal of weed in the latter experiment having a negative effect on *P. elegans* cannot be overlooked. Hull (1987) found that the effect of macroalgal mats on the densities of *P. elegans* and other infaunal species of the Ythan estuary was algal-biomass dependent. With low (0.3kgFW/m^2) and moderate (1kgFW/m^2) densities of *Enteromorpha* spp., *P. elegans* increased in numbers, presumably as a result of an increased detrital-food supply. At high densities (3kg FW/m^2), *P. elegans* decreased in numbers. The decline in abundance of *P. elegans* under high weed biomass was thought to have been possibly due to increased siltation clogging *P. elegans* suspension-feeding mechanism (Hull, 1988) or the physical presence of the weed having a detrimental effect on the worm's feeding behaviour (Everett, 1994). Price and Hylleberg (1992) proposed that the effect was in fact due to a decreased food supply: the alteration in water flow due to the algal mats preventing a continuous settlement of debris onto the sediment surface and around animal tubes.

Hull (1988) carried out an experiment in which the mechanisms of faunal changes due to macroalgal cover were investigated. He used treatments to which organic matter was added, and separate nylon filament treatments, to mimic the enrichment and physical effects of weed respectively. He concluded that the decline in *P. elegans* numbers was due to the enriching effect of weed mats rather than due to its physical presence. However, *P. elegans* has been found to be an opportunistic species and present in high numbers around sewage outfalls (Anger, 1977) and other organic discharges (see Pearson and Rosenberg, 1978) and, therefore, is not likely to decline in abundance due to the reducing sediments under weed mats. Other studies have suggested that the low abundances of *P. elegans* under higher weed mat densities have been an indirect response: *M. fuliginosus* increased in the study by Hull (1987) and it was suggested that *M. fuliginosus* competed with *P. elegans*. Unfortunately, these studies have not compared the sizes of *P. elegans* between weed and control plots and, therefore, it is not possible to determine whether adult mortality or recruitment failure was responsible for the negative effect of weed cover on this species abundance.

A possible cause of *P.elegans* decline in the experiment on Drum Sands could have been sediment accumulation rather than the effect of siltation. During the first few days of the experiment, 5-6cm of sediment had accumulated within the weed treatment plots and it is perhaps unlikely that *P. elegans* individuals were able to cope with such accretion and were therefore buried. This is supported by the size-frequency distributions of *P. elegans*: although sediment accumulation affected all size classes, the smaller ones were more severely affected, as would have been expected from sediment smothering. Sediment accumulation by mats of *Enteromorpha* has been reported elsewhere (e.g., Frostick and McCave, 1979) and is probably a common phenomenon on more exposed sandflats.

In addition to the detrimental effect on adults, this study indicated that the decrease in abundance of *P. elegans* in the long term was likely to have been due to a lack of larval recruitment. Bonsdorff (1992) pointed out that the success of the settling stages of benthic infauna are of crucial importance in determining the structure of the community. It was shown in Chapter 3 that while *P. elegans* is capable of reproducing by both benthic and planktonic larvae, only planktonic larvae were produced by the population at Drum Sands. Size-frequency distributions clearly showed that the decrease in adult density was mostly due to the decrease in the smaller size classes. After 20 weeks, *P. elegans* size-frequency distributions in weed treatment plots were significantly different from those in the control plots, mostly due to the dramatic reduction of those individuals smaller than 0.33mm wide (5th setiger). Therefore, the *P. elegans* larval recruitment which occurred at Drum Sands during

May-June 1997 (see Chapter 3) did not occur with any success in the weed treatment plots of this experiment.

It is not possible to suggest the mechanism responsible for the lack of *P. elegans* recruitment in the weed treatment plots in this study. Although reduced water velocity in weed-affected areas may facilitate planktonic larval settlement, larvae may be 'filtered out' by the weed (Olafsson, 1988) preventing them reaching the sediment surface. However, many studies (see Raffaelli *et al.*, 1999) have suggested that reduced *P. elegans* recruitment to weed-affected areas results from decreased juvenile survival in the more reduced sediments and/or smothering due to siltation. Ragnarsson (1996) found that weed significantly reduced *P. elegans* colonisation of azoic sediments, however, the present study on Drum Sands is the first experimental study which has reported that macroalgal cover has a negative effect on polychaete recruitment to ambient sediments.

The densities of the two bivalves, *C. edule* and *M. balthica*, in this study were not significantly affected by weed cover. Everett (1994) found that *M. balthica* numbers decreased in weed plots compared to algal-free plots and suggested that tellinid bivalves are expected to suffer from the physical barrier formed by algae between the sediment surface and the overlying water column. The results obtained by the algal-removal experiment of Cha (in prep.) supported this. In contrast, Hull (1987) reported greater numbers of *M. balthica* under his experimentally-implanted algal-covered plots compared to unmanipulated controls. Everett (1994) suggested that the contrasting results obtained by his experiment and the one by Hull (1987) could have been due to two factors. Firstly, Hull's method of weed attachment resulted in an unnatural algal-sediment interface. However, this cannot be the reason for the lack of a negative result in the present study because sediment accumulation resulted in the algae being held in place below the sediment surface, similar to natural weed mats. Secondly, Everett (1994) suggested that the *Enteromorpha* spp. Hull (1987) used, in contrast to the *Ulva* spp. in Everett's experiment, being filamentous rather than laminar, may not have formed a barrier between the infauna and the water column to the same extent. However, in Hull's study and the present one on Drum Sands, a significant decrease in the redox profiles occurred under the weed mats leading to black, hydrogen sulphide-smelling sediments, suggesting that oxygen exchange between the sediments and the overlying water column was severely reduced. Raffaelli *et al.* (1999) suggested that the differences observed between the studies by Everett (1994) and Hull (1987) was due to *M. balthica* in Hull's study being settling spat while they were adults in Everett's study. The low ambient abundances of the two bivalve species in the present study were probably partly responsible for the lack of a significant weed effect, although increased food and more reducing sediments could have been two opposing factors.

Macroalgal mats and *P. elegans* patch formation.

The results of this experiment support the conclusion of Thrush (1986a) who proposed that patchily distributed accumulations of macroalgae result in spatial variations in the faunal structure of the benthos. However, the results showed that the *E. prolifera* implanted during this experiment on Drum Sands did not, at least in the short term, result in increased numbers of *P. elegans* and, therefore, did not support the suggestion that macroalgal mat formation has a role in *P. elegans* patch establishment. Instead, the faunal communities under weed mats shortly after implantation, to just after weed disappearance 20 weeks later, were dominated by *C. capitata*, with increased numbers of oligochaetes and gammarids. Unfortunately, monitoring *P. elegans* densities in weed treatment plots in the longer term was rendered impossible due to mussel colonisation onto the plastic netting in the weed treatment and net plots. Therefore, although *E. prolifera* had a negative effect on *P. elegans*, both on the post-larval population and on larval recruitment, the potentiality of *P. elegans* later increasing in numbers remains unresolved. An increase in *P. elegans* population density would only have been possible during late November/early December when larval recruitment occurred (Chapter 3), a time when weed-affected areas would have been numerically dominated by *C. capitata.*

Controlled, manipulation experiments potentially allow a less equivocal way of determining the effects of weed mats on intertidal sandflats. However, since the biotic and abiotic responses are dependent upon factors such as weed type, biomass and timing of establishment, experiments are unlikely to unequivocally link macroalgal mat establishment with invertebrate patch formation in a particular environment unless all these factors in the experiment closely mimic those of naturally occurring weed mats. Logistically, it is very difficult to closely mimic all these factors in an experiment. For this reason, a descriptive survey of the effects of natural weed mats on Drum Sands was considered necessary and is discussed in Chapter 5.

CHAPTER 5

THE EFFECTS OF MACROALGAL COVER ON THE SPATIAL DISTRIBUTION OF MACROBENTHIC INVERTEBRATES : A SURVEY APPROACH

INTRODUCTION

The effects of macroalgal cover on the sediments and invertebrate faunal assemblages of intertidal estuaries and sheltered bays have been investigated by two contrasting approaches (see Chapter 4). Compared to surveys, controlled manipulation experiments allow a more mechanistic approach and the study of the cause and effect of weed cover. These have tended to be small-scale experiments, usually of just a few square metres in area (Raffaelli *et al.*, 1999). Descriptive surveys, although having an intrinsic problem of spatial confounding, allow the investigation of large-scale effects of weed cover.

The results of surveys investigating the effect of weed cover on the faunal communities of intertidal sediments have helped to form the basis for management of these areas with respect to nutrient inputs (e.g., Mathieson and Atkins, 1995). However, this outcome has been problematical because of the different results from surveys. Although many studies have reported increases in opportunists such as *C. capitata* and *M. fuliginosus* and in epibenthic invertebrates such as *H. ulvae*, along with decreases in the numbers of some spionid polychaetes and bivalve molluscs (Perkins and Abbott, 1972; Nicholls *et al.*, 1981), there have been several studies which have not shown significant changes in species composition or diversity (e.g., Soulsby *et al.*, 1982). It has been noted that the responses of invertebrates to weed cover are complex and result from the interplay between many factors (Hull, 1988) associated with both the weed (Sundback *et al.*, 1990; Everett, 1994) and the receiving system (Soulsby *et al.*, 1982). Therefore, as with controlled experiments, the responses of most invertebrate species to weed cover ascertained by any survey within any one system depend upon the weed type and biomass, weed mat size and time of establishment and decay. Comparisons between studies conducted in different areas are further complicated by differences in the ability of the sediments and faunal assemblages to cope with the disturbance (Hull, 1988). Furthermore, Everett (1994) indicated that the responses of the fauna to weed cover vary from year to year, even within the same area. While descriptive studies have weed-affected and weed-free plots in separate areas of the estuary or bay, inconsistencies in the responses shown by different species are expected due to methodological artefacts.

Macroalgal mat establishment on Drum Sands during 1997 provided an ideal opportunity to carry out a descriptive survey to investigate the ecological effects of weed mats on intertidal sandflats and to compare with the results obtained from the weed-implantation experiment (Chapter 4). The two main aims of this survey were:
1 - to investigate the ecological effects of weed mats on an intertidal sandflat;
2 - to investigate whether weed mat establishment could promote patch formation of *P. elegans* on Drum Sands.

METHODS

Survey design - During late August 1997 mats of green algae (*Vaucheria subsimplex*) developed within the study site in approximately the same area as the previous summer (see Figures 4.1 and 5.1). The general appearance of the mats (1-2m^2) closely resembled those which occurred the previous year, except for the absence of *E. prolifera*. The *V. subsimplex* mats covered approximately 30-35% of the sediments within the area affected by weed and approximately 100% within mats. This allowed an ideal opportunity to study the effects of natural macroalgal mats on the sediments and their invertebrate faunal assemblages. The inherent disadvantage of such a descriptive study, i.e., the large-scale spatial separation of weed-affected and weed-free areas, was overcome in this study since weed-free areas remained within the weed-affected area in which non-weed plots could be positioned. Therefore, any large-scale factors affecting the fauna within the study area, independent of the effects of weed cover, should have acted on both the weed and non-weed plots.

On the 18th September 1997 (approximately 4 weeks after *V. subsimplex* first established), 6 'weed' plots and 6 'non-weed' plots, 1m^2 each, were randomly located within a selected area (50×50m) of the sediments affected by macroalgal cover. This was achieved by choosing the nearest weed mat and weed-free area to the randomly generated co-ordinates for the weed and non-weed plots respectively. The layout of the two plot types are shown in Figure 5.1. The assumption that the weed had no effect on the characteristics of the non-weed areas was made. This assumption seemed reasonable with respect to hydrodynamic effects at least since the *V. subsimplex* possessed very short filaments and, therefore, had a very localised hydrodynamic effect.

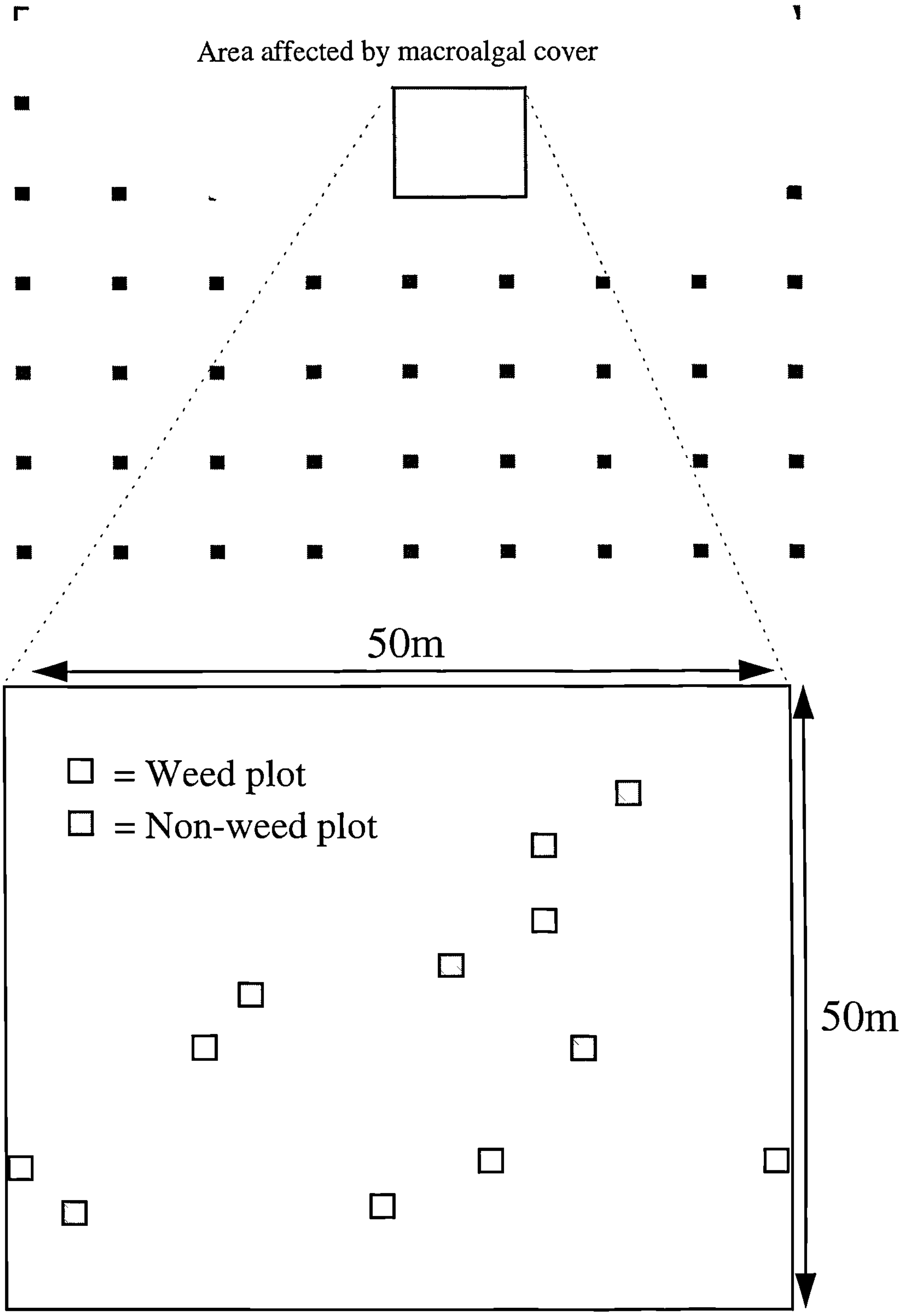


Figure 5.1 : Random layout of the weed and non-weed plots for the weed survey. All plots are $1m^2$ in area. Sample sites for large-scale grid survey (40m survey, Chapter 2) are shown in the top map.

The sediments could not be sampled prior to macroalgal mat development since weed mats had to establish before the two plot types could be positioned. Therefore, the assumption is made that the faunal and sedimentary characteristics in the weed plots were initially similar to the non-weed plots, i.e., that algal mat establishment within the area was random. This assumption seemed reasonable with respect to *P. elegans* densities since the macroalgal mats were not restricted to *P. elegans* patches. Furthermore, the weed and non-weed plots were not placed at any of the previously marked *P. elegans* patches. However, the patchy nature of weed mats suggested that their establishment was probably influenced by some unidentified factor and, therefore, initial conditions within the two plot types may not have been identical.

On 18th September 1997, these plots were sampled for their invertebrate fauna using an identical method to the one described for the controlled, weed-implantation experiment (see Chapter 4). These will be referred to as '4 weeks' samples hereafter since these samples were taken 4 weeks after algal establishment. The sediments were sampled and redox potentials measured in an identical way as described in Chapter 4. Redox measurements were also taken on the 16th of October, i.e., 8 weeks after *V. subsimplex* establishment. Redox profiles were taken at 3 depths only; 1, 2 and 4cm, since the results from the weed-implantation experiment suggested that deeper measurements only showed the same trends as near-surface measurements and were less ecologically significant to the species studied. Sample treatment thereafter was the same as described in Chapter 4.

Sampling was repeated on the 8th of January, 1998, 20 weeks after algal establishment. The weed had been slowly disappearing since mid November and by this time had almost completely disappeared.

One random sample (6×6cm) was taken from each plot for weed biomass determination after 4 weeks and 20 weeks and treated in the same way as described in Chapter 4.

Fifth setiger widths were measured of all *P. elegans* individuals from both the weed and non-weed plots for both the 4 and 20 weeks samples as described in Chapter 3.

Data analyses - Only those species with a mean abundance of 3 or more per core were statistically analysed. The raw faunal data, together with the data from sediment analyses and redox measurements, were tested for normality using the Anderson-Darling test and for homogeneity of variance using the Bartlett test. Raw data, if necessary, were transformed using an appropriate transformation to achieve normality and homoscedasticity (Zar, 1984). A Two-sample t-test was then carried out on either the raw or transformed data to assess if there were any significant differences between the weed and the non-weed plots. A Mann-Whitney U test was carried out on any variable not satisfying the parametric assumptions even after transformation. To assess differences between the diversities of weed and non-weed plot communities, a Hutcheson's modified t-test for Shannon-Wiener diversity index values was used, following the recommendation of Zar (1984). The Hutcheson's modified t-test requires first calculating the Shannon-Wiener diversity index values of the communities by summing all replicates.

Size-frequency distributions were compared between treatments using the Two-sample Kolmogorov-Smirnov (K-S) test and the χ^2 goodness of fit test. Both tests were used since although the former is more appropriate for the data (Zar, 1984), the latter permits the identification of those sizes contributing most to any significant differences. Size classes were grouped so that no expected values were below 5 for the χ^2 test, as recommended by Elliot (1977).

All statistical analyses were performed using Minitab version 10.0 except the Kolmogorov-Smirnov test which was carried out by hand using the formula for large sample sizes given by Smirnov (1948). The Hutcheson's modified t-test was performed by a program written by R. Ladle (pers. comm.).

RESULTS

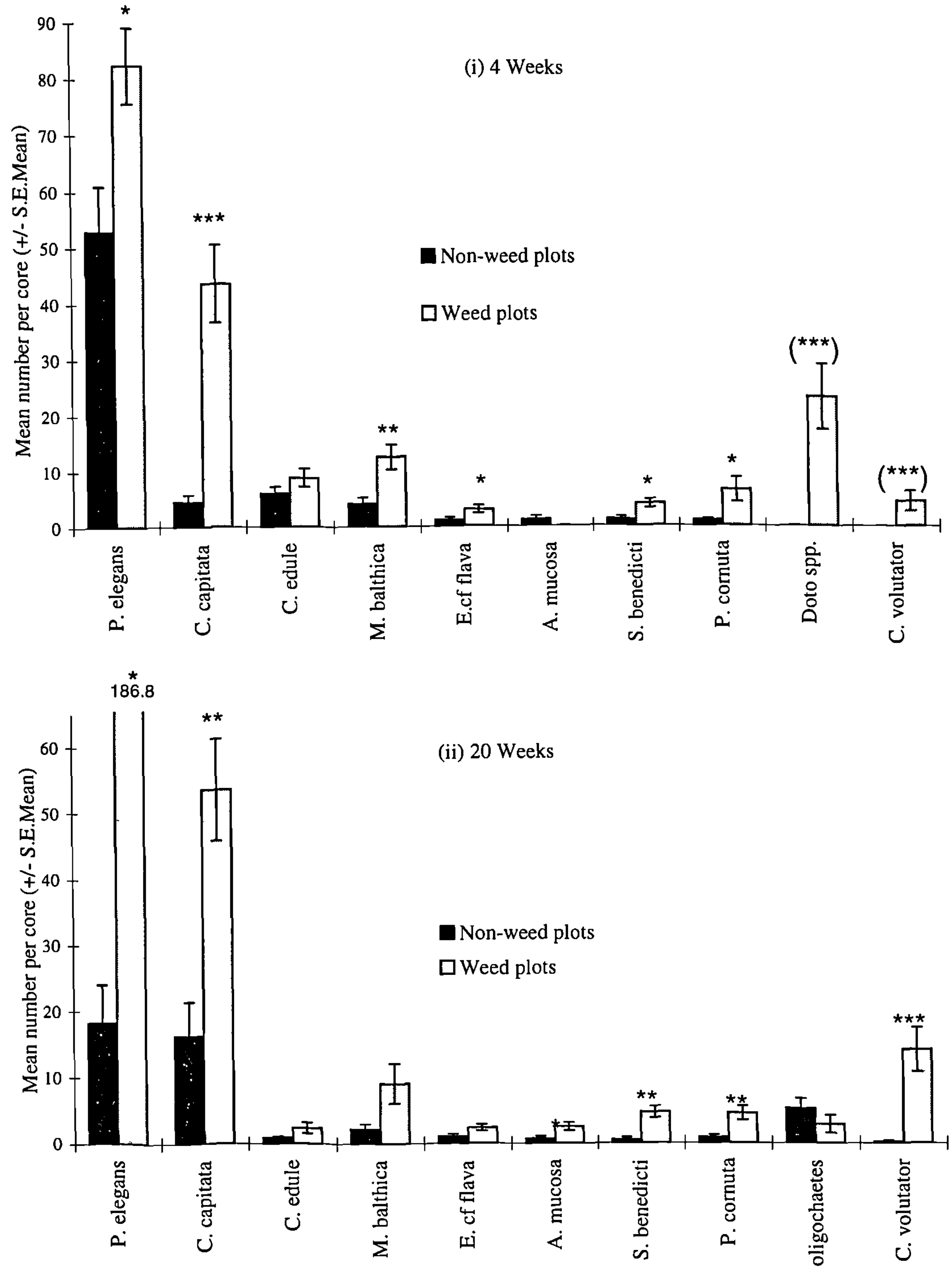
Species abundances - Table 5.1 shows the mean number of species, individuals and Shannon-Wiener diversity index values for the non-weed and weed plots. After 4 weeks of algal cover, the total number of individuals and diversity significantly increased in the weed plots while there was no change in the mean number of species. There was no change in the total number of species: a total of 17 species were obtained from the 6 replicates for both the weed and non-weed plots, 10 being sufficiently abundant for statistical analysis.

The invertebrate abundances for the 4 weeks and 20 weeks samples together with their standard errors are shown in Figures 5.2(i) and (ii) respectively. Eight of the 10 species sufficiently abundant for statistical analysis after 4 weeks showed significant differences in abundance between the two plot types, all being more abundant in the weed plots compared to the non-weed plots (*P. elegans*, $p=0.012$; *C. capitata*, $p<0.001$; *M. balthica*, $p=0.003$; *E.* cf *flava*, $p=0.04$; *S. benedicti*, $p=0.008$; and *P. cornuta*, $p=0.04$; Two-sample t-test; and *Doto* spp., $p<0.001$; and *C. volutator*, $p<0.001$; One-sample t-test). The latter two species, the nudibranch *Doto* spp. and the amphipod *C. volutator*, were only present in the weed plots. *C. edule* and *A. mucosa* showed no significant change in abundance with algal cover and no species was significantly more abundant in the non-weed plots.

After 20 weeks, the mean number of species and individuals in the weed plots were significantly higher than in the non-weed plots, however, due to the numerical dominance of *P. elegans* under algal cover, the diversity significantly decreased (Table 5.1). A total of 16 species were sampled from the non-weed plots and 15 species from the weed plots. Ten species were sufficiently abundant for statistical analysis (Figure 5.2(ii)). Of these 10, 6 species (*P. elegans*, $p<0.001$; *C. capitata*, $p=0.004$; *A. mucosa*, $p=0.03$; *S. benedicti*, $p=0.007$; *P. cornuta*, $p=0.008$; and *C. volutator*, $p<0.001$; Two-sample t-test) showed significant increases in numbers under *V. subsimplex* mats. *C. edule*, *M. balthica*, *E.* cf *flava* and oligochaetes showed no significant differences in abundances. Again, none of the species were significantly more abundant in the non-weed plots compared to the weed plots.

	Mean no. species		Mean no. individuals		Shannon-Wiener	
		p		p		p
4 weeks						
Non-weed	10.6 (±0.61)	N.S.	76.3 (±9.0)	**<0.001**	0.563	*** <0.01**
Weed	10.6 (±0.56)		192.8 (±8.2)		0.733	
20 weeks						
Non-weed	8.5 (±0.34)	**<0.001**	39.7 (±7.9)	**<0.001**	0.789	*** <0.01**
Weed	11.0 (±0.37)		301.2 (±30.0)		0.516	

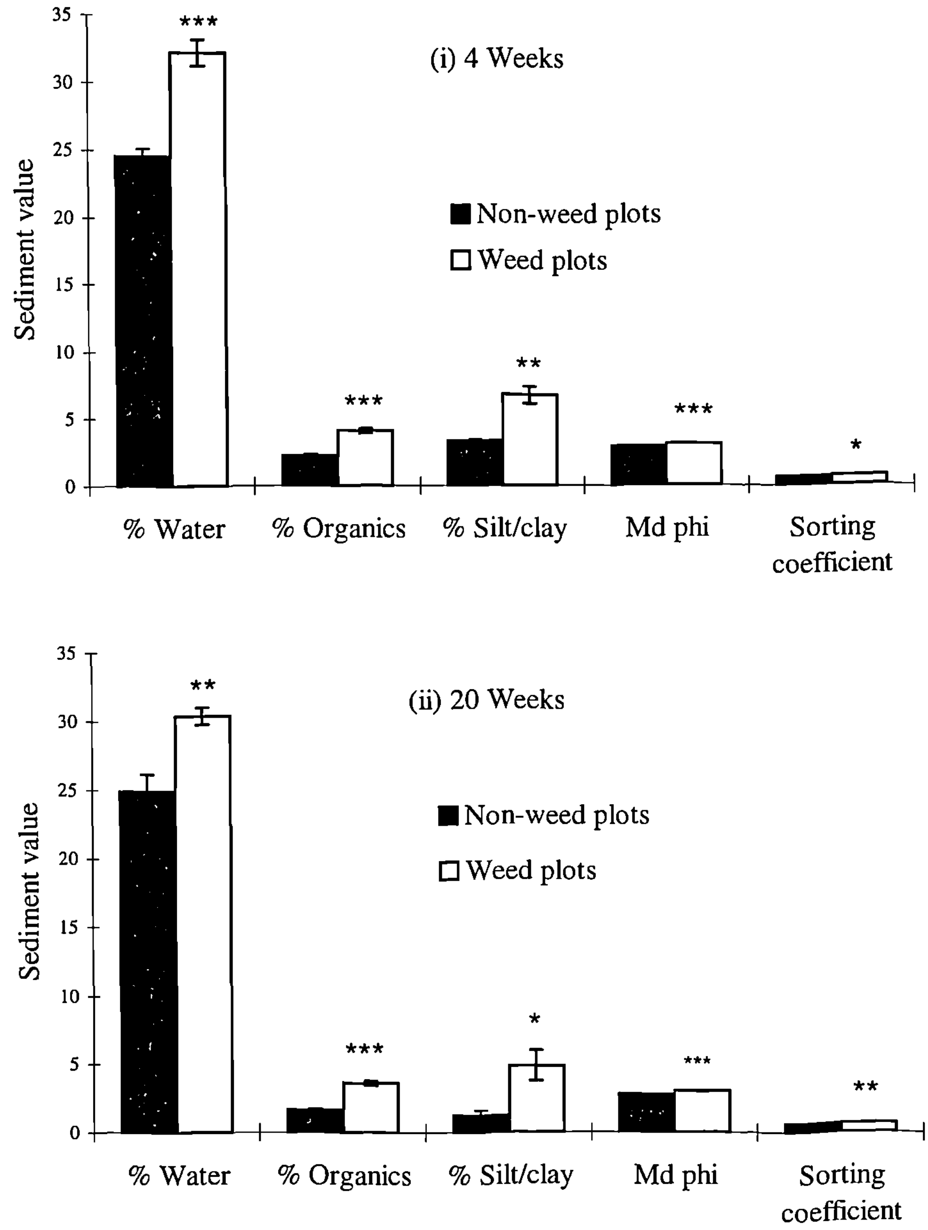
Table 5.1 : Mean number of species and individuals (± S.E. Mean, n=6) and Shannon-Wiener diversity index values for the non-weed and weed plots for 4 and 20 weeks results. Significant differences are indicated by p values while N.S. represents non-significance (Two-sample t-test except for * where significant differences were assessed by Hutcheson's modified t-test).



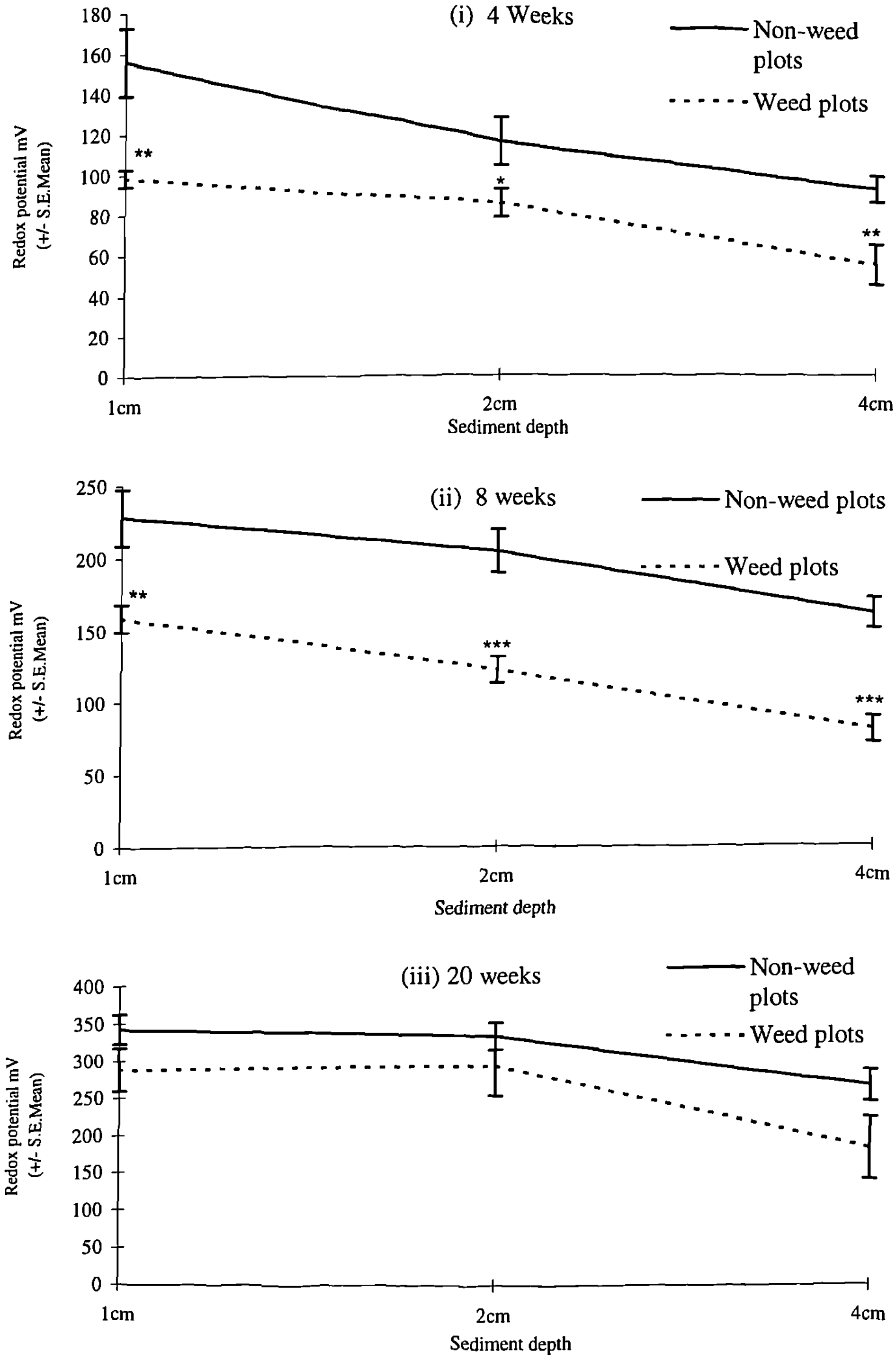
Figures 5.2(i-ii): Faunal results for the weed plots and the non-weed plots (± S.E.Mean, n=6); (i) 4 weeks and (ii) 20 weeks after *V. subsimplex* mat establishment. * Denotes a significant difference between the 2 plot types with $p<0.05$, ** denotes $p<0.01$ and *** denotes $p<0.001$, Two-sample t-test. Brackets imply results from One-sample t-test.

Sediment water, organic and silt/clay contents and granulometry - The results of the physical properties of the sediments (% water, % organics, % silt/clay, Md ϕ and sorting coefficient) for the 4 weeks and 20 weeks samples are given in Figures 5.3(i) and (ii) respectively. All these variables were analysed after an arcsine transformation (Zar, 1984). The results show that after 4 weeks the weed had a significant effect on all the measured sediment variables, increasing their values compared to the non-weed plots ($p<0.001$; $p<0.001$; $p=0.003$; $p<0.001$ and $p=0.046$ respectively, Two-sample t-test). Figure 5.3(ii) shows that after 20 weeks, although the weed had been slowly disappearing for nearly 2 months, the weed plots still had significantly higher values for all these sediment variables relative to the non-weed plots ($p=0.005$; $p<0.001$; $p=0.029$; $p<0.001$ and $p=0.004$; respectively, Two-sample t-test).

Redox potentials - The redox profiles of the sediments of the weed plots and the non-weed plots after 4 weeks, 8 weeks and 20 weeks are shown in Figures 5.4(i-iii). The redox profiles show that the effect of the weed on the sediments' physico-chemical properties and the physical properties (see above) were similar. After 4 weeks, the sediments under the macroalgal mats had become significantly more reducing than those of the non-weed plots ($p=0.008$; $p=0.02$ and $p=0.009$; for 1, 2 and 4cm depths respectively; Two-sample t-test). A similar response was observed for the redox profiles after 8 weeks ($p=0.007$; $p<0.001$ and $p<0.001$; for 1, 2 and 4cm depths respectively; Two-sample t-test). In January, when the weed had almost completely disappeared, the redox profiles no longer showed the significant differences shown by the physical variables at this time, i.e., the redox profiles were no longer significantly different between the two plot types (Figure 5.4(iii)), although the sediments of the weed plots were still slightly more reducing.



Figures 5.3(i-ii): % water, organic and silt/clay contents and granulometry results for the sediments of weed and non-weed plots (± S.E.Mean, n=6) for (i) 4 weeks and (ii) 20 weeks after *V. subsimplex* mat establishment. * Denotes a significant difference between the 2 plot types with $p<0.05$, ** denotes $p<0.01$ and *** denotes $p<0.001$, Two-sample t-test.



Figures 5.4(i-iii): Redox potential profiles of the weed and non-weed plots (± S.E.Mean, n=6); (i) 4 weeks; (ii) 8 weeks; and (iii) 20 weeks after *V. subsimplex* mat establishment. * Denotes a significant difference between the 2 plot types with $p<0.05$, ** denotes $p<0.01$ and *** denotes $p<0.001$, Two-sample t-test.

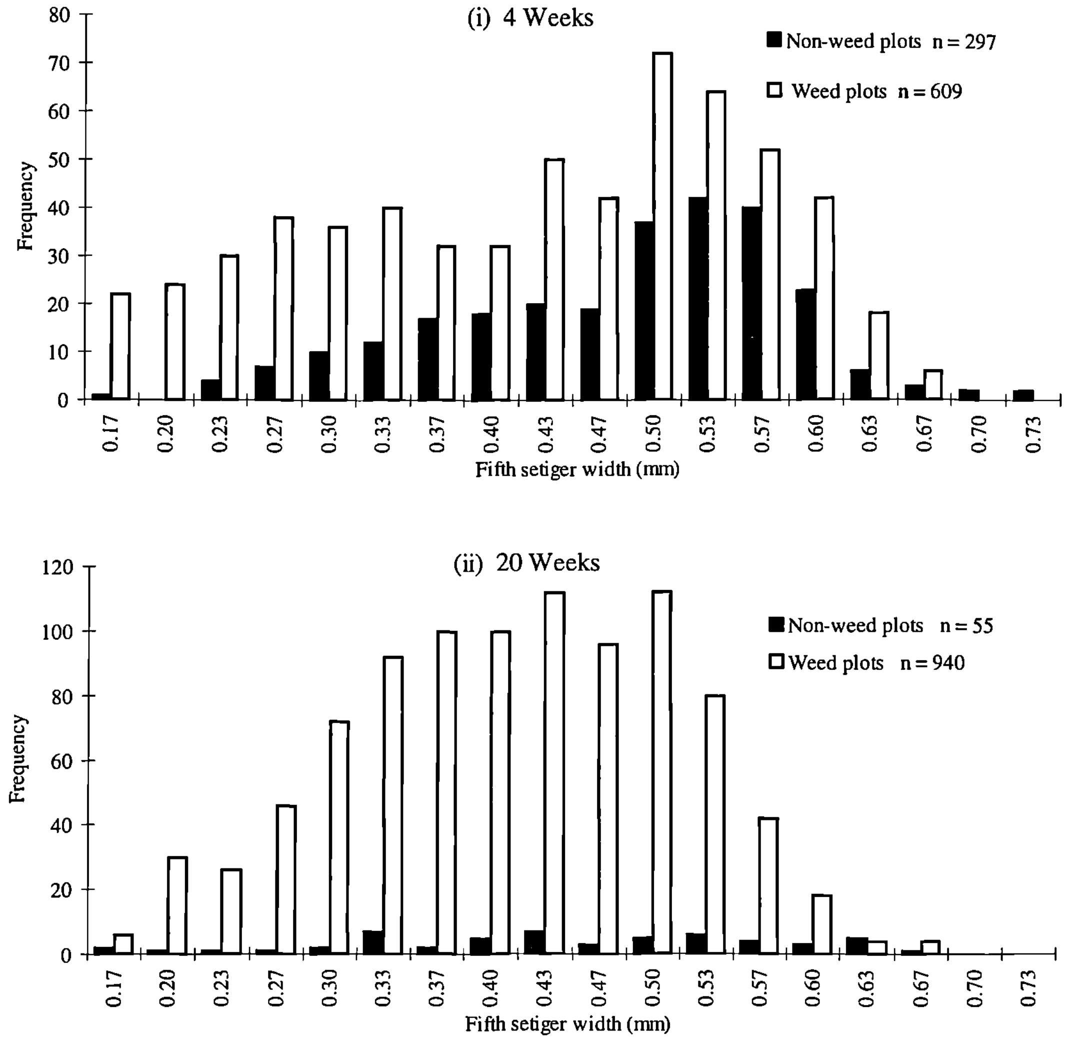
***Pygospio elegans* size distributions** - The 5th setiger widths of *P. elegans* for the weed and non-weed plots after 4 weeks and 20 weeks are given in Figures 5.5(i) and (ii) respectively. The results of the χ^2 goodness of fit and Kolmogorov-Smirnov tests are given in Table 5.2.

5th setiger width (mm)	χ^2 goodness of fit						K-S
	≤ 0.30	0.33-37	0.40-43	0.47-50	≥ 0.53	**p value**	**p value**
4 Weeks	77.1%	1.2%	7.4%	9.0%	5.2%	**<0.001**	**<0.01**
20 Weeks	27.3%	10.1%	12.1%	2.6%	47.9%	0.383	>0.05

Table 5.2 : Results of the χ^2 goodness of fit tests showing the % of the total χ^2 value each size class is responsible for and p values for the 4 weeks and 20 weeks results. The p values for the Kolmogorov-Smirnov tests (two-tailed) are also given.

These results suggest that after 4 weeks, weed cover had a significant effect on *P. elegans* size-frequency distribution and that the main cause of this was a large increase in small individuals under *V. subsimplex* mats, 77.1% of the deviation was due to those individuals with a 5th setiger width of $\leq$ 0.30mm. Therefore, the significant increase in *P. elegans* density observed after 4 weeks (Figure 5.2(i)) was mainly due to an increase in the number of juveniles. This result supports the contention that the numbers of *P. elegans* initially were similar in the two plot types because if the weed preferentially established in areas of high *P. elegans* densities, the number of individuals in the larger size classes would have been much higher in the weed plots compared to the non-weed controls. Although the number of *P. elegans* adults in the weed plots were higher than in the non-weed plots, this only accounted for a relatively small proportion of the deviation of the size-frequency distributions. This difference could have been due to adult migration into these more favourable conditions or due to decreased survivorship in, and/or increased emigration from, the non-weed plots.

After 20 weeks, there was no significant difference between the *P. elegans* size-frequencies in the weed and non-weed plots although this was probably due to the low abundances in the non-weed plots preventing a definite size distribution being ascertained.



Figures 5.5(i-ii): Size-frequency distributions of *P. elegans* for the weed and non-weed plots, (i) after 4 weeks and (ii) after 20 weeks of *V. subsimplex* mat establishment. Numbers of individuals measured are given in the legend.

Algal biomass - The biomass of *V. subsimplex* in the weed plots after 4 weeks was 49.7gDW/m^2 and 3.4gDW/m^2 after 20 weeks. There was never any weed present in the non-weed plots. The weed biomass in this study was very small compared to other areas previously studied (see Table 5.3), although some studies only give % cover which is difficult to compare with quantitative biomass measurements. Furthermore, this is the first detailed investigation into the effects of the green algae *Vaucheria* spp. on the faunal invertebrates of intertidal sediments since other studies have usually investigated the effects of macroalgal species of the genera *Enteromorpha* and *Ulva.*

Algal species	Biomass (gDW/m^2) or % cover	Location	Authors
Enteromorpha spp.	331.6	Montrose Basin	Caudwell and Jones (1994)
Enteromorpha spp.	116.0	Eden Estuary	Owens and Stewart (1983)
Enteromorpha spp.	250.0	Lynher Estuary	Warwick *et al.* (1982)
Enteromorpha spp.	157.24	Ythan Estuary	Cha (in prep.)
Enteromorpha spp. and *Ulva* spp.	42%	Langstone Harbour	Nicholls *et al.* (1981)
Enteromorpha spp.	21%	Firth of Clyde	Perkins and Abbott (1972)
Enteromorpha spp.	almost complete cover	Island of Sylt	Reise (1983a)
Enteromorpha spp. and *Ulva* spp.	no measure given	Medway Estuary	Wharfe (1977)
Enteromorpha spp. and *Ulva* spp.	200-400*	Langstone Harbour	Soulsby *et al.* (1985)
Ulva lactuca	1,100.0 (1984) 300.0 (1986)	Bodega Harbor	Everett (1994)

Table 5.3 : Algal biomasses (gDW/m^2 or % cover) reported in various studies. * Indicates biomasses have been converted from fresh weight to dry weight using the conversion of Ramus and Venable (1987).

DISCUSSION

The two main aims of this study were;

1 - to investigate the ecological effects of macroalgal mats on an intertidal sandflat;

2 - to investigate whether macroalgal mat establishment could promote patch formation of *P. elegans* on Drum Sands.

These were addressed by a descriptive survey by sampling from weed-affected areas and weed-free areas.

The ecological effects of weed mats on intertidal sandflats.

Vaucheria subsimplex mat establishment, which occurred during September 1997, had a marked effect on both the fauna and the sediments of Drum Sands. Four weeks after establishment the mean number of individuals and diversity significantly increased in weed-affected areas compared to non-weed plots. The mean abundances of 8 of the 10 most abundant species significantly increased under weed mats as did the values of % sediment water, organic and silt/clay contents, medium phi and sorting coefficient, while the sediments between 1-4cm depth became significantly more reduced. In January, approximately 20 weeks after *V. subsimplex* mat establishment, the faunal differences between weed plots and non-weed plots were still very marked, *P. elegans* and *C. capitata* numerically dominating the communities of weed-affected sediments. All the sediment variables were still significantly increased in weed plots after 20 weeks although the sediments were no longer significantly more reduced.

The physical and physico-chemical effects of *V. subsimplex* on the underlying sediments during this study were essentially similar to those reported for other macroalgal mat species (see Chapter 4). These include a decreased sediment redox potential, increased silt/clay and organic contents and an increased sorting coefficient due to a reduction in water current velocity. *V. subsimplex* is a green filamentous alga which does not possess the long filaments of other green macroalgal mat forming genera and, therefore, has a very close association with the sediment surface. Consequently, the alga formed a velvet-like carpet over the sediments (pers. obs.). Raffaelli *et al.* (1999) proposed that there was little evidence that the observed differences of macroalgal mats on infaunal species abundances were due to differences in algal morphologies, although Everett (1994) stated that this was the reason why some invertebrates showed mixed responses between studies. However, this controversy mainly revolves around the results of studies investigating the effects of macroalgal genera with very different morphologies from *V. subsimplex* (e.g., *Enteromorpha*, *Ulva* and *Cladophora*) and therefore the effect of this species on macrofaunal abundances could not have been predicted with any certainty without a comprehensive survey. Furthermore, it is possible that since the growth of *Vaucheria* spp. on intertidal sandflats is not a common occurrence, this is possibly the first detailed survey to assess the effects of this macroalgal genera on the invertebrate abundances on intertidal sandflats within this area of Britain.

Many studies have documented the effects of natural macroalgal mat cover on intertidal invertebrates using community parameters such as changes in the numbers of species, individuals and changes in diversity (Nicholls *et al.*, 1981; Soulsby *et al.*, 1982). These studies have found that although the total numbers of individuals may increase due to opportunistic species such as *C. capitata* and oligochaetes, and species such as the gastropod *H. ulvae*, the number of species and diversity decrease. The establishment of *V. subsimplex* mats on Drum Sands, however, appeared to have had an 'enrichment' effect on the faunal assemblages present. Although the number of species were not significantly higher in the weed plots until 20 weeks after establishment, the mean numbers of individuals and diversity showed more rapid responses being significantly higher than weed-free areas after 4 weeks (although diversity was significantly lower after 20 weeks due to the numerical dominance of *P. elegans*). Throughout the period of algal cover, the change in actual species composition was only small - the species present in the two plot types remained similar, i.e., the increase in total abundances and diversity were mainly due to an increased abundance of those species already present. The amphipod *C. volutator* and the nudibranch *Doto* spp. were the only taxa which were found exclusively in the weed plots while no taxa were only present in the control plots.

These results, given the low biomass of *V. subsimplex* compared with biomasses reported in other studies, are fitting with the suggestion that weed has similar effects as those of observed during organic enrichment. While higher densities of weed create a more hostile environment resulting in an impoverished faunal community (e.g., Nicholls *et al.*, 1981; Soulsby *et al.*, 1982), areas with a low weed biomass tend to support higher numbers of individuals due to presumably an increased food supply (this study). Furthermore, it seems that the physical presence of *V. subsimplex* had no detrimental effect on the species present.

Unfortunately, previous surveys of this type have not recorded the redox potentials of the sediments under the weed mats. Although the *V. subsimplex* at Drum Sands rapidly caused the sediments below to become more reduced, it appears this was not severe enough to have had a significant deleterious effect on the species present. Hull (1987, 1988) reported much lower redox potentials in the sediments under his experimentally-implanted *Enteromorpha* spp. than those under the *V. subsimplex* mats in the present study. Although Perkins and Abbott (1972) did not measure redox potentials, they noted that *C. edule* were forced to migrate to the sediment surface by the reduced conditions just below the sediment surface in weed-covered areas; this was never observed at Drum Sands where their numbers actually increased.

Some of the species which increased in numbers with weed cover in this study, e.g., *C. capitata* and oligochaetes (mainly tubificids), have been found to increase under both experimentally implanted and naturally occurring weed mats (Wharfe, 1977; Nicholls *et al.*, 1981; Wiltse *et al.*, 1981). These opportunists increase in numbers due to the increased food supply and their relative tolerance of reduced sediments. However, many species which have been shown to decrease in abundance under weed cover; spionids, bivalves and the amphipod *C. volutator* (Perkins and Abbott, 1972; Nicholls *et al.*, 1981; Wiltse *et al.*, 1981; Reise, 1983a) increased in numbers in the weed plots in this study. The increased abundances of these species in this study presumably resulted from the increased food supply and the more stable sediments afforded by the weed-covered areas, together with the fact that *V. subsimplex*, at least at the density observed, seemed to have no deleterious effect on the feeding mechanisms of most deposit-feeding invertebrates. The nudibranch *Doto* spp. was found only in the weed plots and in moderate abundance. Prescott (1970) suggested that *Vaucheria* spp. harbours its own faunal invertebrate species in marine intertidal benthic environments and proposed that nudibranchs utilise *Vaucheria* spp. as a food source.

This study did not set out to explicitly determine the mechanisms by which many of the species increased in abundance with weed cover. Size-frequency measurements, however, suggested that for *P. elegans*, increased larval settlement, possibly facilitated by reduced water velocity, and/or increased juvenile survivorship, possibly due to fewer epibenthic predators, may have led to the increased densities obtained. This is supported by the results of Chapter 6 in which it was demonstrated that during periods of high larval availability, *P. elegans* was capable of rapidly numerically dominating after small-scale disturbances on Drum Sands. Given its reproductive strategy, *P. elegans* would probably have been able to show this response to the larger-scale disturbances imposed by macroalgal mat development. Furthermore, Hull (1987, 1988) postulated that larval settlement could have accounted for the observed increases in the numbers of several species during his weed-implantation experiment.

The positive effect of *V. subsimplex* on *P. elegans* recruitment in this study is in contrast with the findings of the weed implantation experiment (Chapter 4) in which the main *P. elegans* larval recruitment during May 1997 did not successfully occur in the weed treatment plots. Perkins and Abbott (1972), Nicholls *et al.* (1981) and Soulsby *et al.* (1982) suggested that algal mats had a detrimental effect on particularly the juveniles of many species in their surveys. The positive effect of *V. subsimplex* on larval recruitment during this survey was significant during periods of relatively low larval availability (end September/early October). Therefore, if *V. subsimplex* had been present at the same time as *E. prolifera*, large *P. elegans* densities may have resulted under *V. subsimplex* and the differences between the experiment and the survey may have been appreciably larger (see next section).

It is likely that increased larval settlement and/or survival was probably the process(es) by which many of the other species also increased in abundance under *V. subsimplex* mats, although without size measurements and information on their reproductive strategies and population structure, this cannot be concluded with any real certainty.

The possible role of algal-mat establishment in *P. elegans* patch formation on Drum Sands.

Once established, the *V. subsimplex* mats rapidly increased both the numbers of species present and the numbers of individuals of those species already present on Drum Sands, including large increases in the numbers of *P. elegans.* This effect was not short-lived and became even more pronounced during January, 20 weeks after the weed mats had established. Unfortunately, during February the weed mats, together with their accumulated sediments and associated faunal assemblages, disappeared, presumably due to erosion by winter storms. Therefore, although the *V. subsimplex* mats significantly increased the densities of *P. elegans*, they did not lead to *P. elegans* patch formation during the year this study was carried out.

The possibility that algal mats may have created *P. elegans* patches during other years cannot be ruled out. It is possible that the increased water movement due to storms was unusually strong during the winter of 1997-1998. Indeed, sediment erosion was probably the reason why the numbers of *P. elegans* had decreased in the control plots between October and January (from 52.8 ± 8.1 to 18.2 ± 5.9). However, the majority of the pre-existing *P. elegans* patches appeared unaffected by erosion during this winter. It is perhaps more likely that the timing of weed establishment during 1997 was influential in the erosion of weed plots. During 1997, the weed mats did not appear until September which is much later than weed mats usually establish on sandflats in Britain and much later than it occurred on Drum Sands during 1996 (late May/early June). Since juvenile *P. elegans* numbers in particular increased in sediments covered by *V. subsimplex*, the late development of these mats may not have increased *P. elegans* densities as much as in other years since the large recruitment phase in May/June was missed. Since the numbers of *P. elegans* were possibly lower under weed mats compared to those of previous years, and the period over which sediment accumulation and stabilisation could occur was shorter, the sediments where weed mats developed may have been more prone to erosion during the high-energy wave movement during winter compared to previous years. Furthermore, the unusual presence of the weed during the winter period may also have contributed to sediment erosion.

This reliance upon the early establishment of macroalgae and sediment accumulation has been proposed for *L. conchilega* mound development at Tentsmuir Beach, St. Andrews, by Carey (1987). Carey (1987) suggested that the formation of high-density patches of *L. conchilega*, together with accumulated sediments, were facilitated by *Enteromorpha* spp. development and that their survival during winter storms were dependent upon the presence of the weed to enhance spring recruitment of *L. conchilega*. Similarly, Fager (1964) recognised that increased larval recruitment, allowing worm numbers to build up before periods of high water movement, was a prerequisite for *O. fusiformis* patch formation in Mission Bay.

The present study on Drum Sands did not give any insight as to the possible reasons why *V. subsimplex* establishment was spatially heterogeneous. One would have expected that algal mats would most likely establish on *P. elegans* patches since the hydrodynamic effects of the worm tubes and stabilised sediments (see Chapter 8) encountered there may have facilitated algal spore settlement. However, this was clearly not the case: although macroalgal mats did establish on *P. elegans* patches many of the patches remained weed-free and weed covered many non-patch sediments. This suggests that algal *V. sumbimplex* mat development, at least during the year of study, reflected a cause of the observed faunal changes rather than an effect of the ambient faunal assemblages. It could be concluded that *V. subsimplex* mat formation was determined by other, non-investigated factors.

In conclusion, this study has indicated that *V. subsimplex*, a green filamentous alga with a very different morphology from algal species previously investigated by surveys (Perkins and Abbott, 1972; Nicholls *et al.*, 1981; Wiltse *et al.*, 1981; Reise, 1983a), had an enriching effect on the faunal communities of the intertidal sandflat Drum Sands. It is likely that this effect, which contrasts with those observed in other descriptive surveys (and the controlled algal-implantation experiment in Chapter 4), was due to a relatively low weed biomass although the effect of weed morphology may have also been an important factor. Increased numbers of the most abundant species, *P. elegans*, was due to increased larval recruitment either via increased settlement and/or increased larval survivorship. This study also indicated that a link between V. *subsimplex* mat establishment and the formation of high-density patches of *P. elegans* in previous years may have been possible. Since weed species, biomass, timing of establishment and patch size are all factors which are likely to change from year to year, extending the results obtained here to a conclusion concerning the long-term role of macroalgal mats on the spatial patterns of the invertebrate fauna on Drum Sands is inherently subjective. Long-term studies are needed to investigate this less equivocally.

CHAPTER 6

INITIAL COLONISATION OF DISTURBED SEDIMENTS : THE EFFECTS OF A BIOGENIC SPECIES ON COMMUNITY ESTABLISHMENT

INTRODUCTION

Zajac and Whitlatch (1982a) defined disturbance as 'any stochastic event initiating species population changes'. Although disturbances have been shown to be important factors influencing marine soft-bottom community structure (Johnson, 1970; Dauer and Simon, 1976a; Woodin, 1976, 1978, 1981; Eckman 1979, 1983; Eckman *et al.*, 1981; Thistle, 1981; Probert, 1984; Hall *et al.*, 1991), their spatial and temporal scales vary considerably (Thrush, 1988; Thrush *et al.*, 1992; Hall *et al.*, 1993). Small-scale disturbances ranging from $1cm^2$ to $1m^2$ create mosaics of small patches at different stages of recovery (Johnson, 1970; Thrush 1986b). Grassle and Sanders (1973) suggested that the existence of such a mosaic could permit the persistence of species in a community where they were competitively inferior. These small-scale disturbances, which tend to be biologically mediated and usually occur relatively frequently, include pits created by the feeding activities of rays (Levin, 1984a), Walruses (Oliver *et al.*, 1985), flatfish (Hall *et al.*, 1990), shorebirds (Savidge and Taghon, 1988) and crabs (Thrush, 1986b; 1988; Hall *et al.*, 1991) and by sediment modification by macroinfauna (Reise, 1983b; Woodin, 1985; Brey, 1991; Hall *et al.*, 1991). Large-scale disturbances, ranging from metres to kilometres, occur much less frequently and include storms (Ong and Krishnan, 1995), organic and oil pollution (Rosenberg, 1973; Grassle and Grassle, 1974; Pearson and Rosenberg, 1978) and red tides (Dauer and Simon, 1976a, 1976b).

The spatial extent of the disturbance can influence both the mode and rate of colonisation by the invertebrate fauna (Levin, 1984a; Gunther, 1992). While colonisation of large-scale patches tends to be dominated by species with planktonic larvae (Santos and Simon, 1980a; Levin, 1984a; Strathmann, 1986), experiments have shown that small-scale patches of disturbed sediments are often initially dominated by species with benthic dispersal (Levin, 1984a; Savidge and Taghon, 1988; Frid, 1989; Smith and Brumsickle, 1989). However, the role of post-larval colonisation of disturbed sediments has also been shown to be important at both large and small scales (Dauer and Simon, 1976a; Thistle, 1981; Zajac and Whitlatch, 1982a; Levin, 1984a; Frid, 1989; Smith and Brumsickle, 1989; Gunther, 1992; Thrush *et al.*, 1992; Turner *et al.*, 1997). Santos and Simon (1980b) suggested however that it is possible to incorrectly infer adult colonisation when sampling intervals are too long and/or sieve mesh sizes are too large to detect larval colonisation.

Connell and Slatyer (1977) proposed four generalised models for community assembly during succession. These were the facilitation, inhibition, tolerance and the random colonisation models. Many studies have been performed to elucidate which of these predominate within marine soft-bottom environments (e.g., Woodin 1981; Gallagher *et al.*, 1983; Whitlatch and Zajac, 1985; Trueblood, 1991) and in general, succession proceeds via a mixture of different kinds of interactions rather than one single model prevailing. Whitlatch and Zajac (1985), however, concluded that although biotic interactions between opportunistic organisms were important in controlling successional dynamics, the type of interaction ultimately depended upon the species present, their density and the habitat conditions. Dense aggregations of polychaetes' tubes have been shown to stabilise sediments by altering the characteristics of near-bed flow (Eckman *et al.*, 1981) and have been shown to be particularly important in affecting the early stages of faunal succession (Levin, 1981, 1982; Gallagher *et al.*, 1983; Whitlatch and Zajac, 1985; Noji and Noji, 1991). Therefore, colonisation following disturbances within polychaete tube-beds are likely to have different successional dynamics compared with those outside tube-beds.

Most studies investigating community establishment have followed species and community responses to disturbances which have occurred at only one point during the year and/or within only one type of habitat. However, since the colonisation potential of most species is predominantly governed by their larval availability at any one time (Bonsdorff and Osterman, 1984; Levin, 1984a; Ragnarsson, 1996), the resulting community at any stage of succession is likely to depend upon the timing of the initial disturbance (Zajac and Whitlatch, 1982a; 1982b).

Drum Sands is an ideal location in which to explicitly test certain aspects of population and community responses to disturbances. For example, it has been shown that the study area within Drum Sands contains a mosaic of communities in different successional stages with some species, for example, *P. elegans*, exhibiting pronounced patchiness (see Chapter 2). *P. elegans* has the ability to affect the hydrodynamics of near-bed flow and therefore the potential to affect settlement. Furthermore, this species has been shown to have a wide repertoire of reproductive strategies which was investigated in Chapter 3. Therefore, this system allowed certain questions about initial colonisation to be addressed. These were:

1 - do tube-bed areas have different early successional dynamics from non tube-bed areas?. This will be examined by comparing the initial communities of *P. elegans* patches with those of non-patch areas after a small-scale disturbance;

2 - does the successional stage of a community affect the colonisation mode of early colonisers?. This will be addressed by assessing the dispersal mode of the most abundant species to recently disturbed sediments within *P. elegans* patches with those from disturbances within non-patch sediments;

3 - can sediment disturbance lead to *P. elegans* patch formation on Drum Sands?.

METHODS

Experimental design - Eighty *P. elegans* patches were individually numbered from within the 250×400m study area (Chapter 1) so that patches could be selected randomly for experimentation. Six *P. elegans* patches (hereafter referred to as 'patch' plots) were randomly chosen and a $1m^2$ area marked within each by a small cane at each corner. The patches themselves were approximately $1\text{-}1.5m^2$ in area (Chapter 2). Similarly, 6 plots were chosen outside *P. elegans* patches (hereafter referred to as 'non-patch' plots) by random co-ordinates within the study area and a $1m^2$ area marked in the same way as for patch plots. Six replicates were chosen as this was decided to be the most that could be logistically sampled with respect to the amount of work involved and this was a sufficient number to allow non-parametric statistical analyses to be carried out if necessary. None of these plots had macroalgal mat cover either at the time of sediment implantation or at the time of sampling.

Sediment was obtained by inserting 12 corers, 10cm diameter, into the sand within the study area from non-patch sediments to a depth of 12cm. The sediment was kept in the corers and frozen at -20°C for 3 days, thawed for 1 day and then refrozen. Sediment defaunation by freezing at this temperature has been successfully achieved in many studies (e.g., Bonsdorff and Osterman, 1984; Savidge and Taghon, 1988; Bonsdorff, 1989; Frid, 1989; Thrush *et al.*, 1992). This freeze-thawing was repeated 6 times for each core. After treatment, no animals were found alive (n=6) and all the invertebrate taxa killed by this process were so severely damaged that they could easily be distinguished from invertebrates alive at the time of subsequent sampling (except nematodes). Any *P. elegans* tubes protruding from the treated sediment surfaces were removed. The sediment cores were kept intact throughout the freeze-thawing process, maintaining the original sediment structure was thought to reduce erosion when later replaced in the sand.

The 12 defaunated sediments were implanted on the 18th April 1997, ensuring that the tops were flush with the surrounding sediment surface. One defaunated sediment core was inserted into each of the 6 patch plots and 6 non-patch plots (see Figure 6.1). A $1m^2$ quadrat was located on the predefined $1m^2$ areas (see above), divided into 100 sections (10×10cm) with string and the defaunated sediments inserted after the ambient sediment had been removed. The locations of the defaunated sediments were chosen randomly. This approach allowed the exact position of the treated sediments to be relocated when later sampled and overcame the need for marking them with sticks which would have had hydrodynamic effects. This method was previously tested and the positions of the cores were located exactly (n=12). The outermost sections within the quadrat were ignored to minimise edge effects.

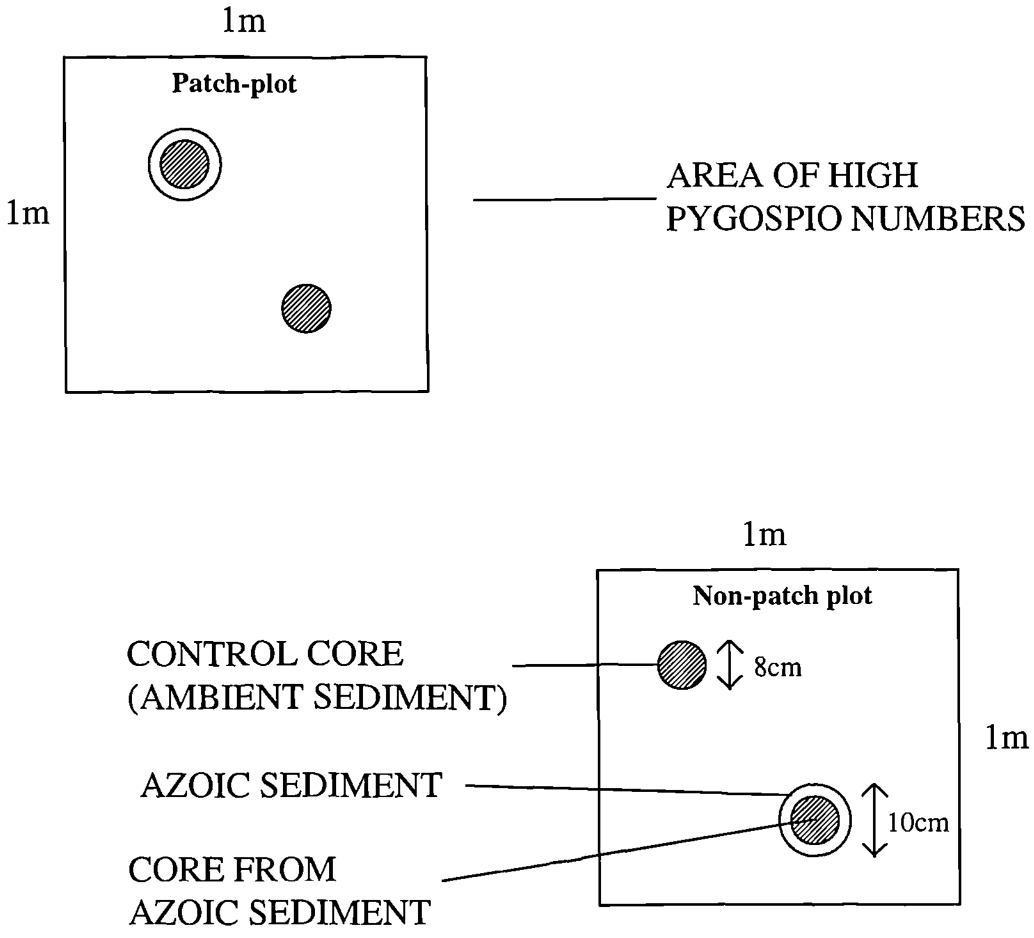


Figure 6.1 : Experimental layout of patch and non-patch plots. One patch plot and one non-patch plot are shown in detail while 6 replicates of each were used in each experiment. The ‘control cores’ (ambient sediment) shown were taken as part of a separate study (Chapter 8) but the results provide useful information as to the background densities of species for this study.

The size of the defaunated sediment core was chosen to approximately represent the area disturbed by small-scale disturbances such as the pits created by feeding flatfish. The scale of disturbance has been shown to result in different successional dynamics only when the disturbed area varies in size by many orders of magnitude (Wilson, 1992; Ragnarsson, 1996). Therefore, although the size of the disturbed areas in this experiment was slightly larger than those created by flatfish, similar successional dynamics would be expected. The sediment cores were implanted without the corers so as not to restrict immigration of infauna from below the sediment surface which would be possible after a natural disturbance. The treatment and implanting of the sediments were identical for both patch and non-patch plots.

The treated sediments were left for 3 weeks before sampling. This time interval was chosen from the results of preliminary studies carried out in March 1997, together with the information obtained on colonisation rates following disturbances at this scale provided by literature review (e.g., Zajac and Whitlatch, 1982a; 1982b; Levin, 1984a; Savidge and Taghon, 1988; Frid, 1989; Hall *et al.*, 1991; Wilson, 1992; 1994; Ragnarrson, 1996). Preliminary studies involved implanting defaunated sediments for 1, 2, and 3 weeks - only after 3 weeks was there a large increase in colonists (*C. capitata* and *P. elegans*) in both *P. elegans* patches and non-patches (n=6). Furthermore, since one of the aims of this experiment was to determine mode of colonisation, it was important to allow colonisation to proceed for as short a time as feasibly possible.

The implanted sediments were sampled after 3 weeks by an 8cm internal diameter corer to a depth of 12cm. Each sample was then sectioned into 2 parts. The top 3cm were removed and preserved in neutralised 10% saline formaldehyde solution with 0.01% Rose Bengal. These samples were later washed through a 500µm and 212µm mesh sieve stack in the laboratory. An elutriation method was used to help remove the fauna from the sediment retained by the 212µm mesh sieve before sorting. This 4-decantation elutriation method separated all the fauna from the sediment (n=25) apart from a small number of nematodes which were not analysed. The elutriant was again sieved on a 212µm mesh sieve and juvenile *P. elegans* and *C. capitata* removed under a dissecting microscope (×10 magnification). These were the only two species removed since they were the only taxa which colonised in sufficient numbers for size-frequency determination (see later). Very few young stages of the other macroinvertebrate species could be observed passing through this sieve. The 3-12cm fractions of the samples were sieved on a 500μm mesh sieve before preserving. These samples, from the treated sediments, are hereafter referred to as 'azoic' samples.

One sample (control core, Figure 6.1) from each plot was also taken at the same time as the azoic sample. The results from these samples will not be presented here. They will be referred to, however, where necessary to give background information on faunal densities in ambient sediments. The results from these samples form part of Chapter 8 which focuses upon the faunal and sediment differences between patches and non-patches. Sampling methods, sample treatment, faunal sorting and identification and statistical analyses for Chapter 8 were carried out in an identical manner to those described here.

The experiment was repeated on the 18th August and the 18th December 1997 using different *P. elegans* patch and non-patch plots in each experiment. The timings of the 3 experiments were aimed to coincide with high *P. elegans* larval availability (April), moderate larval availability (August) and low availability (December)(see Chapter 3). This was later confirmed by the abundances of *P. elegans* juveniles in Figure 6.2(ii).

The *P. elegans* individuals were divided into two groups *a posteriori* based on size. Size measurements were carried out in an identical way to Chapter 3. The smallest group (≤0.27mm, 5th setiger width) were considered to be 'juveniles' and those above this size were considered to be 'adults'. These size definitions were determined from the size distribution histograms (see results) - juveniles are those individuals which, based on the size-frequency histograms, had settled from the plankton within the 3 week experimental period. All juvenile individuals sampled had already begun tube construction at the time of sampling and, therefore, could be classed as settled larvae as opposed to transients.

To determine whether there were any differences in the environmental variables of the disturbed sediments between the two plot types, an additional experiment was carried out concurrent with the faunal experiment on the 18th December. Six patch and six non-patch plots were chosen and defaunated sediments implanted into each in the same way as for the faunal experiments. After 3 weeks, 1 core (2.4cm internal diameter, 3cm deep) was taken from within each of the previously defaunated sediments from each of the 12 plots. These samples were frozen and then later analysed for water, organic and silt/clay contents. Redox potential values were measured at 1, 2 and 4cm depths within each azoic sample, using the technique described in Chapter 4. Water and organic contents were determined in an identical way as described in Chapter 2. It was not possible to carry out a full particle size distribution analysis on the sediments and, therefore, silt/clay fraction was determined for each sample by wet sieving on a 63µm sieve. This method was compared with that used in Chapter 2 and although it produced higher % silt/clay fraction values it gave much more consistent results within replicates.

Data analyses - The invertebrate data were analysed using both univariate and multivariate techniques. For the univariate analysis, only those species with a mean abundance of at least 2 for any plot type were regarded as sufficiently abundant for statistical analysis. The data were checked for normality using the Anderson-Darling test and homogeneity of variances by the Bartlett test. Any data not conforming to either of these two were transformed using an appropriate transformation (Zar, 1984). The transformed data were re-checked using the above tests, any data still not conforming to either test were analysed using an appropriate non-parametric test. Differences in means between azoic samples from patch plots and non-patch plots were otherwise assessed using Two-sample t-tests.

The sizes of *P. elegans* (5th setiger width) and any other taxa with mean abundances ≥20 per core in either plot type were measured. *C. capitata* individuals were measured across their 3rd setiger (Ragnarsson, 1996). Size-frequency distributions were tested for difference between patch and non-patch azoics using the Kolmogorov-Smirnov (K-S) test and the χ^2 goodness of fit test. The relative suitability of these, and the advantage of using the latter test, are given in Chapter 4.

All statistics were performed using Minitab version 10.0, except for the Kolmogorov-Smirnov test which was carried out by hand using the formula given by Zar (1984) and the tables given by Smirnov (1948).

Multivariate analyses were carried out on the faunal data to assess (dis)similarities between community assemblages. All multivariate analyses were performed using the PRIMER (Plymouth Routines In Multivariate Ecological Research) package, version 4.0 (see Warwick and Clarke, 1994). Dendrograms were produced by hierarchical agglomerative clustering with group-average linking from the Bray-Curtis similarity matrices. The raw community data were square-root transformed, this was chosen *a priori* as a compromise between no transformation in which different community assemblages may result from the variability in the most common taxa, and a strong transformation, such as $\sqrt{\sqrt{}}$ or $\log(x+1)$, in which the rarer species have very strong influences on community (dis)similarities (Warwick and Clarke, 1994).

Non-metric Multi-Dimensional Scaling (or MDS) was carried out from which an ordination plot was produced. In ordination plots, the relative distances apart of the samples reflect relative similarity in species composition. Since the MDS ordination represents a multi-dimensional ordination in 2 dimensions, each algorithm has an associated stress value, the influence of which on the reliability of ordination plots is discussed by Warwick and Clarke (1994). The final MDS ordination in each analysis was that with the lowest associated stress value out of 9 iterations. The MDS procedure was repeated 10 times for each analysis to minimise the chance of producing MDS plots with only 'local minimum' stress functions (Warwick and Clarke, 1994), i.e., increasing the number of starting configurations of points in the ordination plots increases the chance of producing the most optimum MDS plot.

Testing for significance between patch and non-patch communities was performed using a One-way ANOSIM test (analysis of similarities) in which the null hypothesis (H_0) in each case was that there were no significant community differences between the two plot types. The ANOSIM test can be regarded as a non-parametric equivalent of the MANOVA test (e.g., Mardia *et al.*, 1979) in which few, if any, assumptions about the data are made. Benthic community data are usually far from normally distributed (Clarke, 1993) and, therefore, a non-parametric test is usually more suitable. However, no corrections are made for multiple pairwise testing (Warwick and Clarke, 1994), consequently, more emphasis should be placed on the value of R, the test statistic, rather than the p value. The test statistic R will always be between 0 and 1; if R≈1 all replicates within sites are more similar to each other than any other replicates from different sites while if R≈0 similarities between and within sites will be the same on average. As with standard univariate tests, it is possible for R to be significantly different from zero yet relatively small if there are many replicates for each site. The ANOSIM test is more reliable for indicating treatment differences than the MDS plot since it works on the full similarity matrix rather than the approximation to it in 2-dimensions (Warwick and Clarke, 1994).

RESULTS

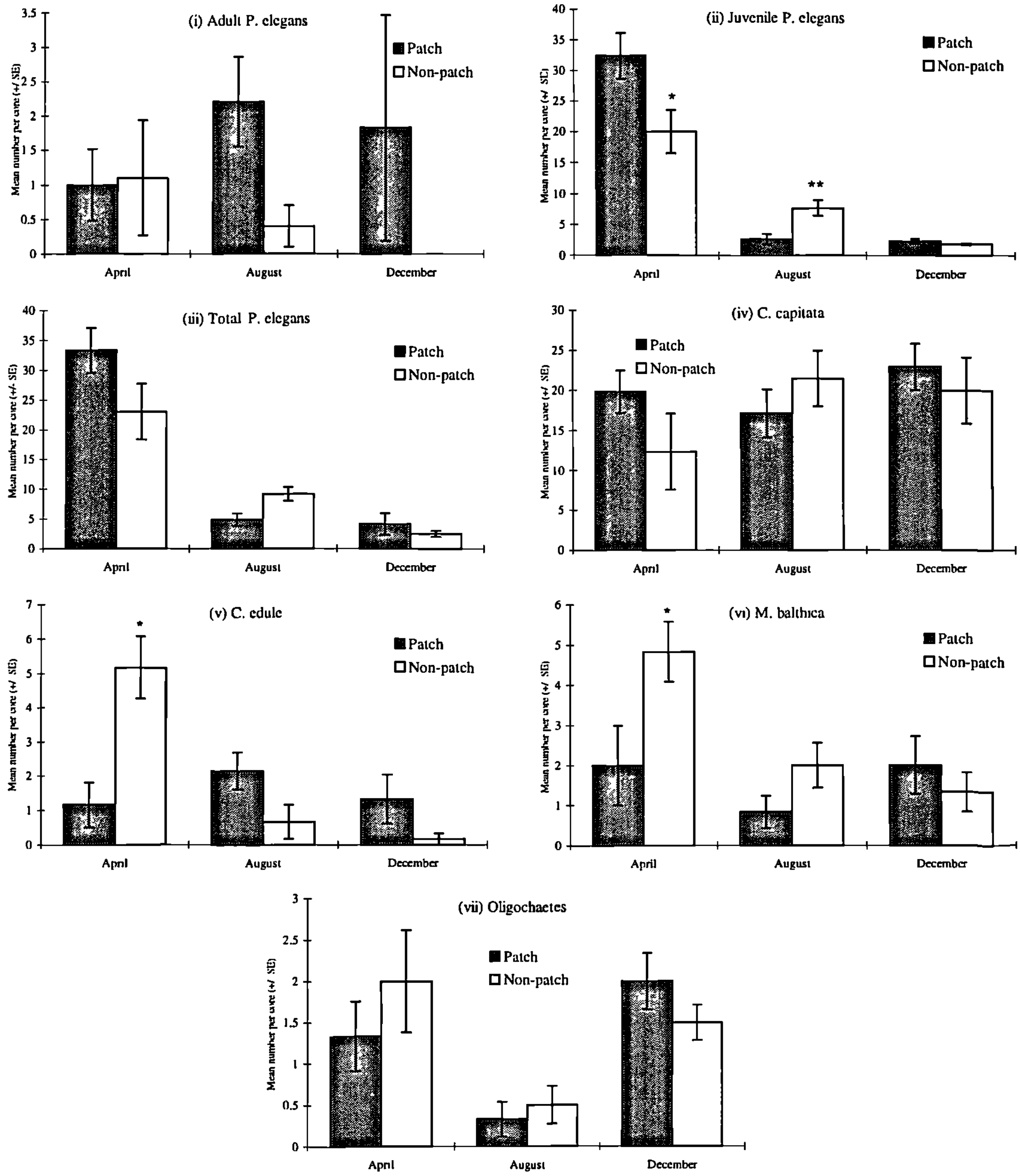
Univariate analysis of species abundances - A total of 14 and 15 taxa were recorded in the patch and non-patch azoic samples respectively, from the April, August and December experiments. Of these, only 5 were sufficiently abundant for statistical analysis. These were the polychaetes *P. elegans* and *C. capitata*, the bivalves *C. edule* and *M. balthica*, and oligochaetes (mainly tubificids). Their mean densities after 3 weeks colonisation, together with standard errors and the results of statistical testing between the two plot types (Two-sample t-test) are shown in Figures 6.2 (i-vii).

Pygospio elegans adults colonised the azoic sediments within 3 weeks in very low numbers. In the August and December experiments, adult *P. elegans* densities in patch samples were higher, although not statistically significant, from those in non-patch samples.

In contrast to the adults, juvenile *P. elegans* colonised the azoic sediments in relatively high numbers when ready-to-settle larvae were present in the water column. This was the case during April when a large peak in *P. elegans* settlement occurred at Drum Sands (see Chapter 3). At this time, a mean density of 32.3 ± 3.7 juveniles per core colonised the patch plots. Moreover, this was statistically higher than the number of juveniles, 20 ± 3.5 per core, successfully colonising non-patch plots, see Figure 6.2(ii). In August, the numbers of juveniles colonising azoic sediments were much lower and in contrast to the situation in April, their numbers were significantly higher in non-patch samples. Larval settlement was lower during December in both patch and non-patch plots, despite a second recruitment peak in the population at Drum Sands in December (Chapter 3). This disparity may have been due to the fact that samples for Chapter 3 were taken at the start of December, while this experiment was not started until the 18th of December, suggesting the acute recruitment phase recorded in Chapter 3 terminated early in December.

Capitella capitata colonised azoic sediments within 3 weeks in relatively high numbers in all three experimental periods. This species was the only one to increase in numbers in the treated sediments compared to numbers in ambient sediments taken at the same time (see Figure 6.2(iv) and Figure 8.1(iv)), although this was not statistically analysed. However, the colonisation of *C. capitata* was similar in numbers between patch and non-patch plots in all three experiments.

The responses of the two bivalves *C. edule* and *M. balthica* to the disturbances were similar to each other. In April, when colonisation by larval *P. elegans* was high, these two bivalve species colonised *P. elegans* patches in significantly lower numbers than outside patches. This was not the case during August or December when colonisation by these two bivalve species continued to be low both in and outside patches (Figures 6.2(v-vi)). Oligochaetes colonised the azoic sediments in very low abundances with no statistical difference between the two plot types (Figure 6.2(vii)).



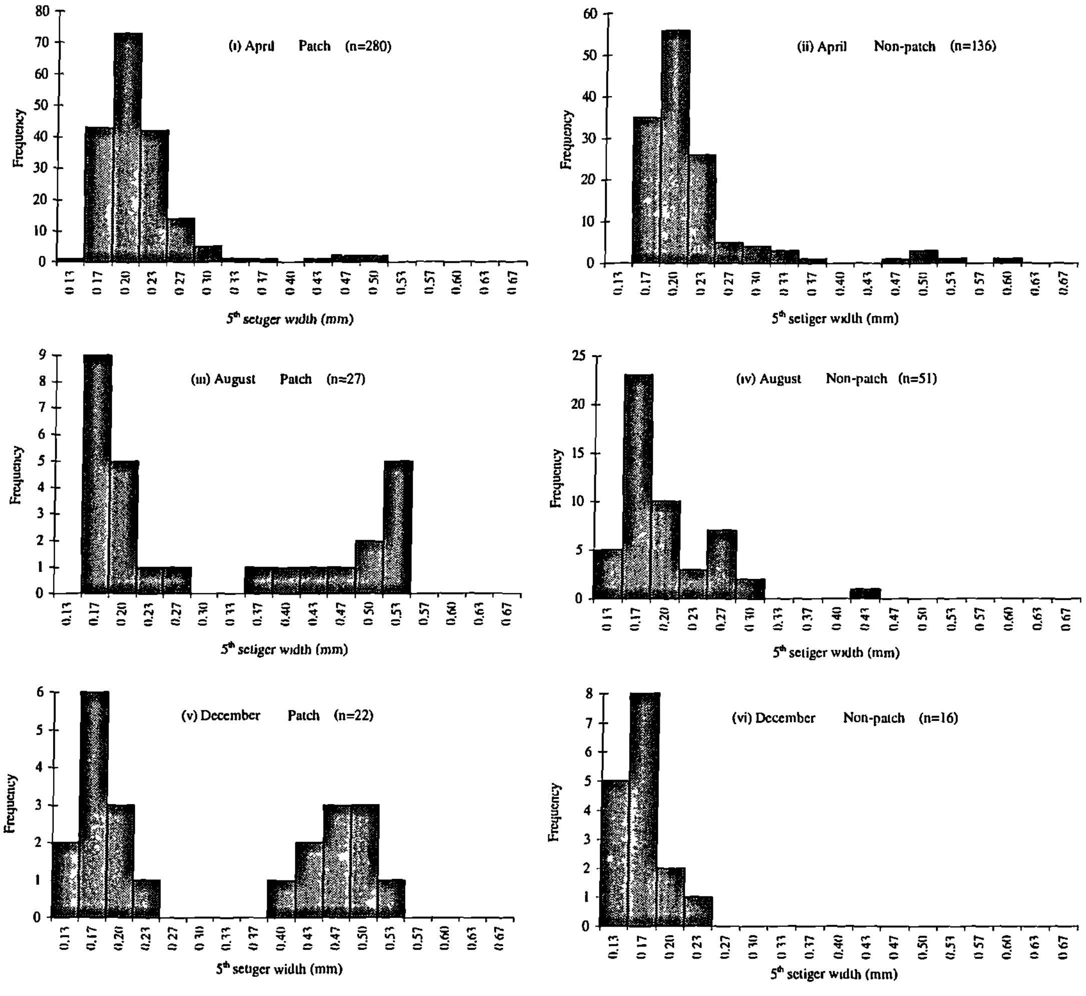
Figures 6.2(i-vii): Mean faunal densities of the taxa sufficiently abundant for statistical analysis after 3 weeks colonisation of azoic sediments (± S.E. Mean, n=6). * Denotes a statistical difference between the means of patch and non-patch plots with $p<0.05$; ** denotes $p<0.01$; Two-sample t-test. Total *P. elegans* means were not statistically tested since *P. elegans* adults and juveniles were tested separately.

Size-frequency analysis - Only 2 species were considered sufficiently abundant to carry out size-frequency measurements, these were *P. elegans* and *C. capitata*. The sizes of the bivalves *C. edule* and *M. balthica* were examined and it appeared that for both these species colonisation was via adults and that no differences between patches and non-patches were apparent.

Figures 6.3(i-vi) show the size-frequencies of the *P. elegans* individuals after 3 weeks colonisation for each of the 3 experiments. In April, colonisation of azoic sediments in patches and non-patches produced similar size-frequency distributions ($p=0.389$, $p>0.05$; χ^2 goodness of fit and K-S tests, respectively; see Table 6.1(i)). Colonisation of azoic sediments occurred predominantly via larval settlement with very low numbers of adults appearing in the azoic sediments after 3 weeks, even within *P. elegans* patches. Since the size-frequency distributions of juveniles in the azoic sediments were very similar to those from ambient sediments at this time (see Chapter 8, Figure 8.2(i-ii)), the beginning of intense larval settlement at Drum Sands probably started at approximately the same time as the azoic sediments were implanted, i.e., 18th April 1997.

In contrast to the results from April, in August there were statistical differences between the *P. elegans* size-frequencies in the patch and non-patch azoic samples ($p=0.001$, $p<0.05$; χ^2 goodness of fit and K-S tests, respectively; see Table 6.1(ii)). This can be explained by the presence of adult individuals colonising azoic sediments in *P. elegans* patches (40% of colonising individuals were adults), while colonisation outside patches remained predominantly due to larval settlement (83.52% of the χ^2 total was explained by size class ≥0.30mm 5th setiger width (Table 6.1(ii)).

During December, 45% of the colonisation by *P. elegans* to patch azoics was due to adults while no adults were recorded in non-patch azoic sediments. This resulted in significantly different *P. elegans* size-frequency distributions due to a bimodal distribution in patch azoics ($p=0.005$, $p<0.05$; χ^2 goodness of fit and K-S tests, respectively; see Table 6.1(iii)). The numbers of juveniles settling in the azoic sediments of the two plot types were similar, but no adults colonised azoic sediments of non-patch areas (Figure 6.3(vi)). Consequently, 72.87% of the χ^2 variation was explained by those individuals ≥0.27mm 5th setiger width (Table 6.1(iii)).



Figures 6.3(i-vi) : Size-frequency histograms of *P. elegans* from patch and non-patch azoic samples for April, August and December 1997 experiments, n denotes total number of individuals.

(i) APRIL

	χ^2 **goodness of fit**						**K-S**
Size (mm)	≤ 0.17	0.20	0.23	0.27	≥ 0.30	**p-value**	**p-value**
% explained	4.32	1.06	12.23	49.25	33.12	0.389	>0.05

(ii) AUGUST

	χ^2 **goodness of fit**					**K-S**
Size (mm)	0.13 - 0.17	0.20 - 0.23	0.27 - 0.30	≥ 0.33	**p-value**	**p-value**
% explained	9.90	0.60	5.97	83.52	**0.001**	**<0.05**

(iii) DECEMBER

	χ^2 **goodness of fit**				**K-S**
Size (mm)	0.13 - 0.17	0.20 - 0.23	≥ 0.27	**p-value**	**p-value**
% explained	25.73	1.41	72.87	**0.005**	**<0.05**

Tables 6.1(i-iii) : Results of χ^2 goodness of fit and K-S tests between *P. elegans* size-frequency distributions of patch and non-patch azoic samples showing p-values and percentage of the total χ^2 value each size class is responsible for. Due to decreasing abundances in August and December, different size classes were chosen to ensure expected values greater than 5 were obtained (Elliot, 1977).

The size-frequency distributions for *C. capitata* are presented in Figures 6.4(i-vi) and the results of χ^2 goodness of fit and K-S tests are given in Table 6.2(i-iii). During April there was no difference between the size-frequency distributions of patch and non-patch azoic samples ($p=0.802$ and $p>0.05$; χ^2 goodness of fit and K-S tests, respectively, Table 6.2(i)). During August, the size distributions of *C. capitata* colonising patch and non-patch sediments were similar, except for the small peak of adult individuals (0.30mm 3rd setiger width, Figure 6.4(iii)) in the former. Although the χ^2 goodness of fit test was significant, the K-S test was not and, therefore, the two distributions were not considered significantly different. However, during December, the individuals colonising patch azoic sediments were distinctly larger than those in non-patch sediments and a skewed size-distribution was apparent for the latter. These tests were significantly different ($p<0.001$, $p<0.01$; χ^2 goodness of fit and K-S tests, respectively; see Table 6.2(iii)) with 37.7% of the χ^2 variation being explained by the smallest size class (≤0.20mm 3rd setiger width).

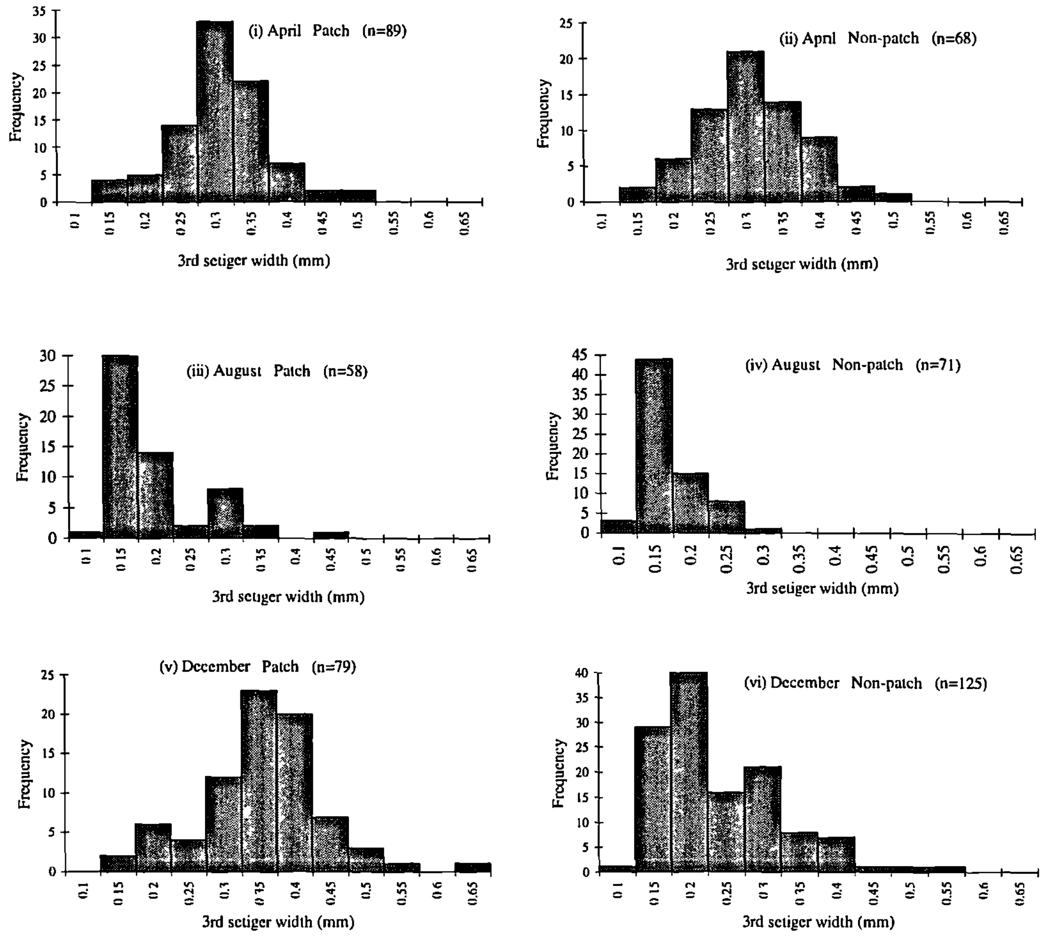


Figure 6.4(i-vi) : Size-frequency histograms of *C. capitata* from patch and non-patch azoic samples for April, August and December 1997 experiments, n denotes total number of individuals.

(i) APRIL

	χ^2 **goodness of fit**						**K-S**
Size (mm)	≤0.20	0.25	0.30	0.35	≥0.40	p-value	p-value
% Explained	3.27	9.11	22.30	14.83	50.41	0.802	>0.05

(ii) AUGUST

	χ^2 **goodness of fit**					**K-S**
Size (mm)	≤0.15	0.20	0.25	≥0.30	p-value	p-value
% Explained	11.26	0.43	2.70	85.61	**0.009**	>0.05

(iii) DECEMBER

	χ^2 **goodness of fit**							**K-S**
Size (mm)	≤0.20	0.25	0.30	0.35	0.40	≥0.45	p-value	p-value
% Explained	37.78	3.33	0.20	24.40	21.11	13.18	**<0.001**	**<0.01**

Table 6.2(i-iii) : Results of χ^2 goodness of fit and K-S tests between *C. capitata* size-frequency distributions of patch and non-patch azoic samples showing p-values and percentage of the total χ^2 value each size class is responsible for. Due to decreasing abundances in August and December, different size classes were chosen to ensure expected values greater than 5 were obtained (Elliot, 1977).

Multivariate analysis of community structure - The complete species matrices were used for multivariate analyses and these are summarised in Table 6.3. In total, 15 species colonised the azoic sediments within 3 weeks, although the majority of these were found in very low numbers.

Pygospio elegans (adult)	*Eteone* cf *flava*
Pygospio elegans (juvenile)	*Anaitides mucosa*
Capitella capitata	*Glycera tridactyla*
Cerastoderma edule	*Scoloplos armiger*
Macoma balthica	*Fabulina fabula*
Polydora cornuta	*Nephtys hombergii*
Streblospio benedicti	oligochaetes
Spio martinensis	polynoids

Table 6.3 : Total species list from patch and non-patch azoic samples for all three experiments.

The dendrograms produced by hierarchical agglomerative clustering, together with the 2-dimensional ordination plots produced by non-metric MDS of the resulting communities from the April, August and December experiments are given in Figures 6.5-6.12. The stress values associated with these MDS ordinations varied from 0.04 to 0.18. Although there is no critical cut-off value for stress values above which a species matrix cannot be represented adequately in a 2-dimensional MDS plot, the lower the stress the better. Warwick and Clarke (1994) suggested that stress values between 0.1-0.2, as the majority of those in the present study, give 'only potentially useful 2-dimensional pictures'. Under these circumstances, they recommended that the MDS plot should be complemented with other techniques such as clustering. Therefore, for ordinations with stress values between 0.1-0.2 dendrograms are included since they can potentially aid interpretation of the MDS plots. However, superimposition of the cluster groups at arbitrary similarity levels from the dendrograms onto the ordination plots, as outlined by Warwick and Clarke (1994), was not performed since this tends to add discrete subdivisions onto a community continuum. To investigate community differences between patches and non-patches, circles enclosing treatments were drawn where the degree of overlap is a reflection of the community similarities/differences between them. These were statistically analysed by One-way ANOSIM tests (Table 6.4).

In April, the invertebrate faunal communities of 5 out of the 6 patch replicates occurred in the same cluster at 70% similarity (Figure 6.5). This suggests that in April, colonisation of disturbed sediments within *P.elegans* patches resulted in distinctly different initial communities compared with those in non-patch areas. The MDS plot supported this, there was no overlap between the clusters formed by the 2 plot types (Figure 6.6). The results of the One-way ANOSIM test also suggested this, the test being statistically significant with a p-value of 0.2% and a test statistic of 0.367. There appeared to be greater replicate variability in the community assemblages in the non-patch sediments compared to patch sediments, the replicates of the former creating 3 clusters at 71% similarity.

Although the initial community structure in patches and non-patches were different to each other in August, the distinction was not as marked as that observed in April. The dendrogram presented in Figure 6.7 suggested that patch replicates 1 and 5 showed some similarity to non-patch communities. This is supported by the MDS plot (Figure 6.8) in which the 2 clusters have a large overlap. The p value for the One-way ANOSIM test was 4.3%. However, in view of the lack of compensation for multiple testing, and an R value of only 0.250, this is not considered significant.

In December, no statistical differences between patch and non-patch communities were observed (p=35.5% and R=0.028; One-way ANOSIM, Table 6.4). Figure 6.9 shows that at 70% similarity, a large cluster is formed containing 5 of the non-patch replicates and 3 patch replicates. Figure 6.10 shows that there is a large overlap between the clusters formed by the 2 plot types in an MDS plot.

Month	Sample statistic (Global R)	No. statistics ≥ Global R	Significance level of sample statistic
April	0.367	1	0.2%
August	0.250	20	4.3%
December	0.028	164	35.5%

Table 6.4: Results of One-way ANOSIM tests between patch and non-patch communities for April, August and December 1997 colonisation experiments. A total of 462 test statistics were permuted in each test.

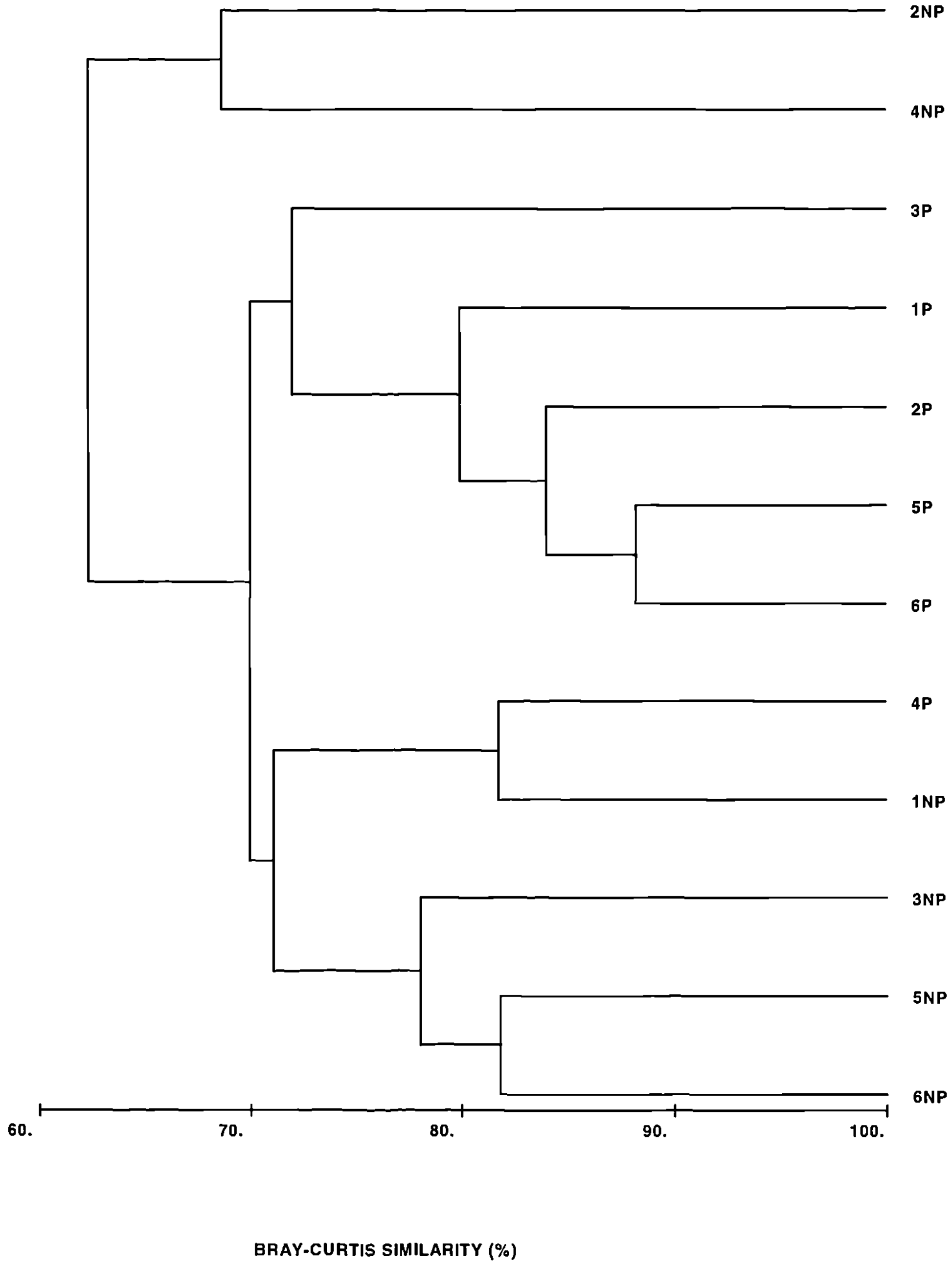


Figure 6.5: Dendrogram of patch (P) and non-patch (NP) replicates for the April experiment, using group-average clustering from Bray Curtis similarities on √-transformed abundances.

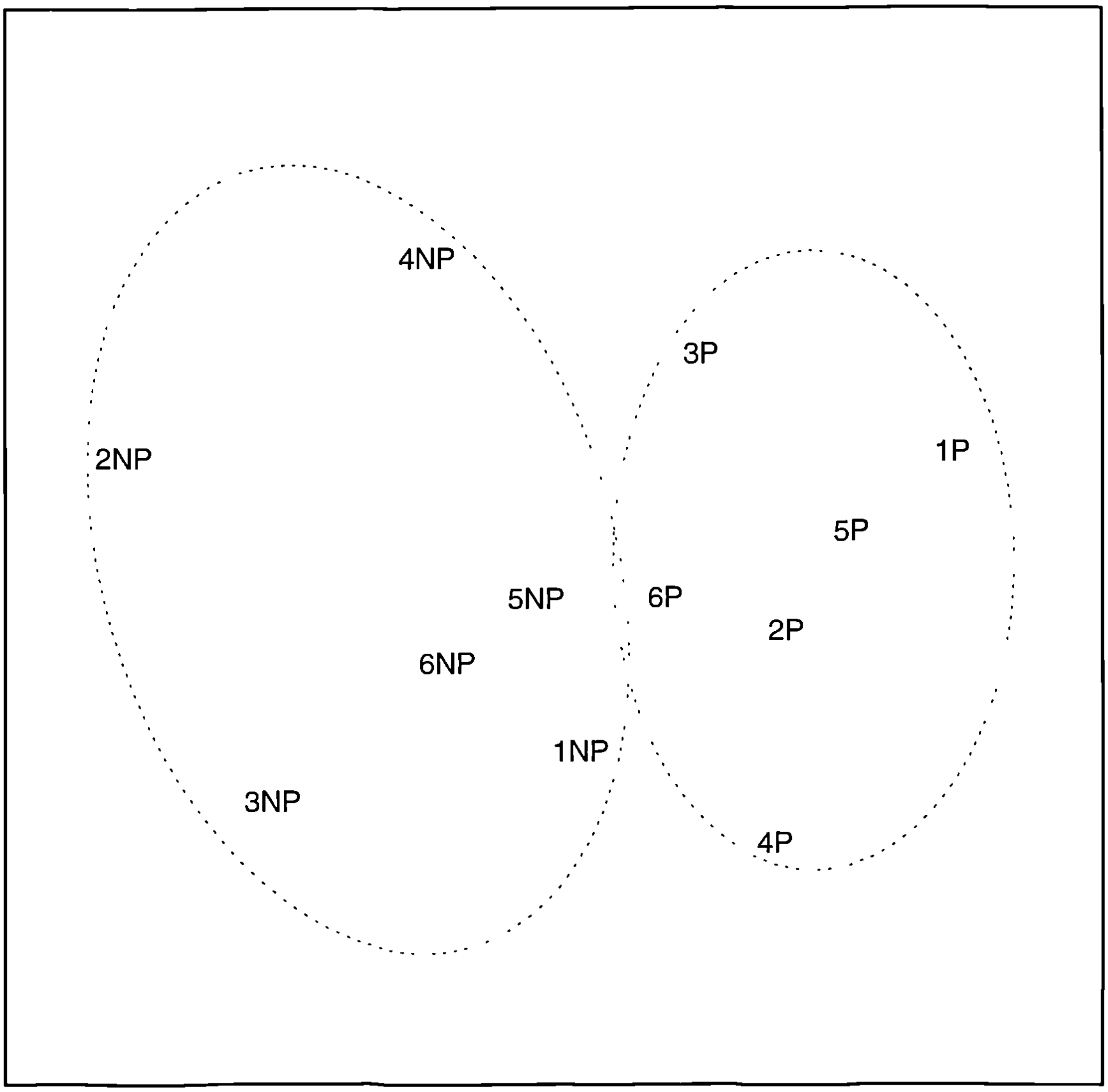


Figure 6.6: Two-dimensional MDS ordination of patch (P) and non-patch (NP) replicates for April experiment. Dashed lines represent clusters formed by the replicates from the 2 plot types. Stress = 0.12.

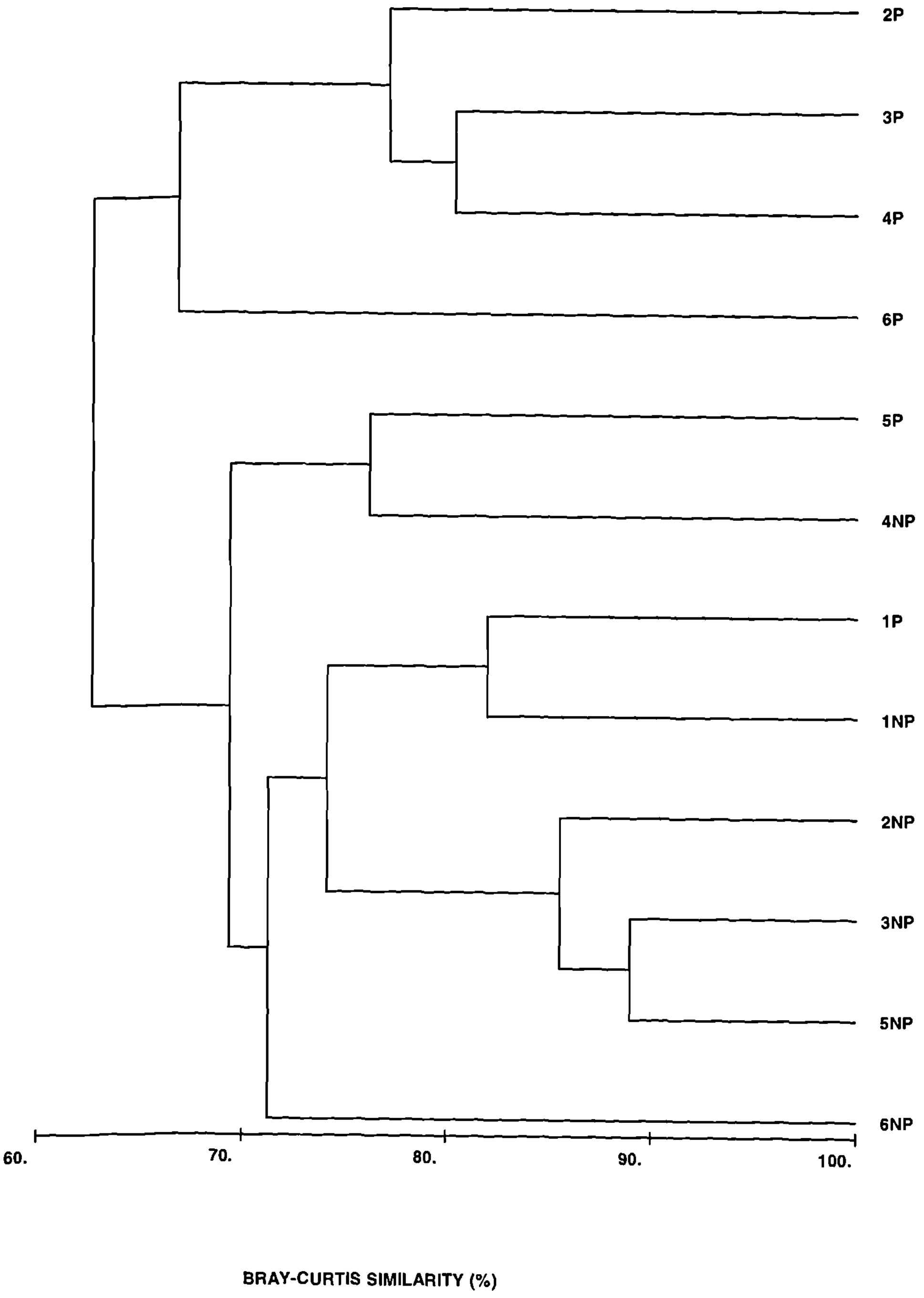


Figure 6.7: Dendrogram of patch (P) and non-patch (NP) replicates for August experiment, using group-average clustering from Bray Curtis similarities on √-transformed abundances.

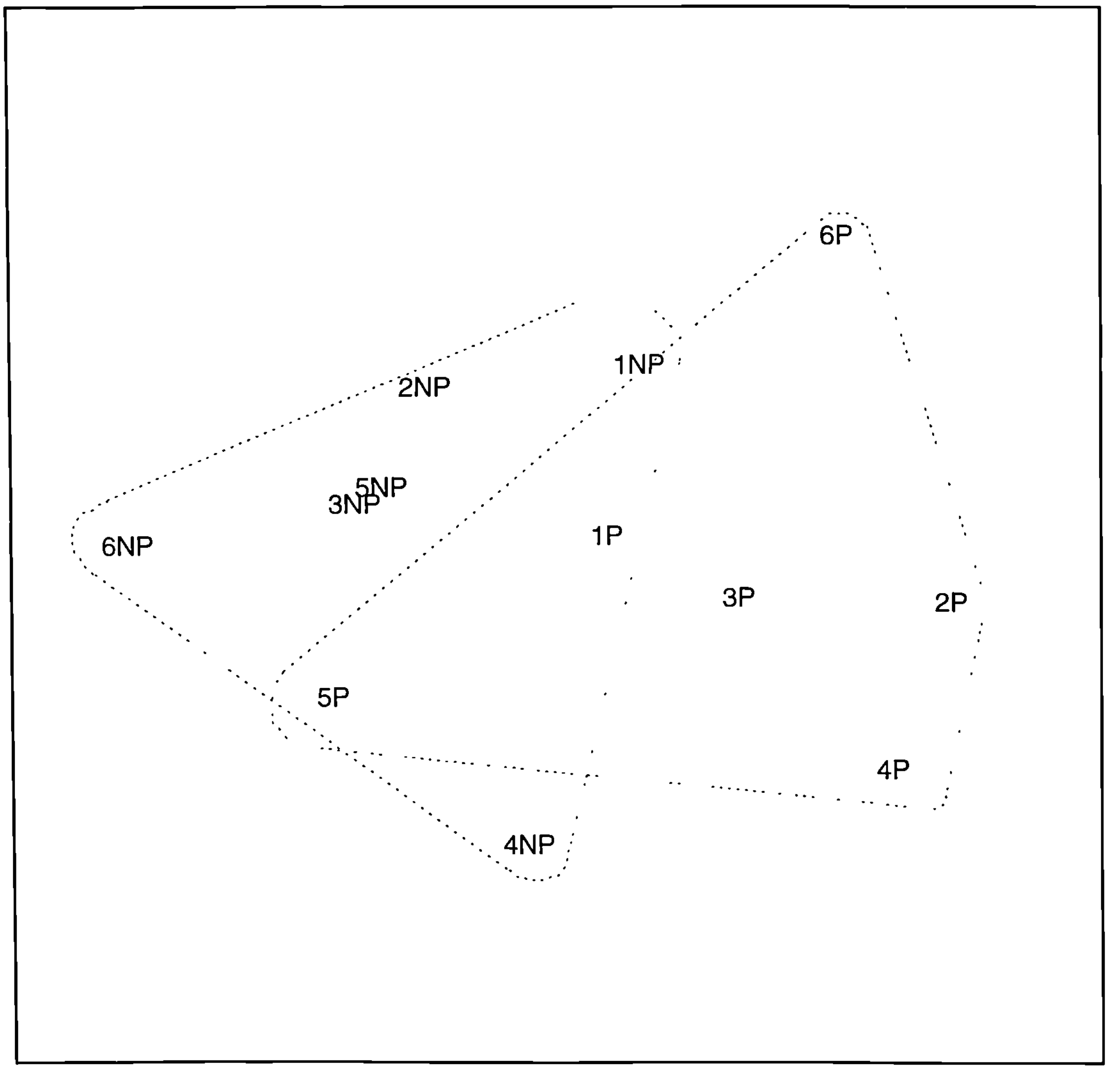


Figure 6.8: Two-dimensional MDS ordination of patch (P) and non-patch (NP) replicates for August experiment. Dashed lines represent clusters formed by the replicates from the 2 plot types. Stress = 0.13.

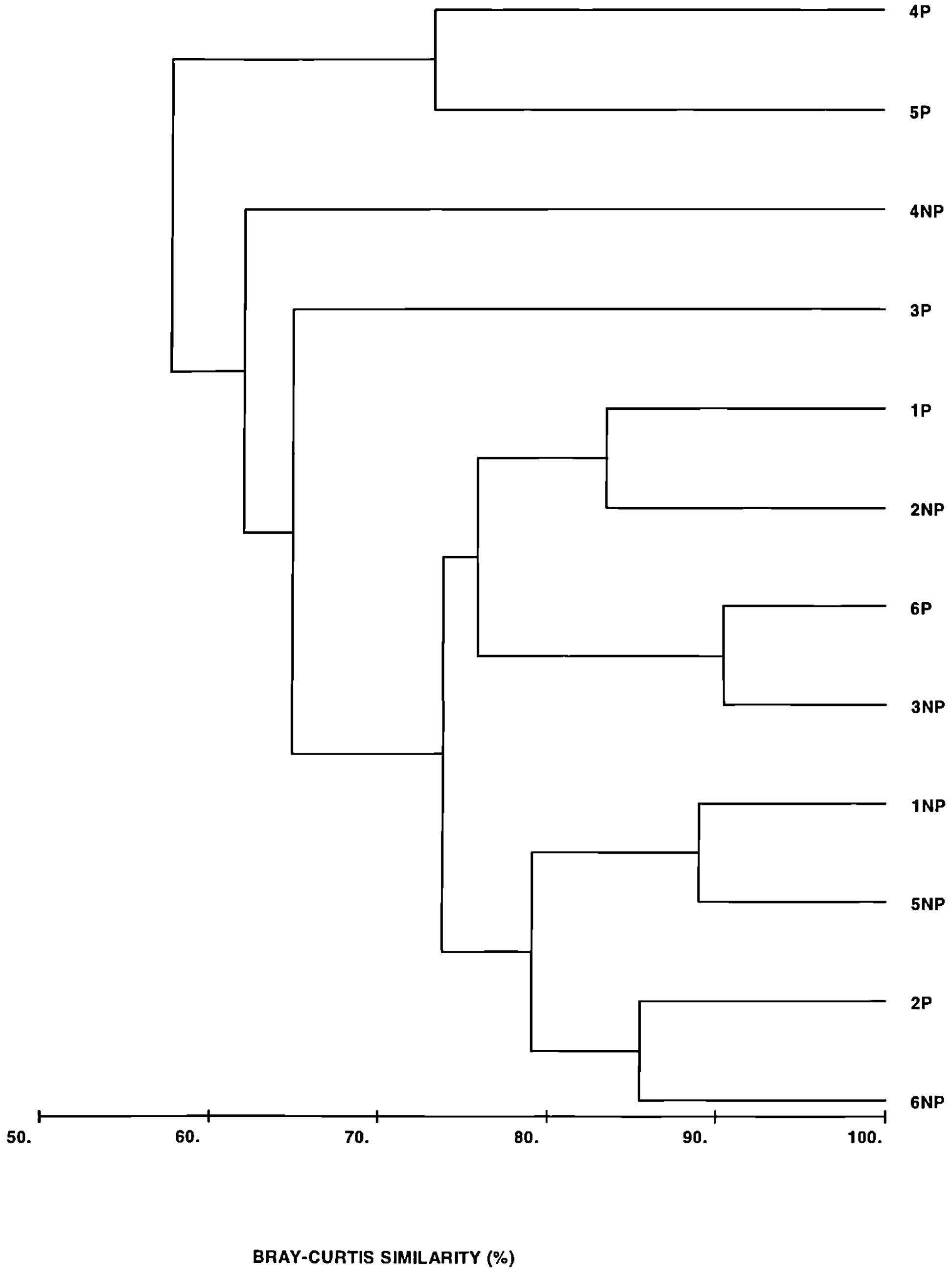


Figure 6.9: Dendrogram of patch (P) and non-patch (NP) replicates for December experiment, using group-average clustering from Bray Curtis similarities on √-transformed abundances.

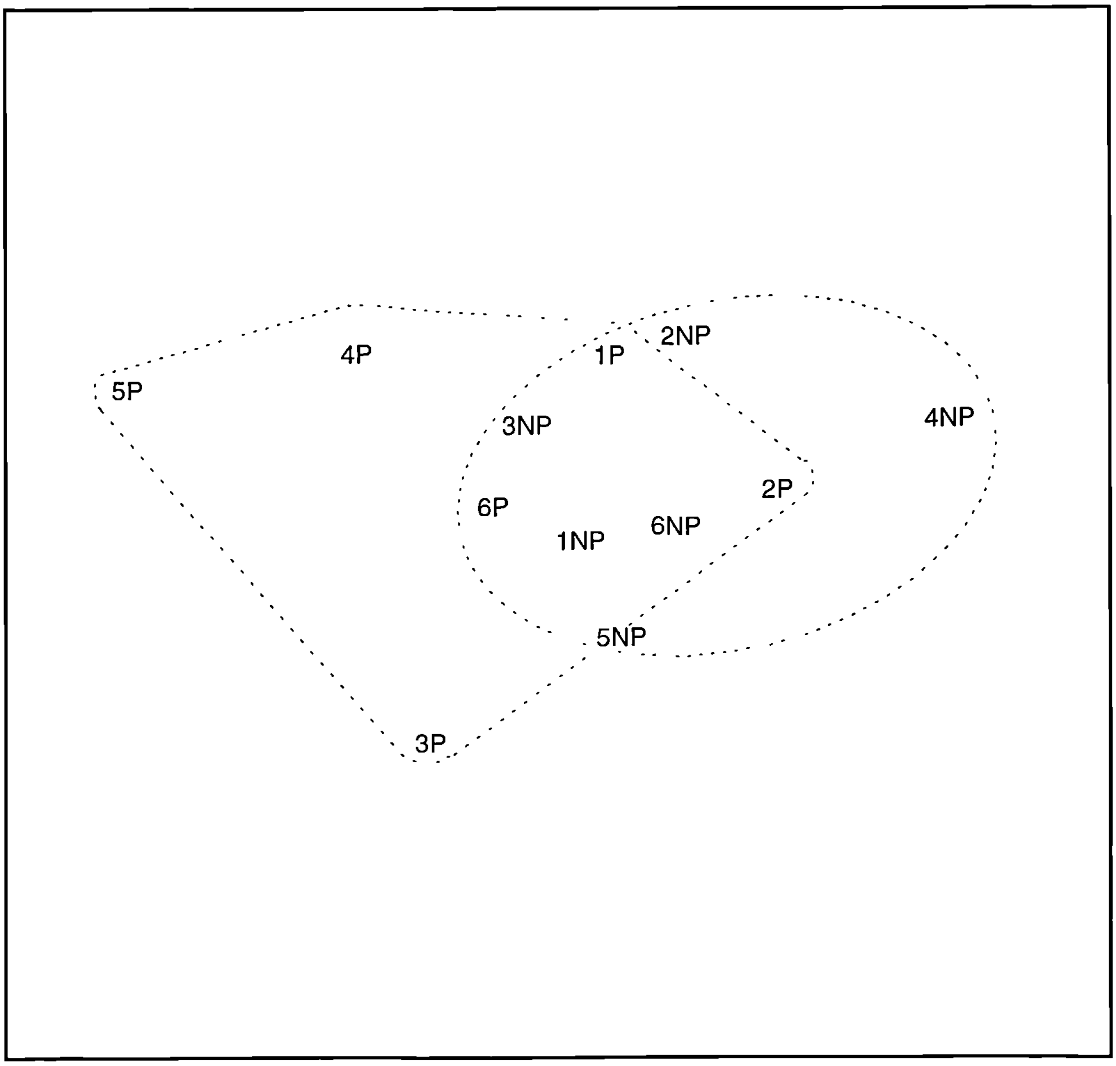
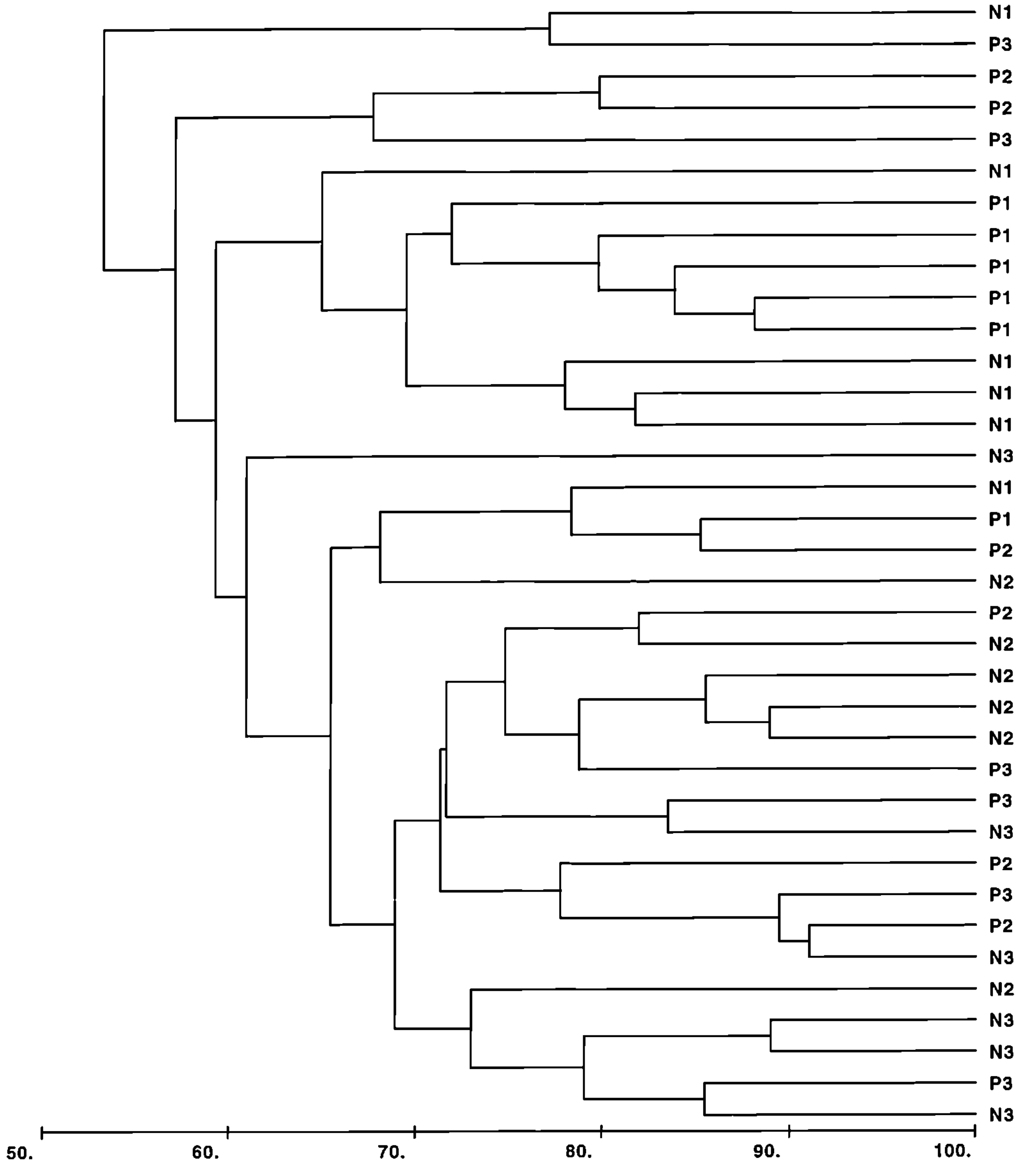


Figure 6.10: Two-dimensional MDS ordination of patch (P) and non-patch (NP) replicates for December experiment. Dashed lines represent clusters formed by the replicates from the 2 plot types. Stress = 0.11.

Figures 6.11 and 6.12 show the dendrogram and 2-dimensional ordination plot of all the patch and non-patch replicates from all 3 experiments. Lines have been superimposed on the MDS plots enclosing the samples from each of the 3 months so that the ordination plot allows an assessment of the effects of season on colonisation and of the strength of this effect in relation to the effect of plot type. The stress value of 0.18 is a little higher than those obtained for each month separately due to the larger number of samples. The MDS plot suggests that there was a noticeable seasonal effect in the initial communities colonising defaunated sediments, April being noticeably different from August and December. This was probably mainly due to changes in the numbers of *P. elegans* larvae settling. Furthermore, during April the patch plots and non-patch plots can be more-or-less separated suggesting that in addition to the seasonal effect, the effects of plot type can be observed. This was not apparent for the August and December experiments when plot type differences were not so pronounced (see Figures 6.8 and 6.10).

Figure 6.13 presents the ordination of the 'average' faunal communities in both azoic and ambient (see Chapter 8) samples for both plot types. 'Average' communities, which were calculated on PRIMER, were used since an MDS plot of all 108 replicates would have been difficult to interpret. The dendrogram is not included here due to the low stress value of 0.04. The ordination, which includes the results from both the April, August and December experiments, allows an estimation of the similarity between azoic and ambient communities after 3 weeks. There is very little overlap between the cluster formed by the azoic communities and that of the control communities. However, it can seen that the azoic patch and non-patch communities from the April experiment are both located very near the cluster formed by the ambient communities and conceivably form one larger cluster. Therefore, while colonisation during August and December was either relatively slow, or produced communities with different species composition to ambient communities, colonisation of azoic sediments during April was relatively rapid and after 3 weeks a community similar to ambient was present.



BRAY-CURTIS SIMILARITY (%)

Figure 6.11: Dendrogram of all patch (P) and non-patch (N) replicates, using group-average clustering from Bray Curtis similarities on √-transformed abundances. The months April, August and December are labelled as 1, 2, and 3 respectively.

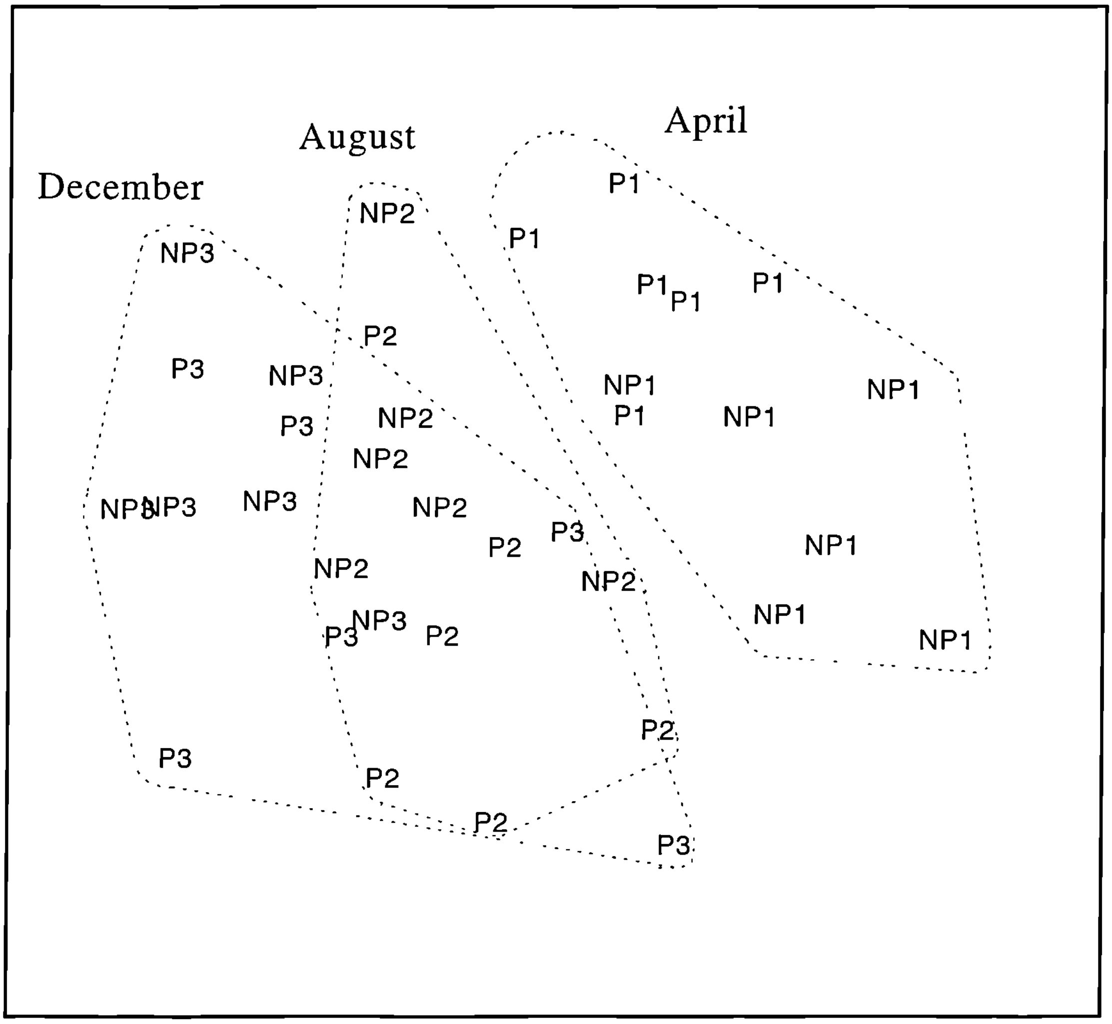


Figure 6.12: Two-dimensional MDS ordination of all patch (P) and non-patch (NP) replicates for the three experiments. The months April, August and December are labelled as 1, 2, and 3 respectively. Dashed lines represent clusters formed by the patch and non-patch replicates from each month. Stress = 0.18.

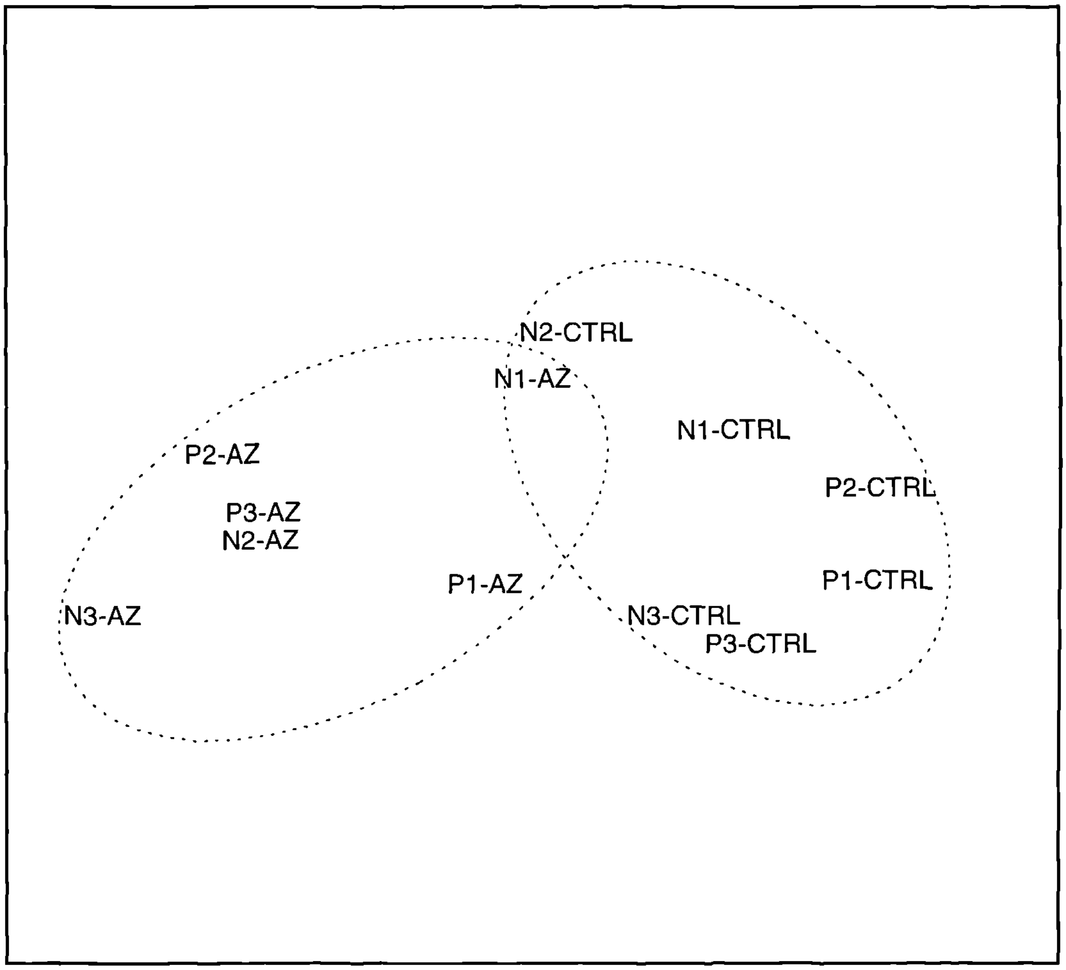


Figure 6.13: Two-dimensional MDS ordination of the ‘average’ azoic (AZ) and ambient (CTRL) communities from patch (P) and non-patch (N) plots. Months are given as numbers where 1= April; 2= August; and 3= December 1997. Dashed lines show clusters formed by azoic and ambient communities. Stress = 0.04.

Sediment water, organic and silt/clay contents - Figures 6.14 and 6.15 present the results of the measured sediment variables in patch and non-patch azoic sediments 3 weeks after implantation. Figure 6.14 suggests that in December, there were no statistical differences after 3 weeks implantation for water content, silt/clay fraction and organic content between patch and non-patch azoics. Additionally, the organic contents of the azoic sediments were similar to those of the ambient sediments (see Figure 8.12(iii), Chapter 8) at this time. Therefore, it is likely that faunal responses were not due to food accumulation in disturbed sediments as concluded in the study by Thistle (1981).

The environmental conditions in the patch plots were not sufficiently different, therefore, from non-patch plots to have any measurable effect on these sediment parameters within 3 weeks. This suggests that faunal differences between patch and non-patch azoic samples during December were not likely to have resulted from differences in any of these three variables. Whether this holds true for the other months cannot be assumed. Furthermore, the lack of a statistical difference for any measured variable between plot type does not necessarily mean that the variable had no effect on the invertebrate fauna since colonisation may be effected by subtle differences in sediment conditions which were not detected. In addition, significant changes in other sediment variables not measured in this experiment may have occurred.

Redox potentials - In contrast to the bulk sediment granulometric characteristics, the 2cm and 4cm redox potentials of the treated sediments were significantly more positive in patch sediments after 3 weeks compared to non-patch sediments. The reason for this is not clear, especially since this was not the case for ambient sediments at this time, (see Figure 8.13(iii), Chapter 8). However, it is unlikely that differences in the redox potential at 2cm and 4cm sediment depths had any effect on faunal colonisation since colonisation was almost exclusively via settlement and/or migration onto the sediment surface (except perhaps for *C. capitata*).

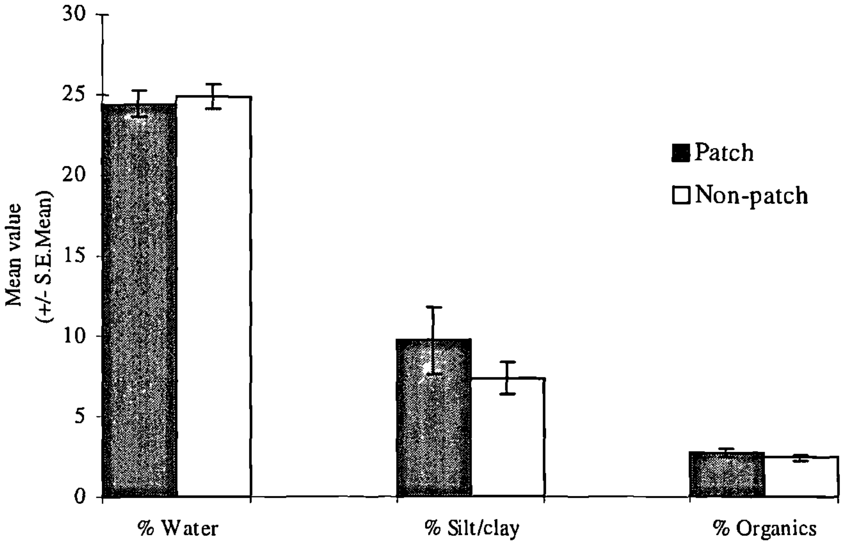


Figure 6.14: Percentage water content, silt/clay fraction and organics (±S.E. Mean, n=6), for patch and non-patch azoic sediments. No statistical differences were found between the 2 plot types using Two-sample t-tests for any variable.

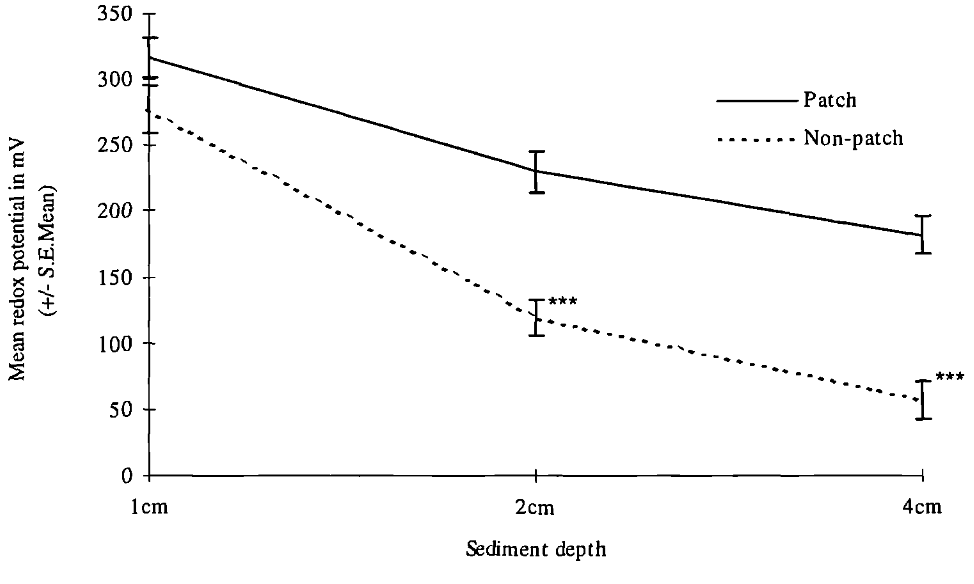


Figure 6.15: Redox potential values in mV (±S.E. Mean, n=6) for patch and non-patch plots. *** Denotes a significant difference between patch and non-patch means where $p<0.001$ using Two-sample t-tests.

DISCUSSION

The present study explicitly addressed three questions with respect to disturbances on intertidal sandflats. These were:

(i) do tube-bed communities have different early successional dynamics from non tube-bed communities?;

(ii) does the successional stage of a community affect the colonisation mode of early colonisers?;

(iii) can sediment disturbance lead to *P. elegans* patch formation on Drum Sands?

Do tube-bed communities have different early successional dynamics from non-tube-bed communities?

These experiments compared the initial (3 week) communities colonising defaunated sediments within *P. elegans* patches with those in non-patch areas. The results indicated that some species colonised the two habitat types in significantly different numbers, at least at certain times of the year. *P. elegans* larvae colonised in significantly higher numbers in patch azoics than non-patch azoics during April 1997, but showed the opposite trend in August 1997 when larval recruitment was relatively low. Adult *P. elegans* colonised patch azoics in higher numbers than non-patch ones during August and December, although this was not significant due to high replicate variability. *C. capitata* consistently colonised in relatively high numbers in all three experiments while *C. edule* and *M. balthica* colonised non-patch azoic sediments in significantly higher numbers than patch azoics during April 1997. Multivariate analyses, together with non-parametric ANOSIM tests, revealed that the community composition of the azoic sediments was significantly different between the two habitat types during April 1997 only. These analyses also indicated that there was a strong temporal effect on initial community composition since the April community was markedly different from those of August and December 1997. Sediment measurements taken during December suggested that there were no significant differences between the levels of water, organics or silt/clay in azoic sediments between the two habitat types although the redox potentials at 2 and 4cm sediment depths were significantly lower in non-patch azoics.

The importance of the ambient community on early community establishment has been demonstrated in other studies (e.g., Zajac and Whitlatch, 1982a) but the effect of dense assemblages of biogenic polychaetes has not previously been investigated. Although several studies have experimentally shown that such tube-builders affect colonisation (e.g., Gallagher *et al.*, 1983; Savidge and Taghon, 1988; Trueblood, 1991; Ragnarsson, 1996), in contrast to this study these studies have implanted tube-building polychaetes or tube mimics into the defaunated sediments and, therefore, their observations apply to the later stages of succession only.

In order to determine which process(es) were responsible for the faunal differences in colonisation between patch and non-patch areas in this study, it is important to indicate how these areas differed hydrodynamically. Flume experiments have shown that isolated animal tubes, and those below a certain threshold density, may cause sediment destabilisation through a sufficiently high transfer of turbulent kinetic energy to the bed (Eckman *et al.*, 1981; Eckman, 1983). At greater densities, the interactions of flow perturbations created by individual tubes may produce a 'skimming flow' (*sensu* Morris, 1955). In 'skimming flow', the region of maximum turbulent kinetic energy and shear stress production occurs away from the bed (Nowell and Church, 1979). The observed effects of animal tubes creating destabilisation on the faunal communities are very different from those where the tubes are dense enough to create sediment stabilisation (Eckman, 1983; Lukenbach, 1986, 1987).

Experiments by Nowell and Church (1979) suggested that the transition from the destabilising effect of low tube density to a stabilising one occurs when approximately 1/12th of the plan area of the sediment is occupied by tubes. For *P. elegans*, with a mean tube diameter of 1mm (Morgan, 1997), this would mean that a tube density of at least 100,000/m^2 is needed to evoke sediment stabilisation. This is far in excess of the densities attained within the patches used for this study, i.e., 22,500/m^2 (April, 1997, see Chapter 8). However, worm density may not be a suitable criteria for estimating the direct role of tubes. Brey (1991) and Morgan (1997) found that many *P. elegans* have tubes with more than one opening, each opening presumably acting as roughness elements, and that many tubes lack an occupant due to emigration (Fauchald and Jumars, 1979; Wilson, 1983) and/or predation (Woodin, 1984). Furthermore, it is likely that the tube structure of dead worms remain intact for some time after the occupant has died. In this way, the direct hydrodynamic effect of *P. elegans* tubes within patches in this study may have been far greater than that estimated from worm densities alone.

Sediment stabilisation by *P. elegans* has been previously demonstrated by shear strength measurements (Meadows and Hariri, 1991; Morgan, 1997). Although such measurements were not taken in this study there is strong evidence to suggest that the sediments within *P. elegans* patches on Drum Sands were stabilised, i.e., the lack of ripple marks in an otherwise rippled area, the increased silt/clay fraction, and the presence of a golden hue, assumed to be diatoms, on the sediment surface. Eckman *et al.* (1981) suggested that these observations, especially the latter, provided strong evidence of sediment stabilisation. In the studies by Sanders *et al.* (1962) and Fager (1964), sediment stabilisation was also assumed by the observations of a golden hue, confirmed to be diatoms by chlorophyll analysis in the former study, and the absence of ripple marks where highest tube densities were found. The polychaete densities producing these effects in their studies were also far below those expected for sediment stabilisation using the empirical formula of Nowell and Church (1979), i.e., observed densities being 600 *C. torquata*/m^2 and 500-1,000 *O. fusiformis*/m^2 in the studies by Sanders *et al.* (1962) and Fager (1964), respectively. For example, Eckman *et al.* (1981) calculated that a density of at least 14,500 *O. fusiformis*/m^2 was necessary for sediment stabilisation.

A number of studies have experimentally shown that extracellular mucus films produced by macrofauna during tube construction (Meadows and Tufail, 1986), and diatoms can stabilise sediments (Frostick and McCave, 1979; Grant *et al.*, 1986; Tufail *et al.*, 1989; Paterson, 1994). Sediments around tubes have been shown to have increased numbers of diatoms (Sanders *et al.*, 1962) and meiofauna (Eckman, 1983; Noji, 1994). The dense films of diatoms observed on the *P. elegans* patch surfaces during this study support the contention that indirect sediment stabilisation was possibly appreciable. Therefore, the observed differences in colonisation between patches and non-patches in this study probably resulted from differences in sediment stability.

In April, when *P. elegans* larval availability in the water column was at its highest on Drum Sands, significantly higher numbers of *P. elegans* larvae colonised azoic sediments in patches compared with non-patch azoic sediments. Many laboratory experimental studies have been carried out to elucidate the precise mechanisms by which differential larval settlement of infaunal species is achieved (Scheltema, 1974; Woodin, 1986; Butman *et al.*, 1988a; Pawlik and Butman, 1993; Hsieh, 1994) but such studies on polychaetes have mainly concentrated on families other than Spionidae, e.g., Capitellidae (Butman *et al.*, 1988b; Grassle and Butman, 1989) and Sabellidae (e.g., Pawlik *et al.*, 1991) and it is likely that mechanisms are species-specific. However, settlement cues associated with adult populations were unlikely to have been responsible for the observed differences in *P. elegans* larval recruitment in the present study because colonisation occurred on totally defaunated sediments.

It is possible that larval behavioural responses to local boundary-layer flow may have produced the observed differences for juvenile *P. elegans* in this study. Such behaviour has been demonstrated for the sabellid *Phragmatopoma lapidosa californica* (Pawlik *et al.*, 1991) and it was proposed that this enabled this species to form large tube-beds.

Savidge and Taghon (1988) showed that in the field, colonisation was dominated by passive advection of larvae (see review by Olafsson *et al.*, 1994). Eckman (1983) suggested that passive larval entrainment can be higher in areas of stabilised sediments. Increased larval entrainment was suggested to have been a possible reason why *C. edule* spat were present in higher numbers in *P. elegans* patches on Drum Sands (Chapter 8). Increased passive entrainment to *P. elegans* patches could, therefore, have been responsible for the increased recruitment of *P. elegans* larvae to patches in this study. However, one must be cautious, apparent increased recruitment to patches could equally have resulted from increased erosion of settled larvae in non-patch areas. Since samples were taken some time after settlement, inferring settlement patterns from observed recruitment patterns can be potentially misleading (Hadfield, 1986; Woodin, 1986). Woodin (1986) suggested that to differentiate between larval settlement and recruitment in field studies is inherently very difficult. Differential mortality and/or erosion were likely to have been factors in this study, i.e., those larvae settling into patches are less likely to have been eroded in the stabilised environment of patches and presumably benefit from the increased food supply.

Zajac and Whitlatch (1982a) demonstrated that initial colonisation following small-scale sediment disturbances were predominantly dependent on the temporal changes in ambient populations. Although such temporal changes in the ambient communities on Drum Sands were important in initial colonisation and presumably in later successional dynamics in the present study, the interspersion of the two plot types demonstrated that the early stages of succession can vary at small spatial scales concurrently.

Does the successional stage of a community affect the colonisation mode of early colonisers?

Two species, i.e., the polychaetes *P. elegans* and *C. capitata*, colonised in numbers sufficiently high for size-frequency analyses. Although no significant differences were observed in the size distributions of *P. elegans* colonising azoic sediments of the two habitat types during April 1997, significant differences during August and December 1997 were observed due to higher numbers of adults colonising patch azoic sediments relative to non-patch sediments. There were significant differences between the size distributions of *C. capitata* colonising the two habitat types in December 1997 which suggested that colonisation in patch azoics was predominantly via adults while that to non-patch azoics was via larvae. The results of the present experiments, therefore, indicated that in addition to affecting initial community composition following a disturbance, dense assemblages of *P. elegans* also affected the colonisation mode of some species. These patches of increased *P. elegans* densities reflected different successional stages from surrounding sediments (Noji and Noji, 1991).

Many studies have found that post-larval immigration can play a substantial role in colonisation after a small-scale disturbance (Dauer and Simon, 1976a; Levin, 1984a; Frid, 1989; Smith and Brumsickle, 1989; Wilson, 1992; 1994). This has been found not only for errant polychaetes, but also for infaunal burrowers and tube-builders (Smith and Brumsickle, 1989; Wilson, 1992; 1994) and for species which clearly relied upon larval recruitment, e.g., *Streblospio benedicti* (Smith and Brumsickle, 1989). Smith and Brumsickle (1989) and Shull (1997) have suggested that post-larval or adult immigration might assume a greater significance during periods of decreased larval availability, although this was not conclusively demonstrated during this study for *P. elegans.* However, the August and December experiments suggested that adult immigration to defaunated sediments was greater in *P. elegans* patches than in non-patch areas. *P. elegans* adults represented 40% and 45% of colonists in patches during August and December, respectively, while only 2% and 0% in non-patch samples.

Adult *P. elegans* (10-12mm long) have been found in the water column above the tidal flats in Konigshafen (Armonies, 1994) which were assumed to be due to active migration. Similarly, adults of other spionid polychaetes have been found in the water column (Levin, 1984a; Armonies, 1988; Cummings *et al.*, 1995). Adult colonisation of azoic sediments in patches during the present two experiments may also have been an active process involving individuals crawling across the sediment surface. Lateral movement (crawling) was proposed to have been the mechanism by which *P. elegans* colonised small patches of azoic sediment in the studies by Wilson (1992, 1994) despite the fact that colonisation by the adults of most species in his studies was by vertical migration and settlement. Density-dependent relocation by crawling across the sediment surface has previously been shown for *P. elegans* (Wilson, 1983). It was concluded that these individuals were able to assess worm density around their tubes (Wilson, 1983) and subsequent relocation enabled a population to prevent over-exploitation of its resources. Furthermore, it is conceivable that an adult worm would be more likely to actively migrate across the sediment surface of the stabilised beds within *P. elegans* patches compared to one in a non-patch area. It is not possible to suggest whether the increased colonisation of adults to patch azoics in this study resulted from vertical migration and subsequent settlement or increased density-dependent relocation.

Capitella capitata has planktonic larvae giving widespread dispersal but also possesses demersal larvae which are completely benthic (Warren, 1976). Shull (1997) demonstrated that this polychaete was capable of colonising azoic sediments by larval settlement, bedload transport and by burrowing. *C. capitata* has a short life cycle, is capable of reproducing all year round and one female may produce up to 10,000 eggs. These characteristics allow this species to quickly colonise suitable unoccupied areas of sediments in vast numbers (Rosenberg, 1973; Grassle and Grassle, 1974). The size-frequency differences between patch and non-patch colonisers for *C. capitata* was only observed during December. It is difficult to suggest the possible reason why those colonising *P. elegans* patches were predominantly adults while those colonising non-patches were mainly larvae but a comparison with the situation in the ambient sediments reveals a possible explanation. Although not significant, there were higher densities of *C. capitata* in patches than in non-patches at this time (23.0±2.9 and 20.1±4.1 respectively, Figure 8.1(iv)). Furthermore, the size-frequency distributions were significantly different at this time (Table 8.2) due to a higher proportion of adults in patch populations. Therefore, the increased proportion of adults colonising azoic sediments in *P. elegans* patches in the December experiment may have been a direct result of the differences in the ambient populations between patches and non-patches at that time. More adults may have colonised via lateral migration through and/or on the sediments in patches.

Can sediment disturbance lead to *P. elegans* patch formation on Drum Sands?

In addition to giving an important insight into differential colonisation of patches compared with non-patch areas and into to the mode of colonisation of *P. elegans* in response to small-scale disturbances, this study has suggested that *P. elegans* patch formation on Drum Sands could possibly have resulted from sediment disturbance. However, since the population relies on a highly seasonal input of planktonic larvae (Chapter 3) the timing of the disturbance is important. Patch formation could only have, therefore, resulted from disturbances occurring during the summer or the winter. It is not always possible to scale-up the results of small-scale disturbance experiments such as this one to those of larger disturbances (Thrush *et al.*, 1997a, 1997b). However, it is likely that the mode of *P. elegans* colonisation following larger-scale disturbances and consequent successional dynamics would be the same as those observed in this study. How crucial the timing of the disturbance would be to the likelihood of patch formation ultimately would depend on the later stages of successional dynamics on Drum Sands, this was not investigated in these experiments. For example, if successional dynamics were slow and disturbed sediments did not become dominated by trophic groups which repressed *P. elegans* colonisation, e.g., suspension feeders, *P. elegans* would be capable of numerically dominating some time after the disturbance. This is a likely scenario on Drum Sands since the creation of 'new' sediments in this study did not result in the presence of species which were absent in the ambient community.

Capitella capitata was the only species to show an opportunistic response (*c.f.*, Zajac and Whitlatch, 1982a) to the disturbance created in this study, i.e., their numbers in azoic samples were higher than those in ambient samples (Chapter 8) at that time. During August and December, when *P. elegans* larval recruitment was low, *C. capitata* was by far the most abundant species colonising the disturbed sediments, in both patches and non-patches. Therefore, depending on time of disturbance, *C. capitata* can dominate early stages of succession even within *P. elegans* patches. The colonisation of disturbed sediments by *P. elegans* during August and December would probably have been relatively slow. This has important implications for the effects of small-scale disturbances within *P. elegans* patches. For example, numerical dominance by *C. capitata* in the early stages of community establishment could lead to different successional dynamics compared with that during April when larval *P. elegans* recruitment dominated recruitment. This implies that for *P. elegans* patch formation following a disturbance on Drum Sands, the timing of the disturbance is critical.

CHAPTER 7

THE MICRO-SCALE SPATIAL PATTERNS OF *PYGOSPIO ELEGANS* WITHIN SMALL-SCALE PATCHES AND THE ROLES OF INTRA- AND INTERSPECIFIC INTERACTIONS AND ABIOTIC EFFECTS

INTRODUCTION

Several studies have reported the presence of spatial aggregations of marine benthic invertebrates at the centimetre (micro-) scale although their sampling regimes were inappropriate to have investigated them fully. For example, Angel and Angel (1967) found clustering of 3 infaunal species at Fanafjorden, Norway, at the scale of their smallest sample size (12.5cm) and reasoned that their core size may have been too large to detect the minimum sizes of the patterns. Similarly, Gage and Coghill (1977) using linear transects of 5cm contiguous cores found clustering at the scale of the sampling unit or smaller for several infaunal species at 2 Scottish sea lochs.

Consequently, later studies investigating the presence and importance of micro-scale spatial heterogeneity of macrobenthic individuals have used smaller contiguous cores or nearest-neighbour techniques and the information obtained from such studies has led to both a greater understanding of both how these populations are regulated and an increased appreciation of the importance of biotic interactions (Eckman, 1979; Reise, 1979; Levin, 1981; Lawrie, 1996; Zettler and Bick, 1996). In general, processes operating at the micro-scale, which tend to act upon the individual rather than the population, can be classed into two broad categories. Processes such as habitat heterogeneity, symbiosis, gregarious behaviour and/or limited dispersal of progeny tend to produce aggregated distributions while negative interactions such as territoriality, avoidance behaviour and/or allelopathy often create uniform distributions (Levin, 1981).

Micro-scale spatial patterns of macrobenthic invertebrates, like those observed at larger scales, have mainly been found to be aggregated. For example, Zettler and Bick (1996) found *Marenzelleria viridis* formed patches down to 0.04m^2 and proposed that these could have been created by sediment structures, substrate preferences, feeding mode and biotic or abiotic attractants. Eckman (1979) combined small-scale manipulative experiments with direct observations and showed that polychaete spatial patterns were affected by the locally varying hydrodynamic environment at the centimetre scale. He suggested that the 1cm patches formed by *Tanais* sp. and *Manayunkia aestuarina* in his experiment resulted from the presence of simulated animal tubes, and that the 10cm periodicities in the abundances of many other species in Skagit Bay, Washington, resulted from the hydrodynamic patterns created by bed ripples. Reise (1979) suggested that the micro-scale patches formed by all 5 species in his study on the intertidal sandflats of the island of Sylt, North Sea, could be related to their feeding modes.

Uniform distributions at this scale are generally ascribed to some type of negative interaction between individuals. Connell (1963) directly observed the development of spatial patterns of the marine amphipod *Ericthonius brasiliensis*. He found that the uniform distributions shown by this species resulted from territorial behaviour by the adults. Similarly, Levin (1981) found, using nearest-neighbour analysis, that *Pseudopolydora* cf. *paucibranchiata* was uniformly distributed while *Streblospio benedicti* was random. She showed that *P.* cf. *paucibranchiata*'s distribution was initiated during larval settlement and enhanced by subsequent interactions (palp-fighting) between post-larval individuals.

In Chapter 2, the small- and meso-scale (m-100m) spatial patterns exhibited by macrobenthic invertebrate species on an intertidal sandflat were investigated. The spionid polychaete *P. elegans* formed patches, 1-1.5m^2, of increased density characterised by smooth, raised sediments. Since there is a limit to the range of scales of heterogeneity investigated by any one survey, the micro-scale spatial patterning of *P. elegans* could not be investigated. Spatial patterns that reflect micro-scale interactions, processes and responses smaller than the sampling unit (25cm) were therefore homogenised.

The presence of these *P. elegans* patches offer an ideal opportunity to investigate the micro-scale spatial patterns of a tube-building spionid polychaete. Firstly, the densities of *P. elegans* have been found to be high within these small-scale patches (Chapter 2), increasing the opportunity for biotic interactions. Secondly, since the sediments are relatively stabilised (Chapter 8) they are more likely to be homogeneous than in non-patch areas which facilitates an investigation into the biotic processes giving rise to spatial patterns. Finally, the population structure and reproductive strategy adopted by this population has been documented (Chapter 3).

Specifically, two main questions were addressed by an investigation of the micro-scale spatial distributions of *P. elegans* within the high density patches found on Drum Sands. These were:

(1) what is the micro-scale spatial distribution of dense populations of tube-building spionids and what does it suggest about intraspecific interactions?;

(2) what are the roles of larval recruitment, interspecific interactions and abiotic variables in determining micro-scale spatial patterns?.

METHODS

Experimental design - A preliminary (pilot) survey was carried out during February 1997 to give an indication of the spatial distribution of *P. elegans* within the small-scale patches which were investigated in Chapter 2, and to determine adult densities so that a suitable core size could be used for the main survey. To achieve this, 1 *P. elegans* patch was randomly chosen and its centre sampled with a box-core containing 49 contiguous 3x3cm cores, together with 32 cores around the edge of the box-core. The survey therefore consisted of 81 contiguous cores forming a 9x9 array, with samples taken to a depth of 10cm (Figure 7.1).

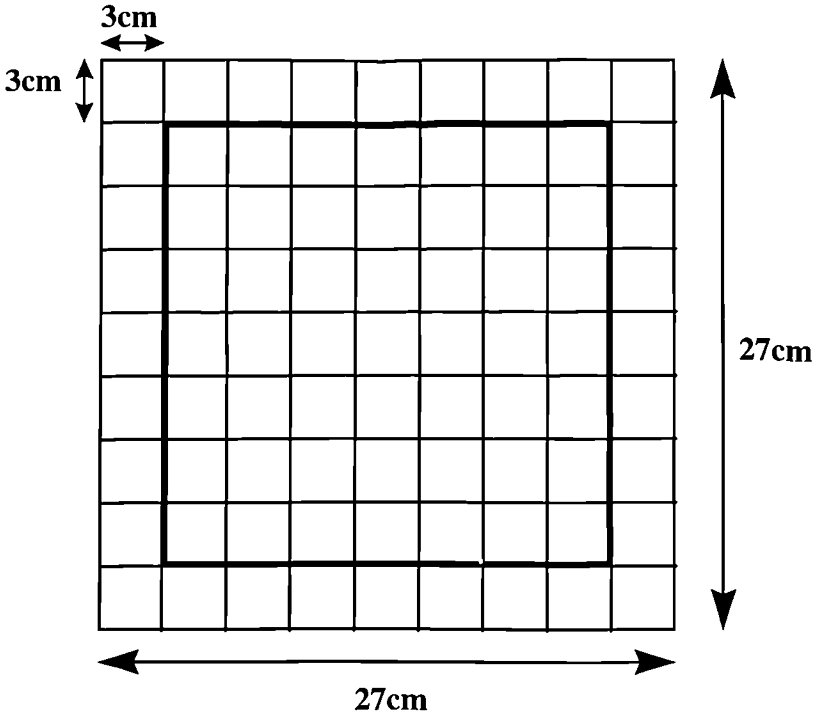


Figure 7.1 : Diagram showing the positions of the 81 3x3cm cores for the pilot survey with the position of the box-core highlighted. Samples were taken to a depth of 10cm.

The sediments from the cores were preserved with 10% saline formaldehyde solution neutralised with 0.2% Borax, stained with 0.01% Rose Bengal and stored. The samples were later washed with water over a 500μm mesh sieve. The samples were then sorted using a magnifying lens and the numbers of *P. elegans* individuals in each sample counted.

A more detailed investigation of micro-scale spatial patterns of *P. elegans* was then carried out. For this, cores were positioned linearly forming a transect rather than forming an array as in the pilot survey. Although with this transect approach the spatial distribution investigated was linear, and thus may have been influenced by the direction of the line, it allowed a larger proportion of the *P. elegans* patch to be sampled. Since each transect consisted of only 32 cores, 3 different patches could be sampled each month. Sampling 3 patches each month overcame the linear bias of the transect to a certain extent. The 3 patches were determined by random numbers each month and the 32 cores forming a contiguous transect taken across them. Taking 3 replicate transects also limited the chance of any variability between *P. elegans* patches being misinterpreted as temporal changes in micro-scale spatial patterns. Thirty-two cores were chosen as a compromise between the practical work involved and the number of samples needed to give enough sample pairs (i.e., 40, Sokal, 1986) for reliable spatial autocorrelation analysis. Furthermore, 32 cores, i.e., 96cm, encompassed most of the patch in one direction for the majority of patches.

The samples, which also provided the data on the population structure and reproductive strategy of *P. elegans* (Chapter 3), were taken at the beginning of each month from March 1997 until August 1997, and then every other month until February 1998. After August 1997, it was decided that sampling alternate months only was necessary since the main recruitment phase of the year had already occurred. It was more important to sample as often as possible during the recruitment phase in order to investigate adult-larval interactions.

The samples were treated and stored in the same way as described for the pilot survey. These samples were washed over a 212μm mesh sieve in addition to the 500μm mesh sieve so that the numbers of newly settled individuals could be determined for each sample. The samples were elutriated as described in Chapter 6 and the numbers of 'adults' (those with a 5th setiger width ≥0.30mm) and new recruits (those below a 5th setiger width of 0.30mm), were counted. The size separation for new recruits was determined from the size-frequency graphs in Chapter 3 (Figure 3.3(iii)) to distinguish those individuals which had settled after the previous sampling occasion. Those individuals above a 5th setiger width ≥0.30mm will be referred to as 'adults' for this study. These individuals would not all have been sexually mature adults (see Chapter 3) but here refer to those individuals which had established a fully-formed tube.

Due to the large total number of samples and the small size of the corers, it was not possible to measure the sediment characteristics of each core and thus correlation analysis between the numbers of *P. elegans* and sediment variables was not possible. Instead, 3 separate transects of 32 contiguous cores were taken from *P. elegans* patches for sediment analysis in the same way as for the fauna during February 1998. Although it would not be possible to carry out correlation analysis of these sediment results with faunal densities, the results would give an indication as to whether the sediment variables were spatially heterogeneous within *P. elegans* patches.

The cores for sediment analyses were taken to a depth of 1cm as this was the minimum depth to provide sufficient sediment for organic and silt/clay content analyses. The samples were then frozen at -20°C for storage. The water and organic contents were determined in the same way as described in Chapter 2 while the silt/clay fractions were determined in the same way as described in Chapter 6.

Data analyses - The spatial distribution of *P. elegans* individuals was determined using the same indices of dispersion as those described in Chapter 2. These were the variance : mean ratio (I), Morisita's index (I_d) and the standardised Morisita's index (I_p). These gave an indication of the intensity of pattern. For new recruits, indices of dispersion were only calculated for those plots in which their mean densities were ≥ 3 individuals per core in order to limit analyses to those months when settlement was relatively high. These indices were calculated using the NEGBINOM program (Krebs, 1989) and tested for significance in the same way as described in Chapter 2. Density plots were produced for *P. elegans* numbers from the pilot survey and the adults and new recruits from the monthly samples. These were produced using the Golden Software Inc. SURFER package version 6.04. The gridding method used for both the pilot survey and the transect survey abundance data was the nearest-neighbour gridding method since this is the most suitable for data from contiguous cores (T. Bresnahan, SURFER; pers. comm.). This method does not interpolate data but uses each data point (abundance) and assigns that value to the grid (Keckler, 1997).

Spatial autocorrelation analysis was performed on the abundance data for adults and new recruits, together with the results from sediment analyses. This was carried out using the SAAP package version 4.3 in an identical way to that described in Chapter 2. The distance classes 1-5 were kept constant through all the analyses and represent inter-sample distances 0-3cm, 3-6cm, 6-9cm, 9-12cm and 12-15cm respectively.

Correlation analyses of adult *P. elegans* abundances with new recruits (for transects with mean abundances of ≥ 3 individuals per core) and other species (with mean densities ≥ 1 individual per core) were carried out. The data were checked for normality using the Anderson-Darling test, any data not conforming to normality were log(x+1)-transformed before Pearson Product Moment Correlation analysis. Any transformed data not conforming to normality were ranked and analysed using Spearman Rank Correlation analysis. The α level, 0.05, was adjusted according to the Bonferroni correction where probabilities were compared to α' where $\alpha' = \alpha/k$ (where k = the number of independent tests; Sokal, 1986; Legendre and Legendre, 1997). Correlation analyses were performed using Minitab version 12.1.

RESULTS

Pilot survey - The pilot survey results indicated that *P. elegans* had an aggregated distribution with a variance : mean ratio of 1.97 ($p<0.001$), a Morisita's index (I_d) of 1.324 ($p<0.05$) and a standardised Morisita's index (I_p) value of 0.501 ($p<0.05$). The density map of *P. elegans* distribution from this survey is displayed in Figure 7.2. The mean density (3.0 individuals per core) was not very high because the samples were taken during February, just before the main annual recruitment phase and adult densities presumably had decreased during the winter months. Furthermore, the samples were sieved with a 500μm mesh sieve only and so some smaller adults were probably not retained. The map suggests that the non-random distribution of *P. elegans* within the patch is explained by small patches of about 3-6cm^2. This is supported by the results from spatial autocorrelation analysis. The analysis gave a significant positive autocorrelation coefficient (Moran's i=0.21) after a Bonferroni correction at distance class 1 which implies that the spatial structure is significant (Figure 7.3). This implies that some *P. elegans* densities were more similar to neighbouring samples than expected from a random distribution, i.e., *P. elegans* formed patches of 3-6cm^2.

Because of the large number of cores containing 0, 1 or 2 adults, it was decided that reducing the core size used for the main survey may have reduced densities too low for statistical analyses.

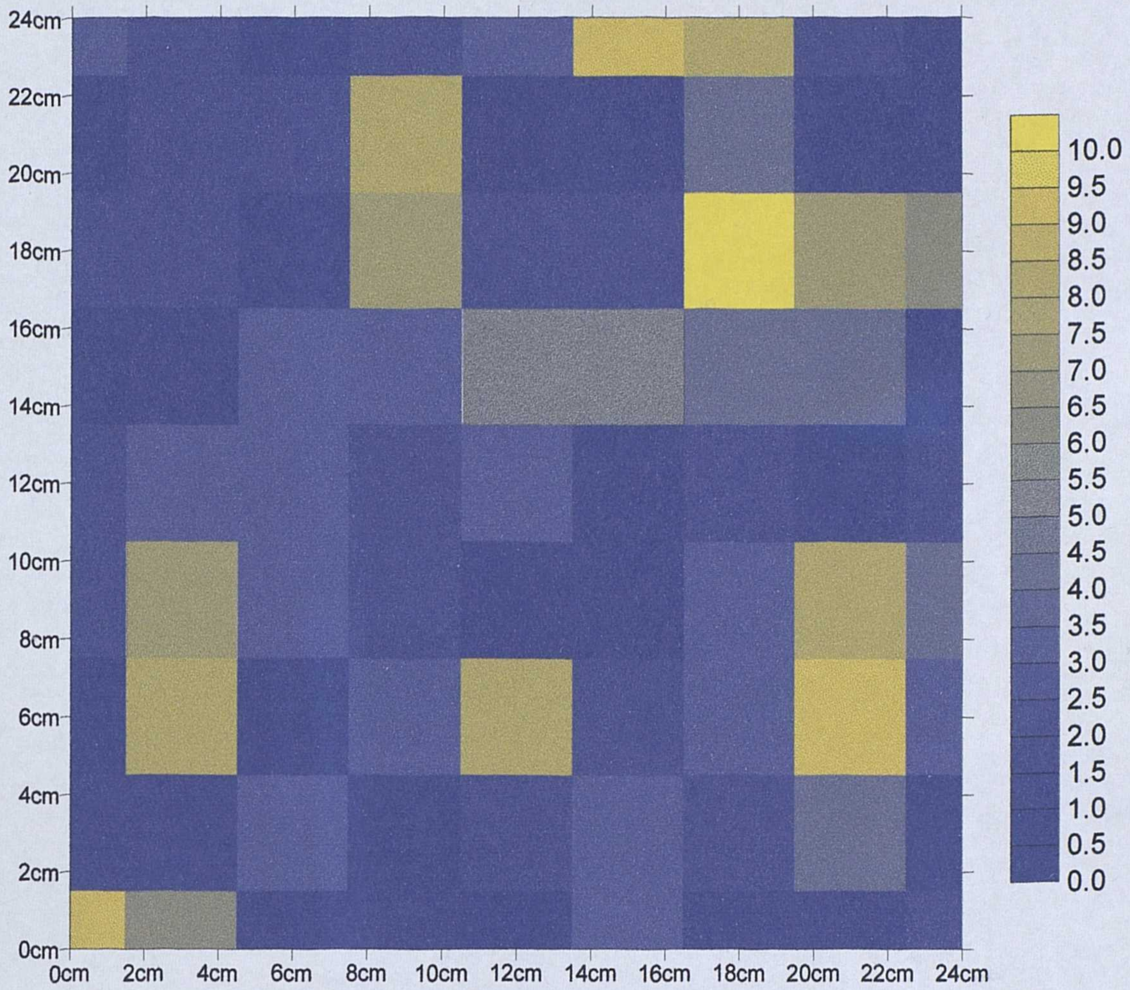


Figure 7.2 : Contour map of P. elegans abundance from pilot survey using nearest-neighbour gridding.

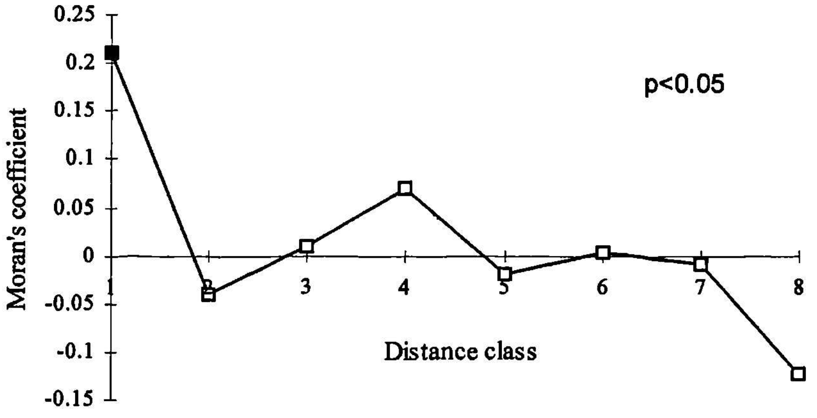


Figure 7.3 : Correlogram of Moran's coefficient against distance class (each 3cm width) of P. elegans density from pilot survey. Whole correlogram is significant after a Bonferroni correction while solid symbol represents significance at 0.05 for that distance class.

Transect survey - Micro-scale patterns of *P. elegans* - Table 7.1 presents the results of the indices of dispersion of adult *P. elegans* densities from March 1997 to February 1998. An overall non-random distribution here is one in which at least 2 indices of dispersion indicated a significant departure from random. The results suggest that adult *P. elegans* exhibited an aggregated distribution all through the year, except during October 1997. The greatest amount of clumping was generally observed during the summer months of June and July (highest v:m ratios). There was some variability between patches - for 4 months (April, May and December 1997 and February 1998) adult *P. elegans* were randomly distributed in one patch replicate while aggregated in the other 2 replicates. There was a good agreement between the 3 dispersion indices, only during May (replicates 2 and 3) and August (replicate 2) were there discrepancies between the results obtained from the variance : mean ratio, I_d and I_p.

Figures 7.4(i-xxvii) present the density plots of *P. elegans* adults throughout the sampling period. The plots of *P. elegans* with random distributions, i.e., April 1997 (replicate 1); October 1997 (replicates 1, 2 and 3); December 1997 (replicate 3); and February 1998 (replicate 3), are included for comparison with plots of non-randomly distributed *P. elegans*. Generally, the plots do not differentiate between random and non-random distributions very clearly. However, it was pointed out in Chapter 2 that a random distribution (according to indices of dispersion) could still have a significant underlying spatial structure (e.g., *N. hombergii*, 1m survey), especially for low-density species. The plots show that for those transects in which *P. elegans* had statistically significant aggregated distributions, patches of *P. elegans* were generally smaller than 3cm across, i.e., less than the size of the sampling unit, for most months. However, since the pilot survey suggested that patches formed tended not to be symmetrical (see Figure 7.2) it is possible that these micro-scale patches were larger than revealed by the transects as some of them may have been perpendicular to the direction of the transect.

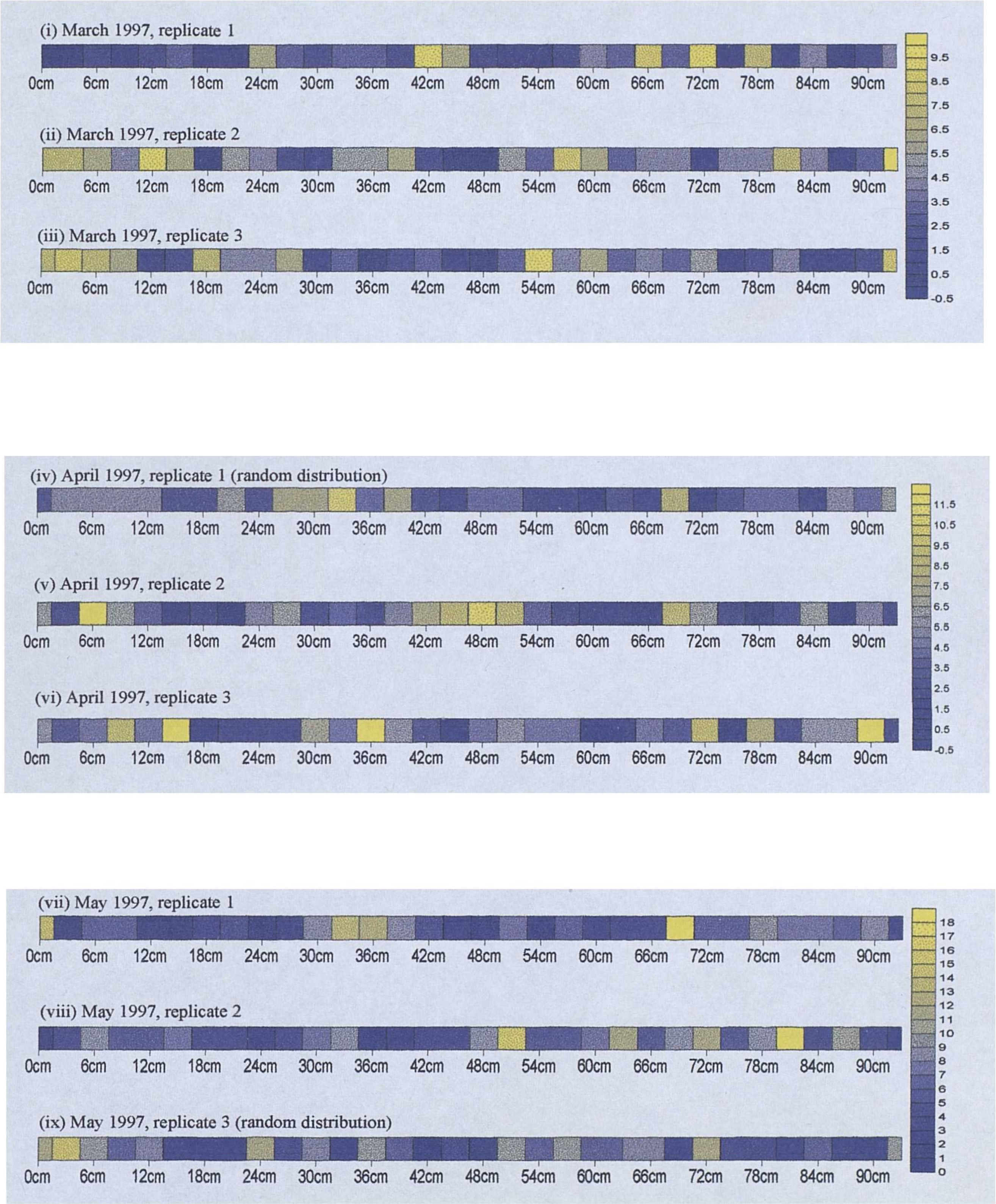
The significant correlograms produced by spatial autocorrelation analysis are presented in Figures 7.5(i-viii). The majority of transects with aggregated distributions of adult *P. elegans* produced non-significant spatial autocorrelation results which supported the density maps, i.e., patches appeared smaller than the sampling unit. April (replicate 1) produced a significant spatial structure function (Figure 7.5(i)) suggesting a patch size of 6-9cm although its dispersion indices suggested a random distribution (Table 7.1). The correlograms suggest that when there was a significant spatial structure in the adult *P. elegans* population, the patch size was usually between 3-12cm (April (1); May (3); July (2 and 3) and October (3)), although these were not evident from their density plots.

Month		v:m ratio	pattern	I_d	pattern	I_p	pattern
March 1997	1	2.110	***A	1.361	*A	0.503	A
	2	1.580	*A	1.133	*A	0.501	A
	3	1.757	**A	1.201	*A	0.501	A
April 1997	1	1.122	Random	1.029	Random	0.101	Random
	2	1.920	**A	1.256	*A	0.502	*A
	3	1.630	*A	1.116	*A	0.501	*A
May 1997	1	2.841	***A	1.306	*A	0.504	*A
	2	1.531	*A	1.112	*A	0.478	Random
	3	1.513	*A	1.171	Random	0.462	Random
June 1997	1	5.447	***A	1.664	*A	0.509	*A
	2	1.773	***A	1.575	*A	0.508	*A
	3	3.161	**A	1.153	*A	0.501	*A
July 1997	1	3.161	***A	1.345	*A	0.504	*A
	2	1.988	**A	1.192	*A	0.501	*A
	3	3.454	***A	1.302	*A	0.504	*A
August 1997	1	2.290	***A	1.220	*A	0.502	*A
	2	1.509	*A	1.092	*A	0.458	Random
	3	1.913	**A	1.148	*A	0.501	*A
October 1997	1	1.149	Random	1.023	Random	0.134	Random
	2	1.144	Random	1.024	Random	0.130	Random
	3	1.166	Random	1.044	Random	0.150	Random
December 1997	1	1.789	**A	1.094	*A	0.501	*A
	2	2.024	***A	1.112	*A	0.501	*A
	3	1.408	Random	1.057	Random	0.367	Random
February 1998	1	1.607	*A	1.072	*A	0.501	*A
	2	2.743	***A	1.203	*A	0.502	*A
	3	1.350	Random	1.033	Random	0.310	Random

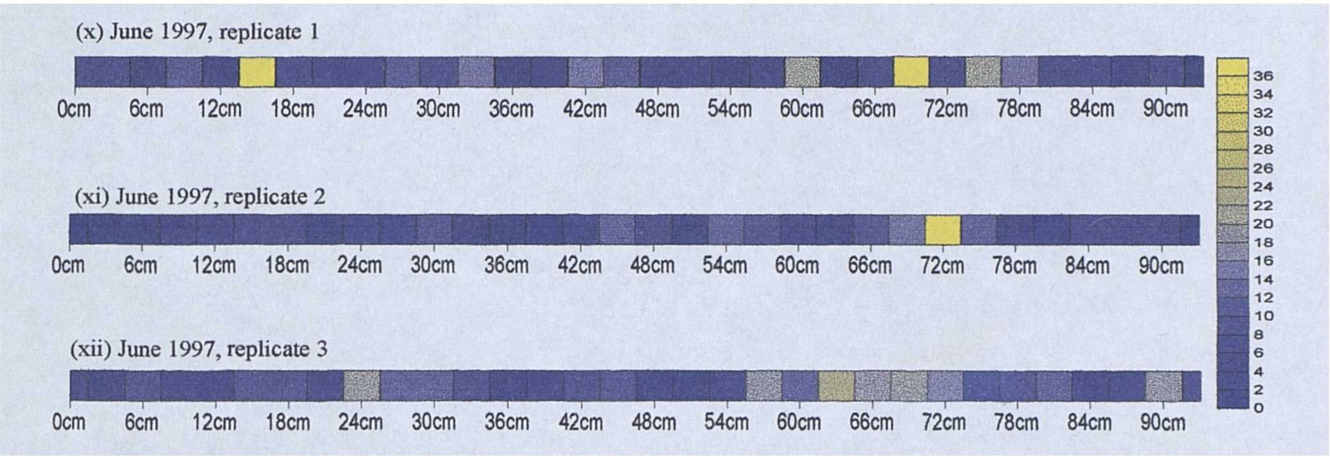
Table 7.1 : Indices of dispersion for adult *P. elegans* individuals from March 1997 to February 1998. A=Aggregated distribution where * represents $p<0.05$; ** $p<0.01$; and *** $p<0.001$.

Month		v:m ratio	pattern	I_d	pattern	I_p	pattern
March 1997	1	2.110	***A	1.361	*A	0.503	A
	2	1.580	*A	1.133	*A	0.501	A
	3	1.757	**A	1.201	*A	0.501	A
April 1997	1	1.122	Random	1.029	Random	0.101	Random
	2	1.920	**A	1.256	*A	0.502	*A
	3	1.630	*A	1.116	*A	0.501	*A
May 1997	1	2.841	***A	1.306	*A	0.504	*A
	2	1.531	*A	1.112	*A	0.478	Random
	3	1.513	*A	1.171	Random	0.462	Random
June 1997	1	5.447	***A	1.664	*A	0.509	*A
	2	1.773	***A	1.575	*A	0.508	*A
	3	3.161	**A	1.153	*A	0.501	*A
July 1997	1	3.161	***A	1.345	*A	0.504	*A
	2	1.988	**A	1.192	*A	0.501	*A
	3	3.454	***A	1.302	*A	0.504	*A
August 1997	1	2.290	***A	1.220	*A	0.502	*A
	2	1.509	*A	1.092	*A	0.458	Random
	3	1.913	**A	1.148	*A	0.501	*A
October 1997	1	1.149	Random	1.023	Random	0.134	Random
	2	1.144	Random	1.024	Random	0.130	Random
	3	1.166	Random	1.044	Random	0.150	Random
December 1997	1	1.789	**A	1.094	*A	0.501	*A
	2	2.024	***A	1.112	*A	0.501	*A
	3	1.408	Random	1.057	Random	0.367	Random
February 1998	1	1.607	*A	1.072	*A	0.501	*A
	2	2.743	***A	1.203	*A	0.502	*A
	3	1.350	Random	1.033	Random	0.310	Random

Table 7.1 : Indices of dispersion for adult *P. elegans* individuals from March 1997 to February 1998. A=Aggregated distribution where * represents $p<0.05$; ** $p<0.01$; and *** $p<0.001$.



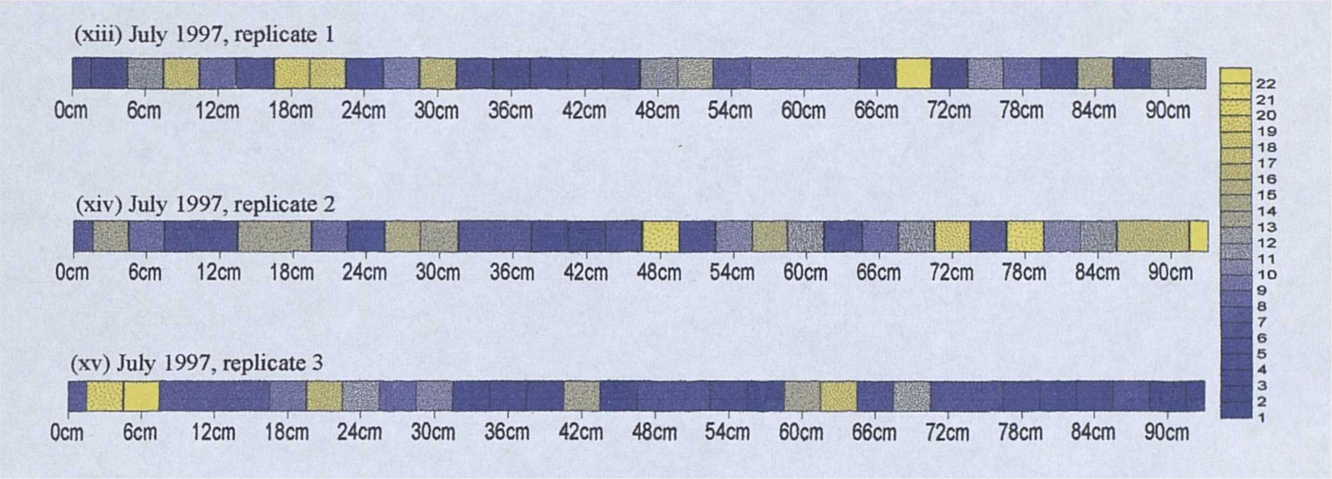
Figures 7.4 (i-ix) : Density maps of adult P. elegans numbers along transects using nearest neighbour gridding.



(x) June 1997, replicate 1

(xi) June 1997, replicate 2

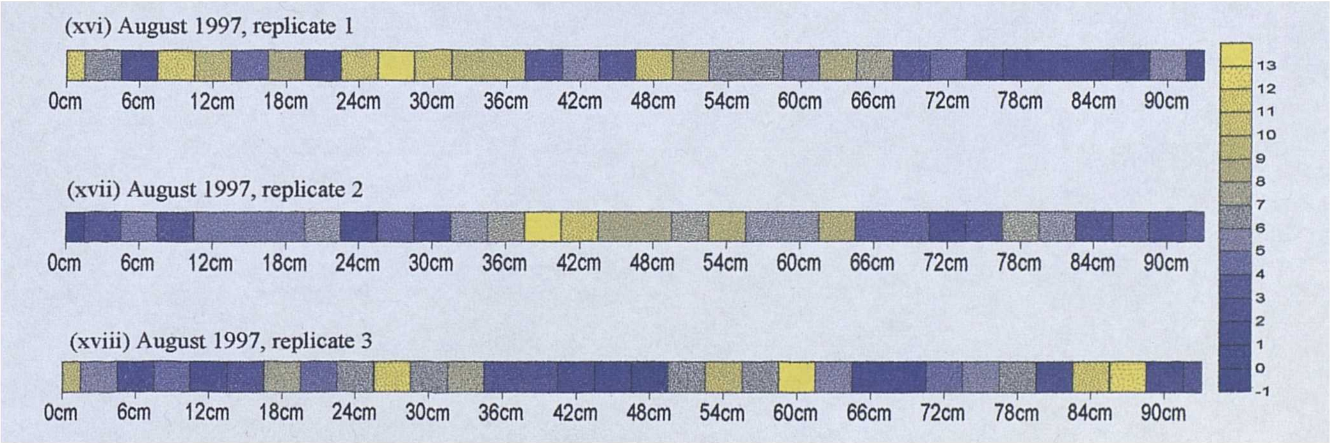
(xii) June 1997, replicate 3



(xiii) July 1997, replicate 1

(xiv) July 1997, replicate 2

(xv) July 1997, replicate 3

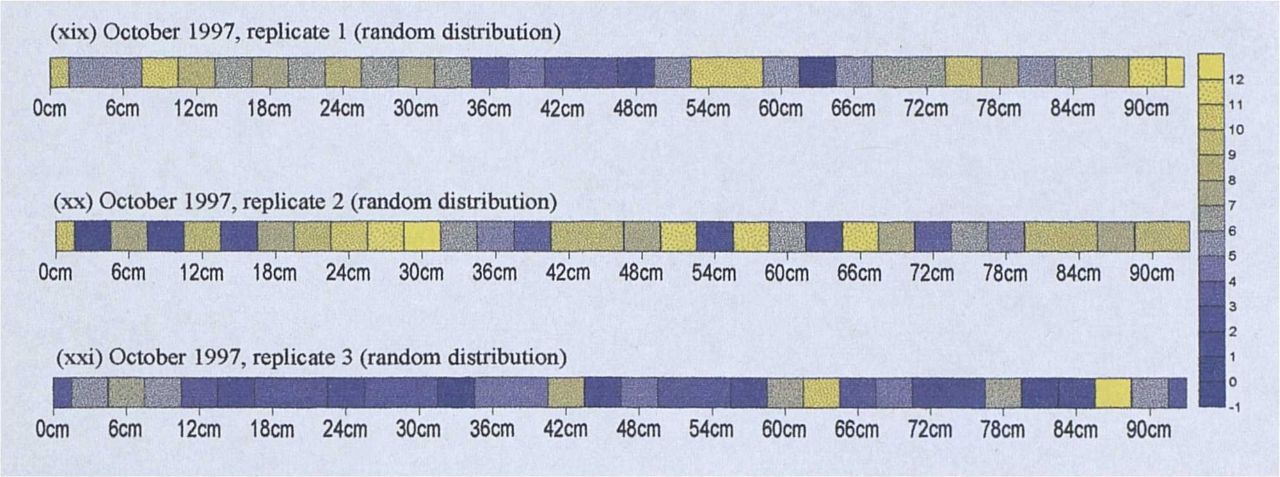


(xvi) August 1997, replicate 1

(xvii) August 1997, replicate 2

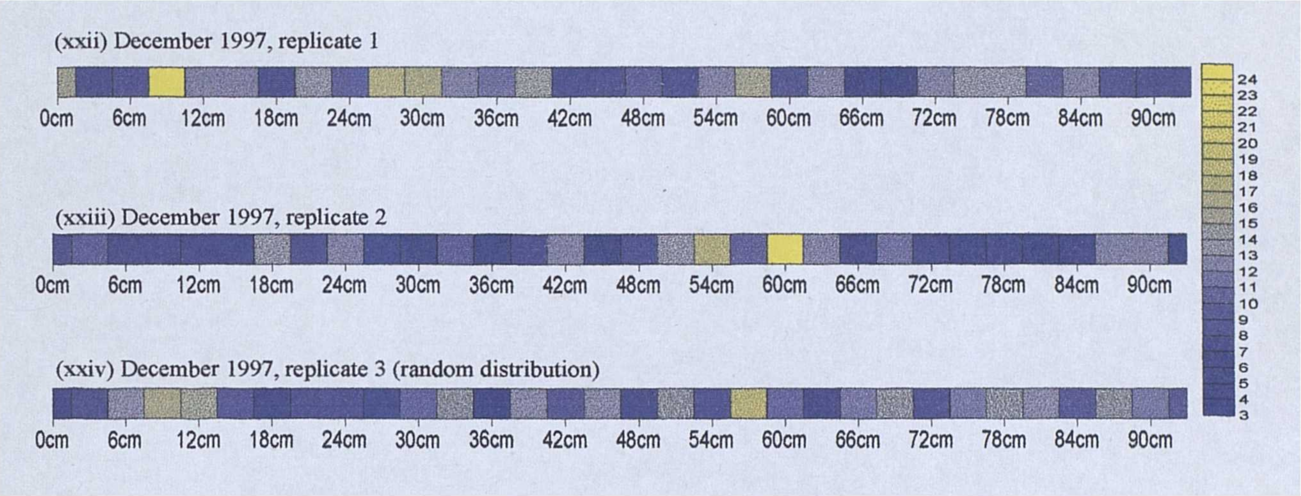
(xviii) August 1997, replicate 3

Figures 7.4(x-xviii) : Continued


(xix) October 1997, replicate 1 (random distribution)

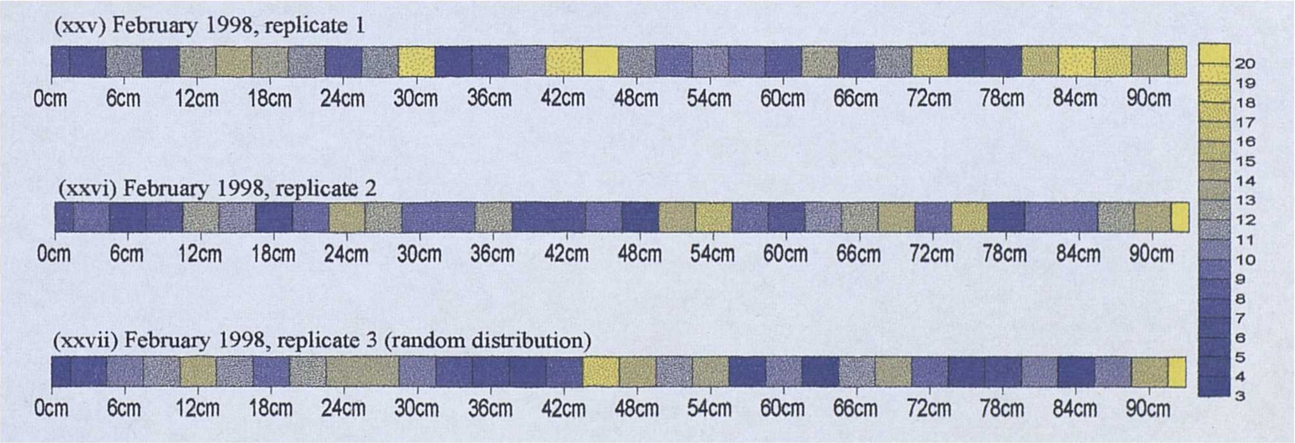
(xx) October 1997, replicate 2 (random distribution)

(xxi) October 1997, replicate 3 (random distribution)


(xxii) December 1997, replicate 1

(xxiii) December 1997, replicate 2

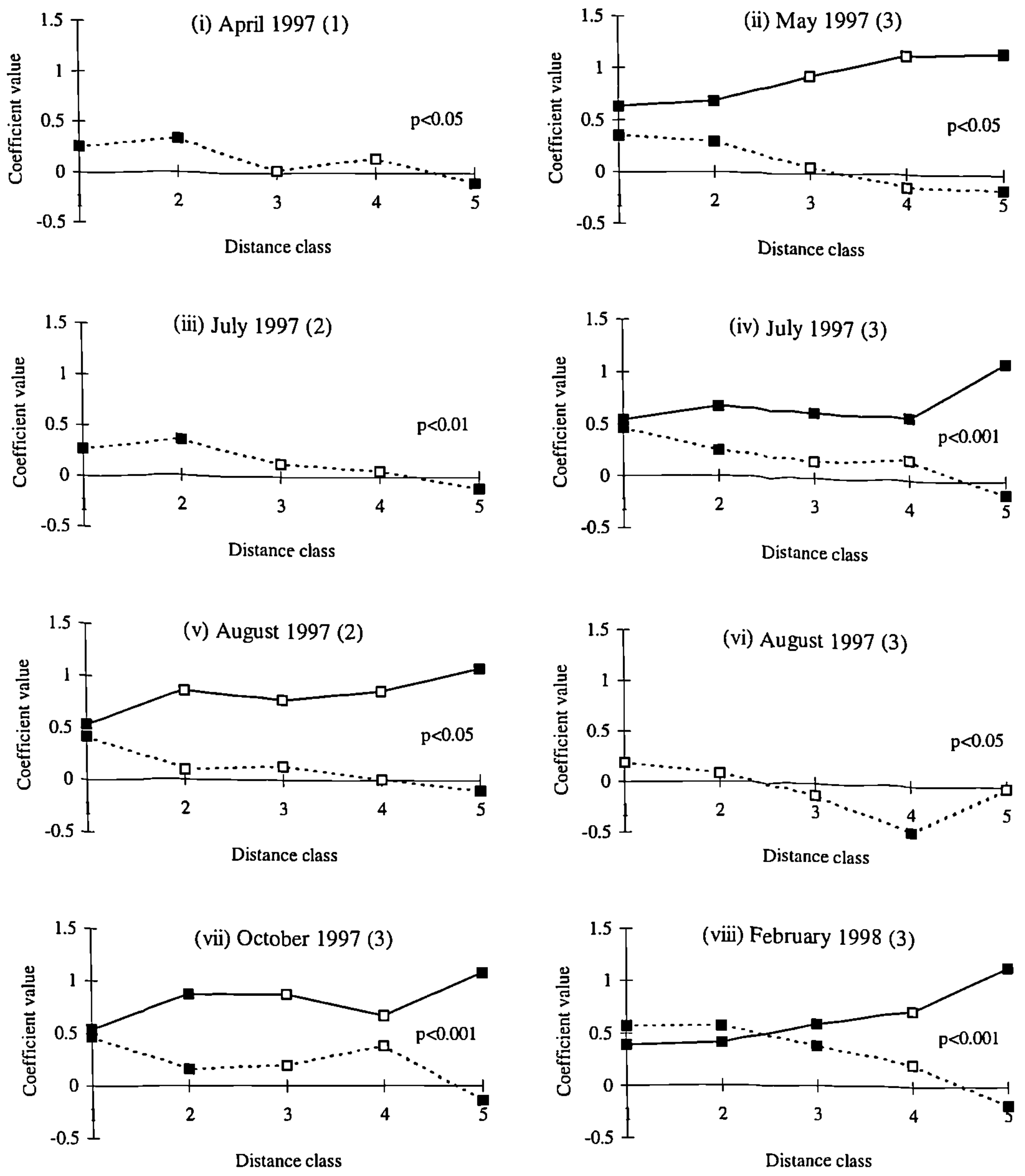
(xxiv) December 1997, replicate 3 (random distribution)


(xxv) February 1998, replicate 1

(xxvi) February 1998, replicate 2

(xxvii) February 1998, replicate 3 (random distribution)

Figures 7.4 (xix-xxvii) : Continued.



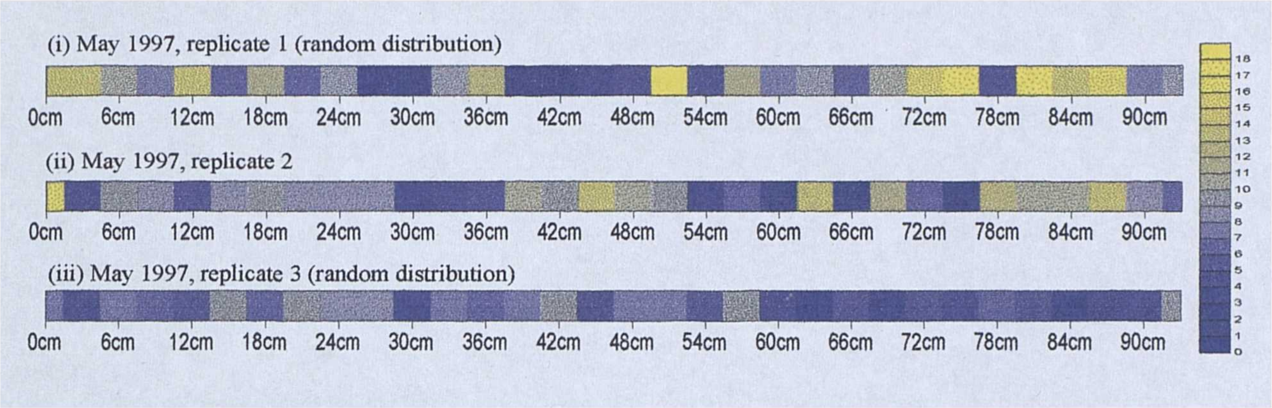
Figures 7.5(i-viii) : Correlograms of significant autocorrelation coefficients for adult *P. elegans* between March 1997 to February 1998 (number in bracket refers to replicate number). Dashed lines represent Moran's coefficients while solid lines represent Geary's coefficients. P-values refer to whole correlogram of Moran's coefficients after a Bonferroni correction while individual points significant at 5% are shown as solid symbols.

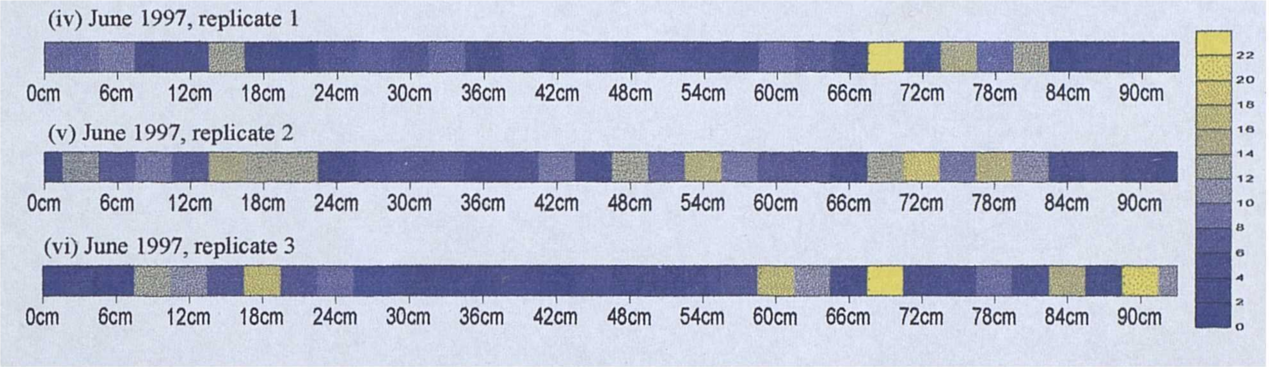
The new recruits were only sufficiently abundant for statistical analyses during May, June and December 1997 and February 1998. Mean abundances per core of new recruits for these months were rather similar for each patch replicate and, therefore, all 3 replicates were analysed for these months. The results of their indices of dispersion are displayed in Table 7.2. These results suggest that new recruits, i.e., individuals benthic for less than 1 month, were generally randomly distributed except during June 1997 when they were aggregated.

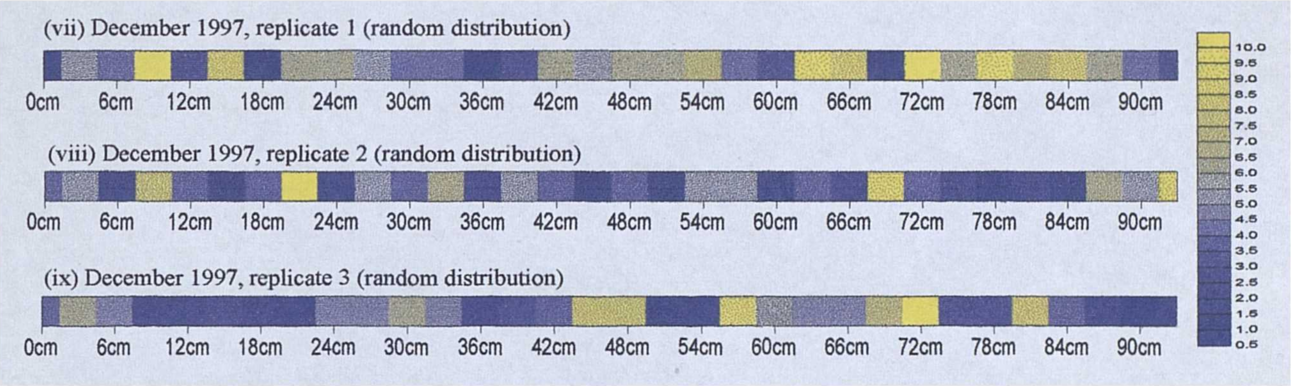
Figures 7.6(i-xii) present the density plots of the abundances of new recruits for these months. Spatial autocorrelation analysis performed on these distributions revealed no significant spatial structuring and the correlograms are therefore not shown. The density plots suggest that the non-random distributions of new recruits during June 1997 probably resulted from patches which were smaller that the sampling unit, 3cm, which probably explains why their spatial correlograms were non-significant.

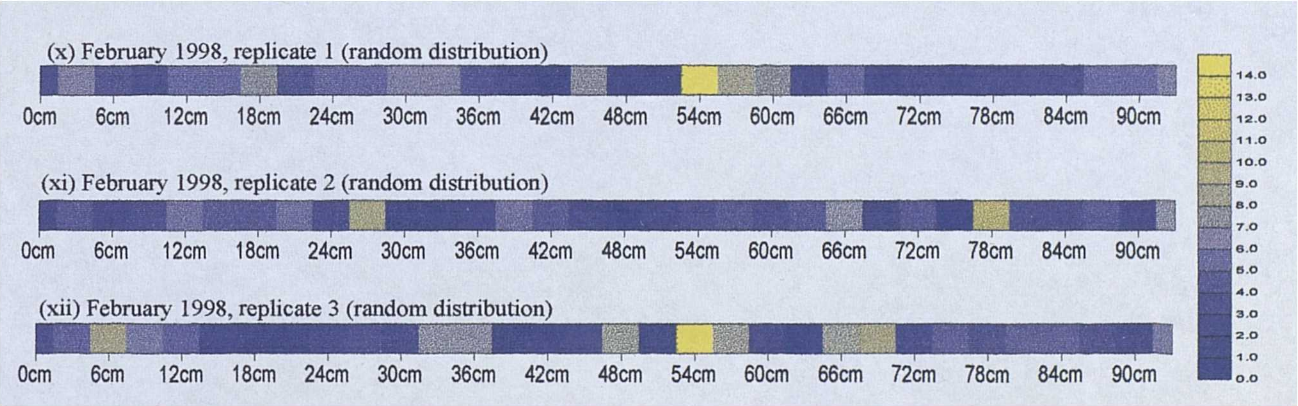
Month		v:m ratio	pattern	I_d	pattern	I_p	pattern
	1	1.428	Random	1.037	Random	0.385	Random
May 1997	2	1.841	**A	1.106	*A	0.501	*A
	3	0.916	Random	0.986	Random	-0.096	Random
	1	3.677	***A	1.522	*A	0.507	*A
June 1997	2	2.217	***A	1.194	*A	0.502	*A
	3	4.938	***A	1.563	*A	0.508	*A
	1	1.208	Random	1.038	Random	0.187	Random
December 1997	2	1.163	Random	1.050	Random	0.146	Random
	3	1.423	Random	1.042	Random	0.213	Random
	1	0.832	Random	0.961	Random	-0.191	Random
February 1998	2	1.228	Random	1.066	Random	0.206	Random
	3	1.441	Random	1.098	Random	0.397	Random

Table 7.2 : Indices of dispersion of *P. elegans* new recruits for the months with mean densities greater than 3 individuals per core. A=Aggregated distribution where * represents a statistical significance from random at $p<0.05$, ** $p<0.01$ and *** $p<0.001$.









Figures 7.6 (i-xii) : Density maps of new recruits for May, June and December 1997 and February 1998 using nearest neighbour gridding method.

The results of correlation analyses between adult *P. elegans* abundances and those of *P. elegans* new recruits, together with those of other species with mean abundances greater than 1 per core, are presented in Table 7.3. The results suggest that in general, *P. elegans* densities were not significantly correlated with those of any other species (except a positive correlation with *C. edule* during July (replicate 3)). The non-significant results obtained were supported by their scatter plots which indicated a lack of correlation in each case. However, the results also suggest that there appeared to be a significant positive correlation in the abundances of adult *P. elegans* adults with the abundances of new recruits during June 1997 (replicates 1 and 2). These significant correlations were supported by their scatter plots (not shown) and to a certain extent by their density plots.

Sediment water, organic and silt/clay contents.

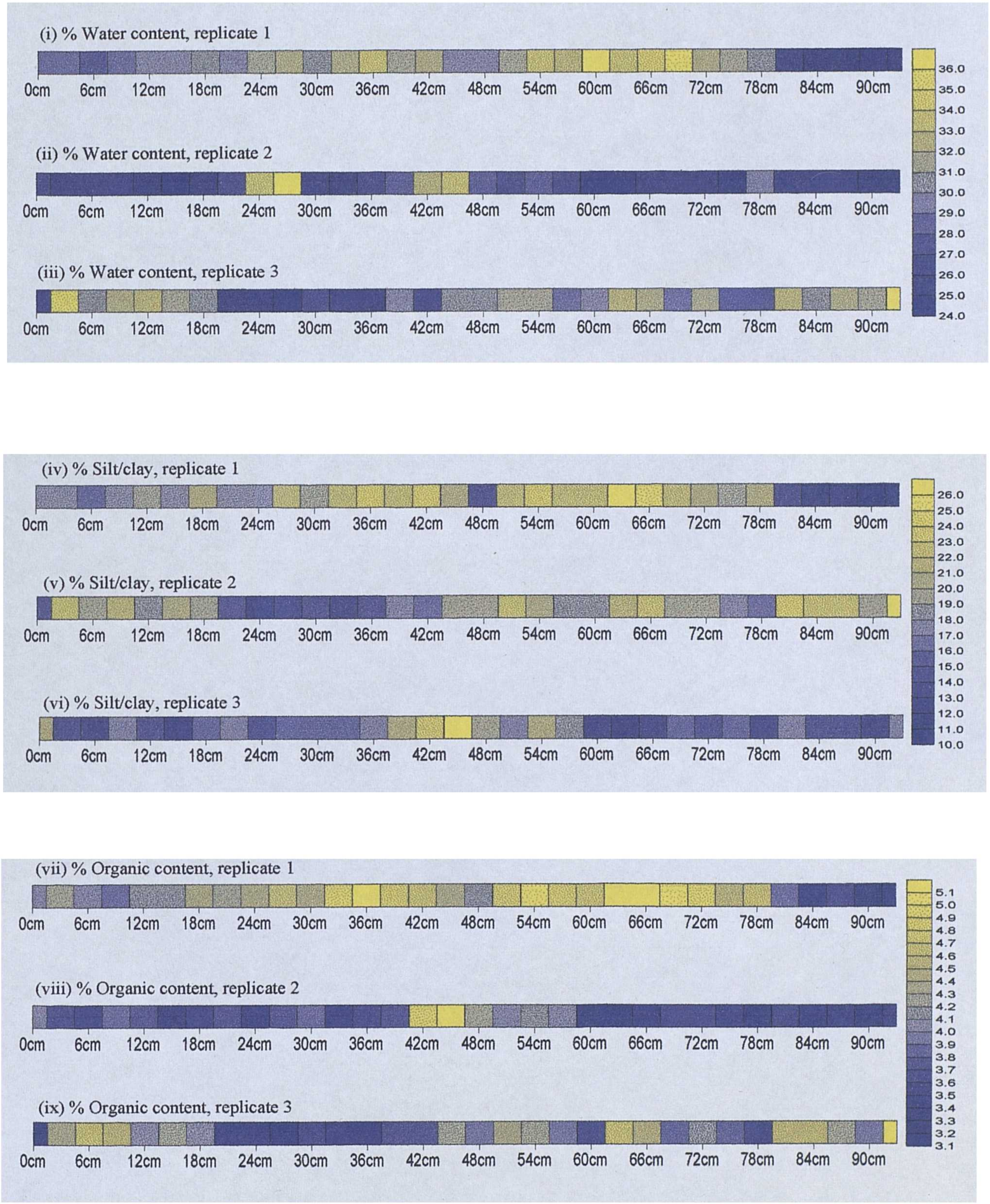
The density plots of the sediment variables % water, % silt/clay and % organic contents for replicate transects 1-3 are presented in Figures 7.7(i-ix). All of these variables produced significant correlograms (Figures 7.8(i-ix)) suggesting that they were all spatially structured within *P. elegans* patches. Within replicate 1, the density plots and autocorrelation analysis suggested that all 3 variables appeared spatially correlated, forming patches up to 25cm across. In patch replicate 2, these variables appeared less positively correlated and formed smaller patches, between 3-9cm. Within replicate 3, % water and % organic contents appeared positively correlated, forming patches between 3-9cm while % silt/clay content, which appeared less correlated from the density plots, formed patches of approximately the same size. Within none of the patches did the sediments contain patches of increased % water, % silt/clay or % organic contents at the same scale (<3cm) as the majority of the adult *P. elegans* populations during this study.

		March 1997			April 1997			May 1997			June 1997			July 1997		
		1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Juvenile	r_p	-	-	-	-	-	-	*0.153	*0.121	*0.123	***0.459**	***0.488**	*0.381	-	-	-
P. elegans	p-value	-	-	-	-	-	-	0.359	0.509	0.502	**0.009**	**0.005**	0.032	-	-	-
C. capitata	r_s	-0.058	-0.036	-	0.184	0.224	0.089	-	0.055	-	-	-	-	-	-	-
	p-value	0.754	0.847	-	0.313	0.219	0.629	-	0.765	-	-	-	-	-	-	-
C. edule	r_s	0.111	0.230	0.081	0.286	0.021	-0.045	0.183	0.233	0.306	0.106	0.268	0.269	-0.138	0.128	**0.458**
	p-value	0.545	0.205	0.660	0.112	0.910	0.807	0.317	0.200	0.089	0.564	0.139	0.136	0.451	0.484	**0.008**
C. volutator	r_s	-	-	-	-	-	-	-	0.186	-	-0.079	-0.329	-0.109	-	-	-
	p-value	-	-	-	-	-	-	-	0.308	-	0.664	0.066	0.553	-	-	-

Table 7.3 : Results of correlation analyses between adult *P. elegans* abundances per core and *P. elegans* new recruits (≥3 per core) and other, abundant species abundances (≥1 per core). * Represents Pearson Product Moment Correlation (r_p) on log(x+1)-transformed data, otherwise a Spearman Rank Correlation (r_s) was performed. P-values in bold represent those statistically significant after a Bonferroni correction.

		August 1997			October 1997			December 1997			February 1998		
		1	2	3	1	2	3	1	2	3	1	2	3
Juvenile *P. elegans*	r_p	-	-	-	-	-	-	*0.292	*0.002	*0.087	-	-	-
	p-value	-	-	-	-	-	-	0.105	0.993	0.637	-	-	-
C. capitata	r_s	-	-	-	-0.307	-0.180	0.364	-0.296	-0.315	-0.004	0.037	-0.173	0.051
	p-value	-	-	-	0.087	0.324	0.041	0.100	0.079	0.984	0.840	0.344	0.780
C. edule	r_s	0.236	0.237	0.159	-	-	-0.333	-	-	-	-	-	-
	p-value	0.193	0.192	0.384	-	-	0.062	-	-	-	-	-	-
C. volutator	r_s	-	-	-	-	0.252	-	-	-0.142	-	-	-	-
	p-value	-	-	-	-	0.171	-	-	0.438	-	-	-	-

Table 7.3 : Continued.



Figures 7.7(i-ix) : Density plots of sediment variables using nearest neighbour gridding method.

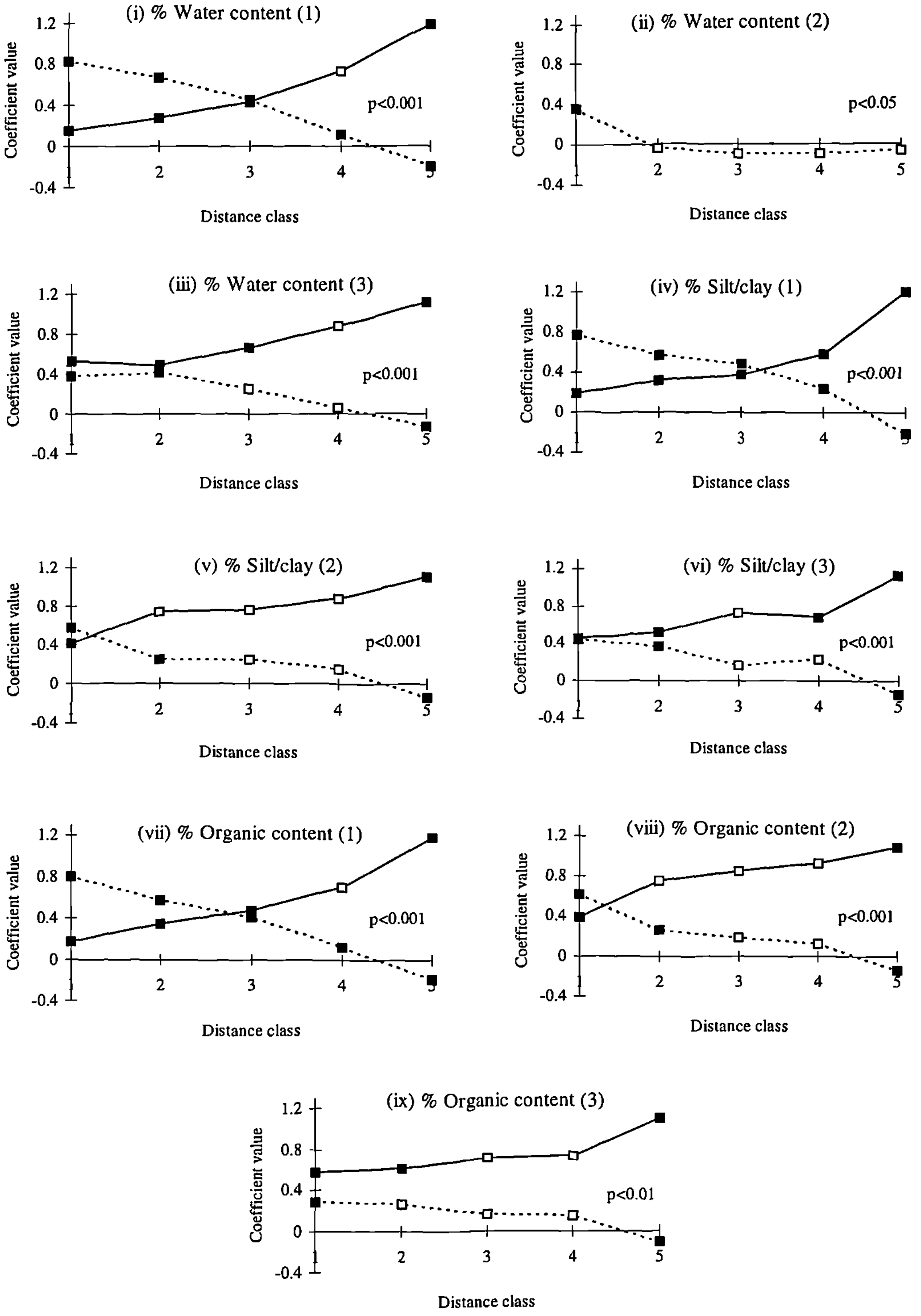


Figure 7.8(i-ix): Correlograms of significant autocorrelation coefficients for the sediment variables (replicates 1-3). Dashed lines represent Moran's coefficients while solid lines represent Geary's coefficients. P-values refer to whole correlogram of Moran's coefficients after a Bonferroni correction while individual points significant at 5% are shown as solid symbols.

DISCUSSION

This study specifically addressed 2 questions, these were:

(1) what is the micro-scale spatial distribution of dense populations of tube-building spionids and what does it suggest about intraspecific interactions?;

(2) what are the roles of larval recruitment, interspecific interactions and abiotic variables in determining spatial patterns?

These questions were addressed using *P. elegans* as an example.

The micro-scale spatial patterns of *P. elegans* within high density patches on Drum Sands.

Linear transects of 32 contiguous cores were taken monthly from 3 small-scale *P. elegans* patches from March to August 1997, and then every other month until February 1998. Dispersion indices suggested that all through the sampling period (except October 1997) the distribution of adult *P. elegans* individuals showed a significant departure from random (in at least 2 of the 3 replicates), all of these were aggregated distributions, i.e., their variances were significantly greater than their means. There was generally a very good agreement between the 3 dispersion indices used (I, I_d and I_p) which suggests that confident statements can be made about these results (Myers, 1978).

The form of these patterns were investigated using mapping (nearest-neighbour gridding technique) and spatial autocorrelation analysis. Spatial autocorrelation analysis allowed the nature of patterns and estimates of patch sizes to be made. In general, these patches of increased adult *P. elegans* densities were smaller than the sampling units (i.e., <3cm^2) and produced non-significant spatial correlograms. However, significant correlograms indicated that some patch replicates, for example, April 1; May 3; July 2 and 3; August 2 and October 3 1997; and February 3 1998 contained *P. elegans* patch sizes between 3-9cm (or up to 12cm for February, 1998). These patches contained abundances of up to 36 adults per 3x3cm core (equivalent to 40,000/m^2).

Quadrat-sampling and multiple cell-corers of various sizes have previously been used in conjunction with indices of dispersion and spatial autocorrelation analysis to examine the micro-scale spatial patterns of spionids in soft sediments. Different inter-individual patterns have been observed which have been related to, and supposedly generated by, intraspecific interactions. For example, Levin (1981) found individuals of *Pseudopolydora* cf. *paucibranchiata* to be uniformly distributed on the intertidal mudflats of Mission Bay, San Diego. She suggested, following observations on its feeding behaviour, that this distribution in this large, aggressive spionid resulted from defensive behaviour and guarding of food, space and tube-building materials. She also found that *Streblospio benedicti*, a smaller spionid polychaete, was randomly distributed suggesting a greater tolerance to intraspecific encounters. However, at their highest densities, 16,500/m^2, Levin (1981) found that *S. benedicti* was also uniformly distributed indicating some density-dependent competition. Morgan (1997) found, by superimposing a 10×10 grid of 2mm^2 squares onto the surface of a larger core, that *P. elegans* was randomly distributed at high densities (47,500/m^2-82,500/m^2). That *P. elegans* did not exhibit a uniform distribution at these densities suggested that this species was very high-density tolerant, in contrast to *P.* cf. *branchiata* and *S. benedicti*, the latter being similar in size and having a similar feeding behaviour to *P. elegans*. This is supported by the observations of Brey (1991) who reported no signs of aggressive behaviour between *P. elegans* individuals.

It is difficult to relate the present findings with those of the above studies because of sampling-scale differences. Since *P. elegans* abundances were too low to sample at the scale of an individual's influence (i.e., 2mm^2) in this study, the results cannot unequivocally be compared with the results of Morgan (1997) or the plotless sampling methods of Levin (1981). For example, plotless sampling, within the micro-scale *P. elegans* patches observed in this study, might have revealed a localised uniform distribution (and hence possibly negative intraspecific interactions) and similarly, sampling with 3cm^2 cores in the studies by Levin (1981) and Morgan (1997) might have revealed clumped distributions in much the same way as in the present study.

The relatively low overall *P. elegans* densities within small-scale patches on Drum Sands indicated that in order to investigate the inter-individual spatial distribution and hence provide evidence for intraspecific interactions, plotless sampling would have been necessary. However, what this study has revealed is the presence of micro-scale patchiness within which *P. elegans* abundances were high enough to allow the possibility of inter-individual interactions. The presence of these patches support the view that *P. elegans* is relatively tolerant of intraspecific interactions. The processes possibly giving rise to such patches are discussed below.

The roles of larval recruitment, interspecific interactions and abiotic variables in determining micro-scale spatial patterns of *P. elegans*.

The results from this study indicated that the micro-scale patches of adult *P. elegans*, within the 1-1.5m^2 patches of increased density defined in Chapter 2, were neither positively nor negatively correlated with any other species of sufficient abundance for analysis during the study period (except for a positive correlation with *C. edule* in one replicate during July 1997). The abundances of *P. elegans* new recruits (<1 month benthic life-span) were significantly positively correlated with those of conspecific adults during periods of high adult micro-scale patch densities (June 1997). This was supported by their scatter plots and density plots. Sediment measurements indicated that the measured sediment variables (% water, % organic and % silt/clay contents) were significantly spatially structured within small-scale *P. elegans* patches during February 1998 and were, therefore, possibly spatially structured all through the sampling period.

Aggregation at the scale of centimetres may result from one or more factors including habitat heterogeneity, symbiosis, gregarious behaviour, limited dispersal of progeny and/or interspecific interactions. While the aggregated distributions of many mobile polychaete species can be generated by their feeding mechanisms (Reise, 1979), those of sessile tube-builders are more likely to have been generated by processes during larval recruitment. Limited dispersal of progeny has been shown to give rise to micro-scale aggregated distributions of *Scoloplos armiger* (Reise, 1979) which produces benthic larvae. However, Chapter 3 indicated that the *P. elegans* population on Drum Sands produced only planktotrophic larvae during 1997 which probably spent approximately 2-3 weeks in the plankton before settlement and, therefore, patterns could not have been generated by limited larval dispersal.

Invertebrate larvae, those of polychaetes in particular, are known to be capable of complex settlement behaviour and substrate selection (see reviews by Wilson, 1958, and Scheltema, 1974). The significant positive correlation of new recruits with *P. elegans* adults during June (replicates 1 and 2) indicate that adult-juvenile interactions, or at least the hydrodynamics associated with adult's tubes, may perhaps have helped generate the *P. elegans* micro-scale patches. Eckman (1983) proposed, using field observations and experimental manipulation experiments, that species heterogeneity at this scale may be created by the localised hydrodynamic effects of polychaete tubes. Facilitation of larval colonisation by tube-builders on intertidal sandflats has previously been demonstrated (Gallagher *et al.*, 1983; Savidge and Taghon, 1988; Thrush *et al.*, 1992). Eckman (1979) suggested that local flow patterns were important in producing the observed micro-scale gregariousness of several species in Skagit Bay, Washington. In the present study, a significant positive correlation between new recruits and adults only occurred during June 1997, when adult densities, and presumably hydrodynamic effects of adult's tubes, in micro-scale patches reached their highest. Hadfield (1986) and Bachelet (1990) pointed out that one must be careful when inferring processes responsible for larval recruitment patterns from field observations. Since some time must elapse between larval settlement and subsequent sampling, the patterns observed will have resulted from not only initial settlement but from a number of subsequent processes, each capable of affecting juvenile distribution patterns. Therefore, it is not possible to suggest whether the non-random patterns and positive correlations of new recruits with adult micro-scale patches resulted from non-random larval settlement patterns or from differential mortality/survivorship of juveniles (Woodin, 1986).

The lack of a significant correlation between *P. elegans* adults and any other species indicated that the micro-scale patchiness of *P. elegans* adults within patches were probably not generated by interspecific interactions. All other species present within *P. elegans* patches were of relatively low abundance and it is likely that none of them were present in sufficient abundances to significantly affect the spatial distribution of *P. elegans*. One possible explanation for the lack of association between *P. elegans* and other species (or at least those with planktonic larvae) may be the high densities of *P. elegans* within micro-scale patches. For example, the potential feeding area of *P. elegans* is likely to have been over-exploited within these localised patches (Brey, 1991) and since spionids are known to predate on settling larvae of other species (Breese and Phibbs, 1972; Daro and Polk, 1973; Tamaki, 1985; Whitlatch and Zajac, 1985) there may have been no refuges from predation for settling larvae. However, such interactions would presumably have resulted in significant negative associations.

It was not possible to determine sediment heterogeneity along each transect in this study. Therefore, correlation analysis between the abundances of adult and juvenile *P. elegans* with the measured sediment variables (% water, % organic and % silt/clay contents) were not possible. *P. elegans* patches appeared as smooth plateaus with no visual sign of topographical variability within them. Samples taken from 3 patches during February 1998 revealed micro-scale spatial patterning of the 3 sediment variables. These sediment patches were at least $3cm^2$ with apparent correlation between at least 2 of the variables in 2 of the 3 replicates. These patches were not of the same scale as patches exhibited by adult *P. elegans* or by new recruits during most of the study period (less than $3cm^2$), however, sediment patterning of this scale for other variables, or for these variables during other times of the study period cannot be ruled out. The possibility that micro-scale patchiness of *P. elegans* was generated by aggregated larval settlement patterns in response to sediment heterogeneity cannot be falsified with the results from this study.

Although *P. elegans* is a sessile tube-building spionid, adults of this species may be capable of some mobility. Armonies (1994) found adult *P. elegans* individuals in the water column, and Wilson (1992, 1994) suggested that adults of this species were capable of lateral crawling. *P. elegans* is the only reported spionid species in which direct spermatophore transfer is used during sexual reproduction (Schlotzer-Schrehardt, 1987, 1991). This involves a special pattern of reproductive behaviour including active seeking of the females by males and therefore adults may actively seek to relocate near conspecific individuals to enhance their reproductive chances. This factor may also have been partly responsible for the micro-scale aggregations of adults observed in this study, at least at certain times during the year. Direct laboratory observations are needed to confirm whether mature males relocate towards females, or vice versa, to confirm this.

In conclusion, this study has shown the presence of aggregated distributions of a tube-building polychaete within small-scale ($1\text{-}1.5m^2$) patches of increased density. These patches were generally smaller than the sampling unit ($3cm^2$) and persisted all through the year. The presence of these patches support previous studies indicating that *P. elegans* are very tolerant of conspecific encounters. The process(es) generating these patterns were probably positive adult-juvenile interactions (passive and/or active), adult movement and/or sediment heterogeneity. However, since correlation analysis should not be used to imply causation, controlled laboratory experiments and observations, in addition to field observations, need to be carried out to test these hypotheses.

CHAPTER 8

THE FAUNAL COMMUNITIES OF *PYGOSPIO ELEGANS* PATCHES

INTRODUCTION

Epibenthic biogenic structures are conspicuous features of many marine soft-bottom habitats. Of these, the most widespread include seagrasses (e.g., Thistle *et al.*, 1984), mussels (e.g., Ragnarsson, 1996), macroalgal mats (e.g., Hull, 1987, 1988; Everett, 1991, 1994; Raffaelli *et al.*, 1999; Chapters 4 and 5 of this study) and high densities of tube-dwelling polychaetes, or 'tube-beds' (e.g., Fager 1964; Daro and Polk, 1973; Noji, 1994; Morgan, 1997). The ecological importance of the tube-beds of many polychaete species has been studied including the terebellids *Lanice conchilega* (Jones and Jago, 1993; Ragnarsson, 1996), *Loimia* sp. and *Axionice* sp. (Trueblood, 1991), the oweniid *Owenia fusiformis* (Fager, 1964), the maldanids *Clymenella torquata* (Sanders *et al.*, 1962; Featherstone and Risk, 1977) and *Axiothella rubrocincta* (Weinberg, 1979) and the spionids *Pygospio elegans* (Dupont, 1975; Morgan, 1997), *Polydora ciliata* (Noji, 1994) and *Spiophanes* cf. *wigleyi* (Featherstone and Risk, 1977).

The general inference arising from such studies is that tube-mats play a major role in determing soft-sediment community structure (Woodin, 1981; Gallagher *et al.*, 1983). Both meio- and macrofaunal communities, together with many physical variables, of those sediments with biogenic structures have been found to differ from those of adjacent areas lacking such structures. The factors responsible for these differences are many and the effects of tube-beds on community composition and sediment structure ultimately result from the interaction of many complex and interrelated processes. Furthermore, since the fauna associated with tubes may have a marked effect on sediment structure and community composition themselves, quantifying the effects of tube-beds is inherently difficult since it involves both the direct alterations

CHAPTER 8

THE FAUNAL COMMUNITIES OF *PYGOSPIO ELEGANS* PATCHES

INTRODUCTION

Epibenthic biogenic structures are conspicuous features of many marine soft-bottom habitats. Of these, the most widespread include seagrasses (e.g., Thistle *et al.*, 1984), mussels (e.g., Ragnarsson, 1996), macroalgal mats (e.g., Hull, 1987, 1988; Everett, 1991, 1994; Raffaelli *et al.*, 1999; Chapters 4 and 5 of this study) and high densities of tube-dwelling polychaetes, or 'tube-beds' (e.g., Fager 1964; Daro and Polk, 1973; Noji, 1994; Morgan, 1997). The ecological importance of the tube-beds of many polychaete species has been studied including the terebellids *Lanice conchilega* (Jones and Jago, 1993; Ragnarsson, 1996), *Loimia* sp. and *Axionice* sp. (Trueblood, 1991), the oweniid *Owenia fusiformis* (Fager, 1964), the maldanids *Clymenella torquata* (Sanders *et al.*, 1962; Featherstone and Risk, 1977) and *Axiothella rubrocincta* (Weinberg, 1979) and the spionids *Pygospio elegans* (Dupont, 1975; Morgan, 1997), *Polydora ciliata* (Noji, 1994) and *Spiophanes* cf. *wigleyi* (Featherstone and Risk, 1977).

The general inference arising from such studies is that tube-mats play a major role in determing soft-sediment community structure (Woodin, 1981; Gallagher *et al.*, 1983). Both meio- and macrofaunal communities, together with many physical variables, of those sediments with biogenic structures have been found to differ from those of adjacent areas lacking such structures. The factors responsible for these differences are many and the effects of tube-beds on community composition and sediment structure ultimately result from the interaction of many complex and interrelated processes. Furthermore, since the fauna associated with tubes may have a marked effect on sediment structure and community composition themselves, quantifying the effects of tube-beds is inherently difficult since it involves both the direct alterations of tubes on near-bed flow and the indirect effects of the resulting biogenic changes (Lukenbach, 1986).

Polychaete tubes are thought to exert important and complex effects on near-bed flow. While isolated tubes, or 'roughness elements' in hydrodynamic terms (Eckman, 1983), destabilise sediments by creating local currents which result in sediment scour and local deposition (Eckman *et al.*, 1981; Lukenbach, 1986; 1987), there is a widely accepted notion that sediments are stabilised by arrays of tubes. This opinion has developed from both field studies (Sanders *et al.*, 1962; Fager, 1964; Daro and Polk, 1973) and laboratory flume studies (Nowell and Church, 1979; Nowell *et al.*, 1981; Eckman, 1983). Tube size, geometry, and numerical density determine the properties of near-bed flow, including the magnitude of the shear stress exerted on the bed (and hence its susceptibility to erosion, i.e., stability), the rate of fluid transport, and the production of turbulence (Eckman *et al.*, 1981; Nowell *et al.*, 1981). The shear stress exerted on the bed affects emigration of established individuals and the composition of the sediments, while fluid transport near the bed will affect immigration rates of fauna dispersed passively by lateral advection. It is conceivable that these hydrodynamic processes alone may result in the distinct faunal communities observed in field studies. The effects of tube-beds on fluid transport have been shown to facilitate colonisation by micro-organisms which further helps stabilise the sediments (Eckman *et al.*, 1981; Lukenbach, 1986) by mucus binding (Grant *et al.*, 1986). Since the velocity of near-bed flow generally exceeds the swimming speeds of larvae (Chia, 1989), larvae are generally advected horizontally as passive particles along the bed (Butman, 1987) and deposition to the bottom is usually predominantly via passive entrainment (Hannan, 1984; Pawlik and Butman, 1993; Snelgrove *et al.*, 1993). Eckman (1983) however, using flume experiments suggested that the velocity of near-bed flow was reduced using seagrass mimics to such an extent that larvae would be passively deposited. In addition to the hydrodynamic effect of their tubes, tube-building organisms themselves significantly affect processes at the sediment-water interface by their behaviour, e.g., feeding, burrowing, defecation and tube irrigation (Rhoads and Young, 1970; Frithsen and Doering, 1986; Noji and Noji, 1991).

Other theories have been postulated for the observed community differences within tube-beds. Woodin (1978, 1981) suggested that the observed effects result from the 'refuge' provided by the high numbers of tubes. Both predation and local disturbances have been shown to be important structuring forces for soft-bottom infauna (Reise, 1978; Woodin, 1978; Zajac and Whitlatch, 1982a; Ambrose, 1984; Thrush, 1988; Hall *et al.*, 1993) and Woodin (1978) suggested that refuges may be created by organisms whose structures buffer the impact of physiological stress or inhibit the access of predators. Woodin (1976) viewed soft-bottom community structuring from the perspective of 'functional group' interactions in which 'tube-dweller', 'bioturbator' and 'suspension-feeder' functional groups should each be unfavourable to each other. This 'functional group' interaction hypothesis implied that the maintenance of discrete dense assemblages in infaunal systems was due to interactions between established infaunal individuals and settling larvae. Therefore, a tube-building species would be expected to exhibit increased densities within an assemblage of other tube-builders by this interaction, whilst bioturbators and suspension-feeders would be expected to exhibit lower densities.

The main tube-building polychaete species forming dense tube-beds in northern European shallow waters tend to be either *Lanice conchilega* or *Pygospio elegans*. Several studies such as Eagle (1973, 1975), Carey (1982) and Ragnarsson (1996) have described the fauna within *L. conchilega* tube-beds, however, relatively few studies have focused on the beds formed by *P. elegans* (e.g., Dupont, 1975; Morgan, 1997). The dense tube-beds at Drum Sands allowed an investigation of the effects of this tube-builder on an intertidal sandflat. Specifically, the differences in the biology and the sediments within *P. elegans* patches and non-patch areas of sand were studied.

METHODS

The sampling for the investigation described in Chapter 6 was carried out at the same time and within the same patch and non-patch plots as those for the present study. However, a further survey was also carried out in August 1998 for this study. Faunal sampling methods, sample treatment and sorting, faunal identification and statistical analyses for this chapter are as described in Chapter 6.

While sediment variables were only measured on one occasion for the investigation described in Chapter 6, the same variables were measured at each sample date for the present study, i.e., April, August and December 1997, and August 1998.

In addition to the size measurements of *P. elegans*, individuals of other species with mean abundances above 20 per core in patch and non-patch samples were measured. *P. elegans* and *C. capitata* were measured as 5th setiger and 3rd setiger widths respectively. Small bivalves were measured as shell width using a microscope (×20 magnification) fitted with an eyepiece graticule while larger ones were measured with a pair of calipers.

RESULTS

Univariate analysis of species abundances - A total of 22 taxa for the patch samples and 20 for non-patch samples were recorded from the 4 sampling months, only 6 of these were sufficiently abundant for univariate statistical analysis (i.e., mean abundances ≥2 for either plot type). These were the polychaetes *P. elegans* and *C. capitata*, the bivalves *C. edule* and *M. balthica*, the amphipod *C. volutator* and oligochaetes. Mean densities, together with standard errors and statistical differences between patch and non-patch densities, are presented in Figures 8.1(i-viii). Statistical analysis was not carried out on total *P. elegans* numbers since they were the sums of the adult and juvenile means and these stages were analysed separately. Statistical analysis was not carried out for *C. capitata*, *C. volutator* and oligochaetes for August 1998 due to insufficient numbers in the samples.

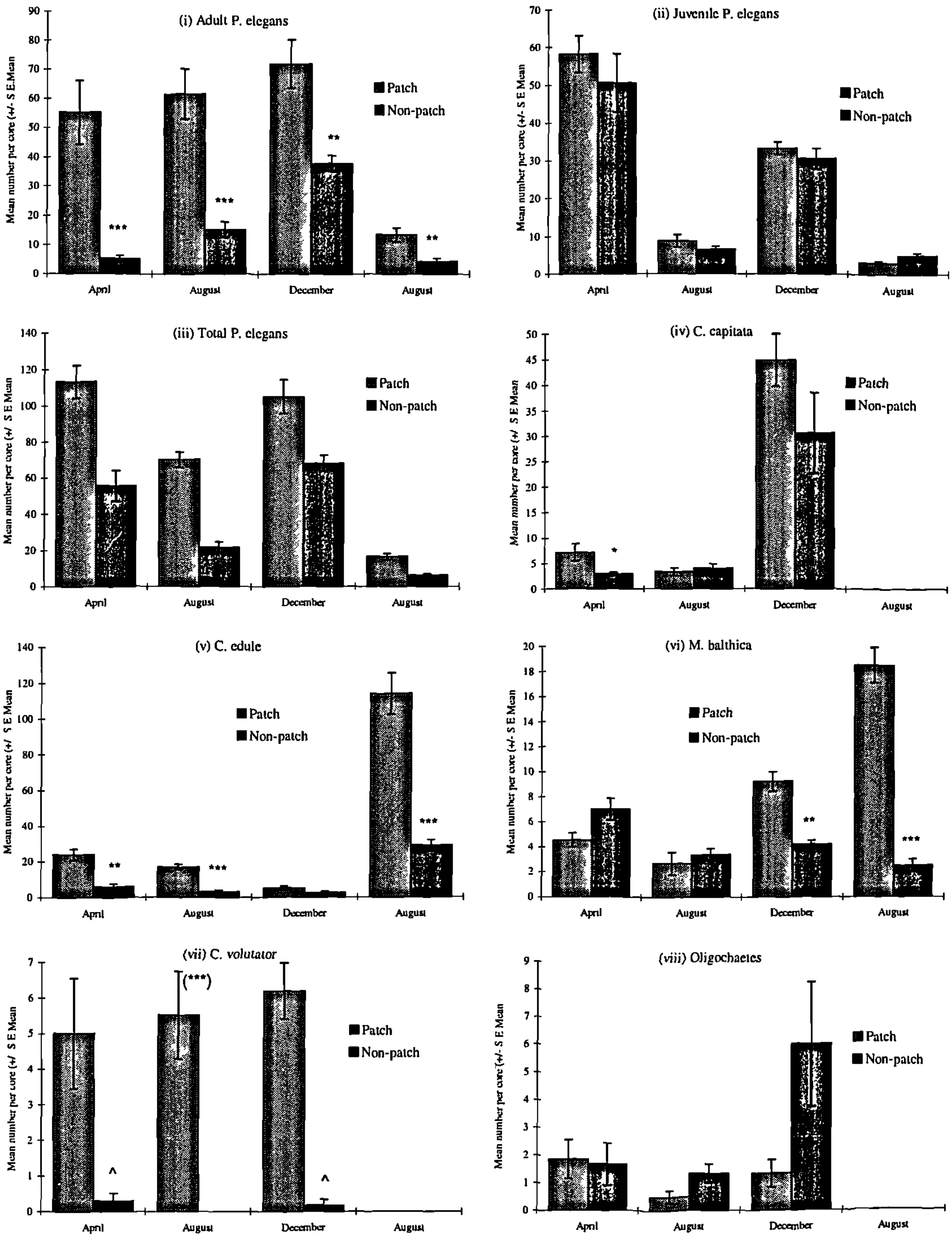
The numbers of adult *P. elegans* were always significantly higher in patches than outside patches (Figure 8.1(i)). Since the sampling was stratified into patches and non-patches this result is not surprising. Their numbers increased from April to December 1997 in both plot types. However, in August 1998, there was a large decrease in the numbers of *P. elegans* adults both inside and outside patches from 72 ± 8.4 to 13.6 ± 2.34 and 37.8 ± 2.76 to 4.3 ± 1.13; for patch and non-patch samples respectively. Juvenile *P. elegans* densities were high during April 1997 as this coincided with the peak of new recruits for this year (see Chapter 3). Their densities were much lower the following August but increased again in December 1997, corresponding to a second, smaller peak of new recruits during the winter (see Chapter 3). Their numbers were again low in August 1998. Additionally, the numbers of juveniles in patches and non-patches were never significantly different, suggesting there was no preferential juvenile recruitment to the ambient sediments of patches compared with non-patch areas (this contrasts with the findings of Chapter 6 with respect to azoic sediments).

The densities of *C. capitata* were relatively low during April and August 1997, approximately 5 per core. However, there was a dramatic increase in their densities during December when densities rose to 44.8 ± 5.1 and 30.7 ± 7.9 per core in patch and non-patch samples respectively (Figure 8.1(iv)). They were practically absent from both sample types during the following August.

The numbers of *C. edule* dramatically rose in *P. elegans* patches during August 1998 to very high densities of 114 ± 11.5 per core (Figure 8.1(v)). This is far greater than the numbers in patches the same time the previous year (16.7 ± 1.5 per core) suggesting that the spat-fall of 1998 and/or juvenile survival was possibly higher than the previous year. A similar trend was shown by *M. balthica*, whose densities within *P. elegans* patches rose from 2.67 ± 0.88 per core in August 1997 to 18.5 ± 1.4 per core in August 1998 (Figure 8.1(vi)).

Corophium volutator was found almost exclusively in *P. elegans* patches, with mean densities between 5-6 per core from April to December 1997, but was totally absent in August 1998. Oligochaetes were present in relatively low numbers from April to August 1997, but peaked in abundance in non-patch samples (6.0 ± 2.25 per core) in December 1997. Although present in August 1998, oligochaetes were not sufficiently abundant for statistical analysis.

These results suggest that for the majority of the most abundant taxa, significantly higher densities were attained in *P. elegans* patches than outside patches, at least at certain times of the year. For example, significantly higher densities of *C. capitata* (April, 1997; Figure 8.1(iv)); *C. edule* (April and August, 1997 and August 1998; Figure 8.1(v)); *M. balthica* (December 1997 and August 1998; Figure 8.1(vi)); and *C. volutator* (April to December 1997; Figure 8.1(vii)) were found in *P. elegans* patches compared to outside patches. Furthermore, this pattern was also shown by the meiofauna. Although not counted, harpacticoid copepods and nematodes were much more abundant on the 212μm sieve fractions from patches compared with those from non-patch samples.



Figures 8.1(i-viii) : Mean abundances (±S.E.Mean, n=6) of the most abundant taxa together with the results of statistical tests between patch and non-patch values. * Denotes a statistical difference between patch and non-patch means using a Two-sample t-test at 0.05 level of significance; ** at 0.01; and *** at 0.001. (***) Denotes a significant difference from zero at 0.001 level of significance using a One-sample t-test. ^ Indicates a statistical difference at 0.05 level of significance using Mann-Whitney U test.

Size-frequency analysis - In addition to *P. elegans*, two species were sufficiently abundant (i.e., mean abundance ≥20 in either plot type) in samples to allow size-frequency measurements and the statistical assessment of differences between patches and non-patches. These were *C. capitata* (December 1997 only) and *C. edule* (April 1997 and August 1998).

The size-frequency histograms of *P. elegans* throughout the sampling period are given in Figures 8.2(i-viii) and the results of the χ^2 goodness of fit and Kolmogorov-Smirnov (K-S) tests are shown in Table 8.1.

In April 1997, the size distributions of *P. elegans* were significantly different ($p<0.001$, $p<0.01$; χ^2 goodness of fit and K-S tests, respectively) between patch and non-patch individuals with the greatest χ^2 differences being due to both the smallest size class, 0.13-0.20mm (23.8%) and the >0.40-0.47mm size class (25.9%). This was due to the bimodal distribution in patches where large numbers of juveniles and adults were present and the skewed distribution in non-patches where there were very few adults.

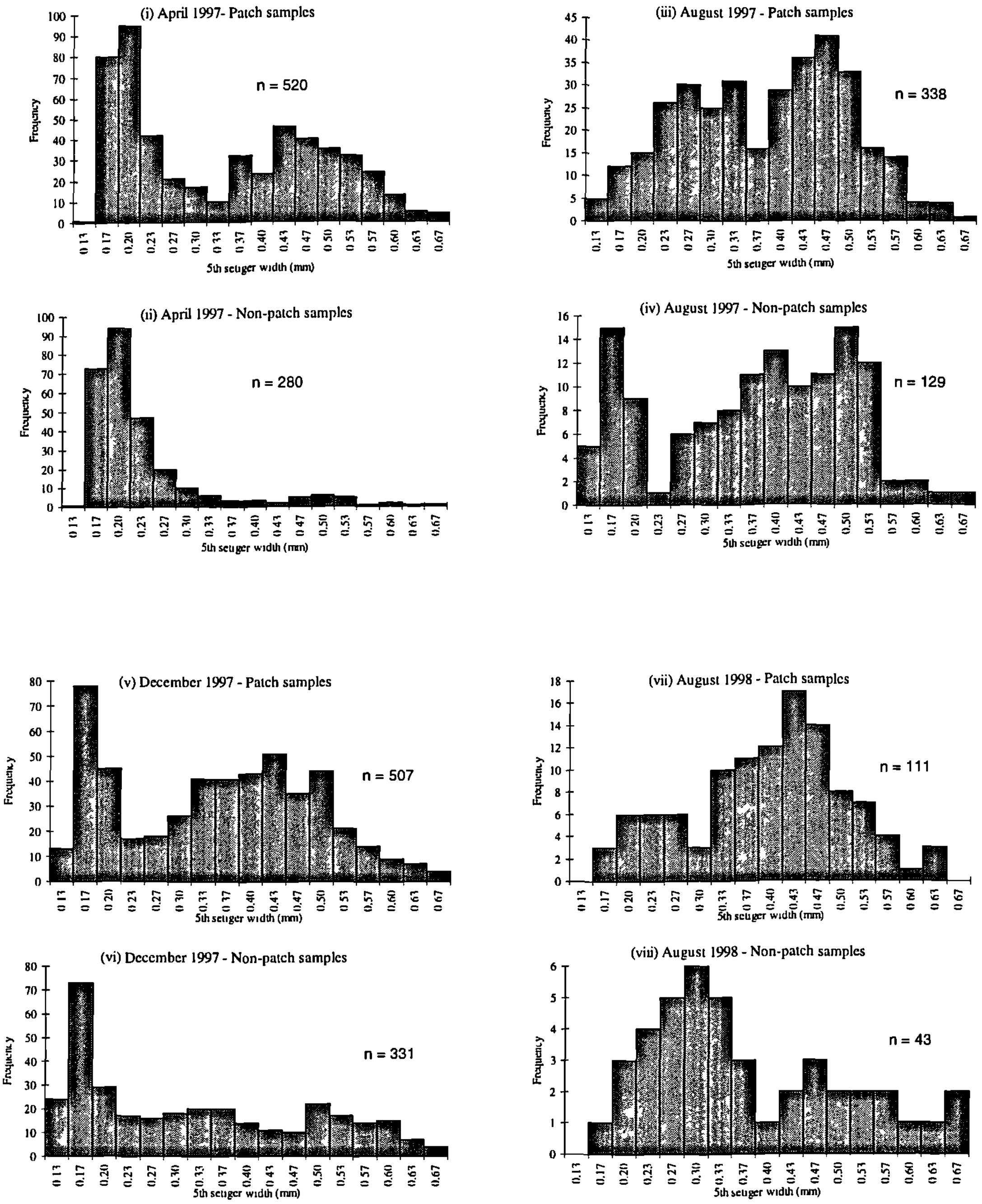
The results for the *P. elegans* distributions in August 1997 were more equivocal: although the two distributions were statistically different ($p<0.001$, $p<0.05$; χ^2 goodness of fit and K-S tests, respectively), the reasons why are less obvious than those for April. The χ^2 goodness of fit results suggest that the majority of the difference, 41.9% and 29.7%, lie in the two smallest size classes, 0.13 ≤0.20mm and >0.20 ≤0.27mm, respectively. In other words there were fewer *P. elegans* individuals in the smallest size class and more individuals in the >0.20 ≤0.27mm size class in *P. elegans* patches compared to those of the non-patch distribution. This can be seen in Figures 8.2(iii-iv) in which the modal size in the peak of juveniles appears to be smaller in non-patch samples compared to the corresponding modal size in patches.

The *P. elegans* size-frequencies for December 1997 were similar to those in April of that year. A second recruitment period of *P. elegans* occurred in December resulting in significant differences in size distributions ($p<0.001$, $p<0.01$; χ^2 goodness of fit and K-S tests, respectively) due a bimodal distribution in patch samples and a skewed distribution in non-patches. Consequently, the greatest χ^2 differences were in the same size classes as those in April: 20.6% for 0.13-0.20mm and 42.9% for the $>0.40 \leq 0.47$mm size classes.

In August 1998, there were no longer any significant differences between the size distribution of *P. elegans* in patches and non-patches ($p=0.06$, $p>0.05$; χ^2 goodness of fit and K-S tests, respectively). The greatest χ^2 difference, 32.8%, was due to the size class $>0.40 \leq 0.47$mm, i.e., there were fewer adults of this size in non-patch samples. However, this result could alternatively be viewed as fewer juveniles in patches compared with non-patches (see Figure 8.1(ii)).

	χ^2 goodness of fit								K-S
	0.13- ≤0.20	>0.20 ≤0.27	>0.30 ≤0.37	>0.37 ≤0.40	>0.40 ≤0.47	>0.47 ≤0.53	>0.53	**p value**	**p value**
April	23.8	12.9	0.1	14.2	25.9	12.6	10.6	**<0.001**	**<0.01**
August	41.9	29.7	5.2	6.1	6.5	8.2	2.4	**<0.001**	**<0.05**
December	20.6	5.5	1.2	13.8	42.9	0.5	15.6	**<0.001**	**<0.01**
August	5.0	11.6	20.2	14.6	32.8	1.8	14.0	0.06	>0.05

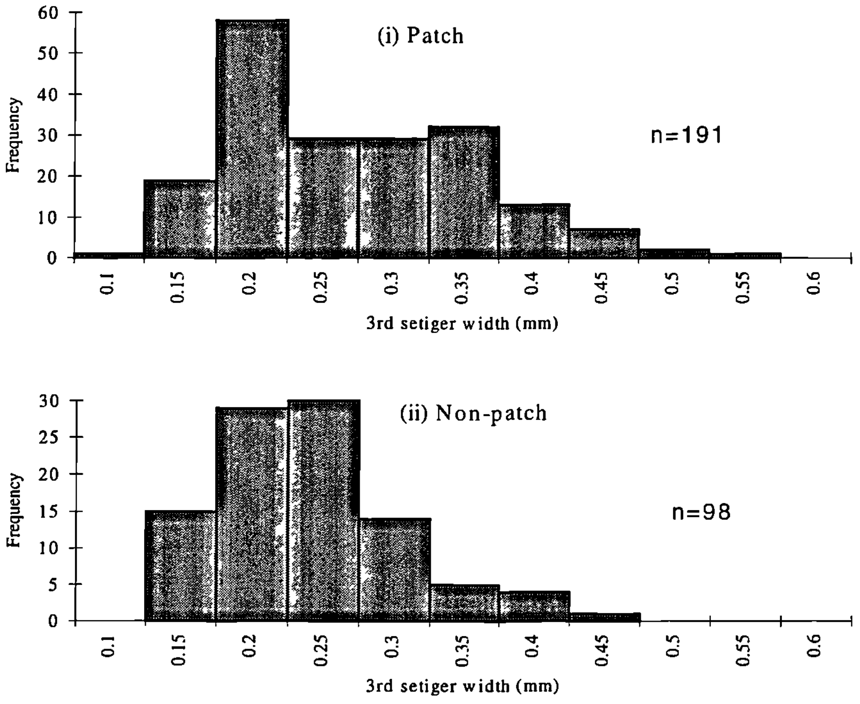
Table 8.1: *P. elegans* size-frequency distribution χ^2 goodness of fit and Kolmogorov-Smirnov (K-S) tests results between patches and non-patches for April 1997 until August 1998. The percentage of the total χ^2 values are given for each size class together with the p-values for both the χ^2 goodness of fit and the Kolmogorov-Smirnov tests.



Figures 8.2(i-viii) : Size-frequency histograms of *P. elegans* in patch and non-patch samples for each sampling occasion, 'n' denotes the total number of individuals measured for each plot type.

The size-frequency distributions of *C. capitata* in patch and non-patch samples are presented in Figures 8.3(i-ii). There were statistical differences between these two distributions (p=0.002, p<0.05; χ^2 goodness of fit and K-S tests, respectively, Table

8.2). This was mainly because of the smaller numbers of individuals with a 3rd setiger width of 0.25mm and higher numbers with 3rd setiger widths of 0.35mm in patches, i.e., there was a greater proportion of larger individuals in patches compared to non-patches.

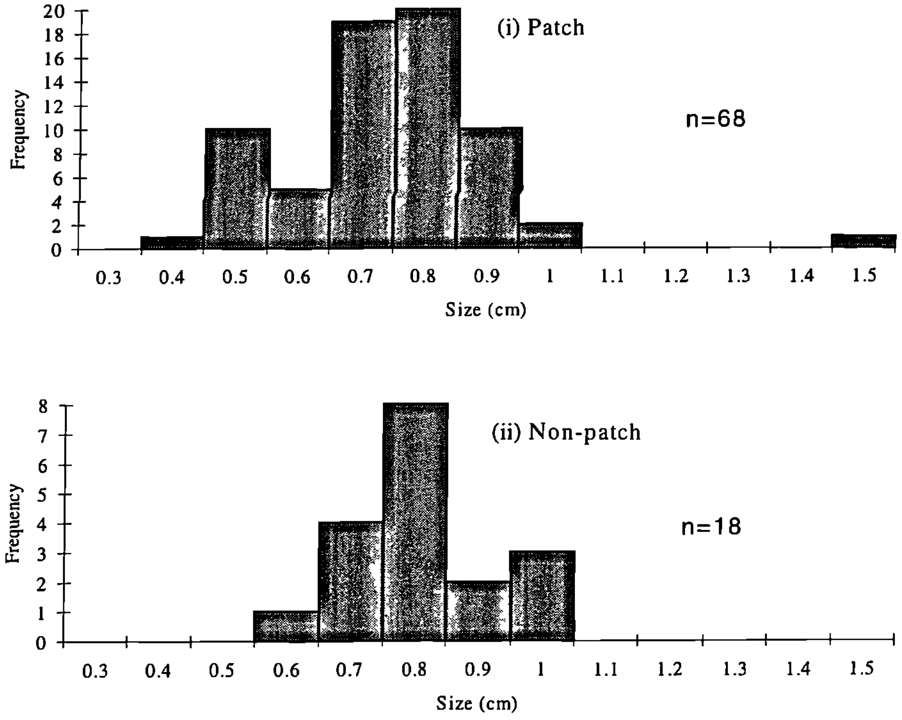


Figures 8.3(i-ii) : Size-frequency histograms of *C. capitata* from December 1997 patch and non-patch samples, 'n' denotes the total number of individuals measured for each plot type.

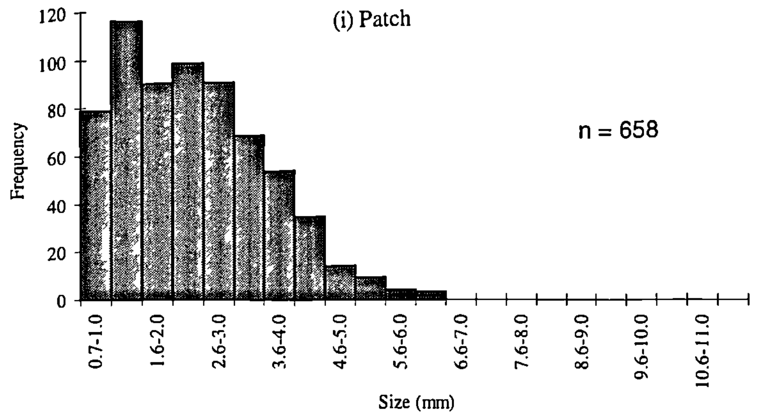
	χ^2 goodness of fit							K-S
size (mm)	≤0.15	0.20	0.25	0.30	0.35	≥0.40	**p value**	**p value**
% explained	6.60	0.07	39.88	0.18	36.27	17.00	**0.002**	**<0.05**

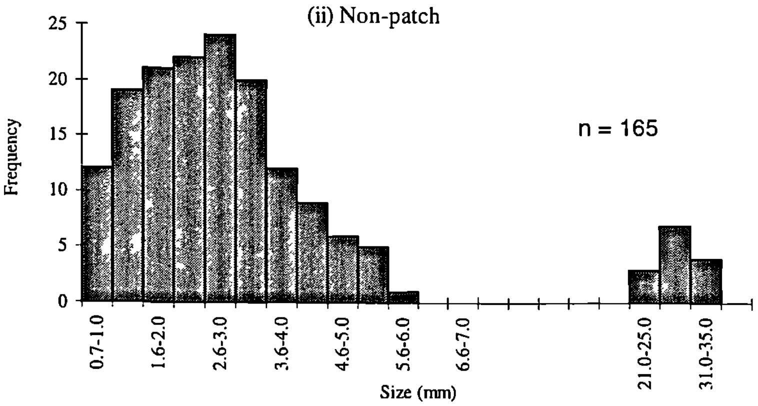
Table 8.2: *C. capitata* size-frequency distribution χ^2 goodness of fit and Kolmogorov-Smirnov (K-S) tests results between patches and non-patches for December 1997. The percentage of the total χ^2 values are given for each size class together with the p-values for both the χ^2 goodness of fit and the Kolmogorov-Smirnov tests.

The size-frequency distributions of *C. edule* in patch and non-patch samples for April 1997 are shown in Figures 8.4(i-ii). Sampling must have occurred before the annual settlement of spat and the mean shell widths in both patches and non-patches were 0.7-0.8cm with no significant differences between the two plots types (p=0.201, p>0.05; χ^2 goodness of fit and K-S tests, respectively). The size distributions for August 1998 are shown in Figures 8.5(i-ii). The size distribution of the individuals with shells less than 6.6mm long is highly skewed. These individuals had no obvious growth rings on their shells and were much smaller than individuals which possessed growth rings. This suggests that all the individuals found in the patches were that year's cohorts. Although there was no difference in the size-frequency distributions (p=0.536, p>0.05; χ^2 goodness of fit and K-S tests, respectively), large individuals, at least one year old, were only found outside *P. elegans* patches.



Figures 8.4(i-ii) : Size-frequency histograms of *C. edule* from April 1997 patch and non-patch samples, 'n' denotes the total number of individuals measured for each plot type.





Figures 8.5(i-ii) : Size-frequency histograms of *C. edule* from patch and non-patch samples in August 1998, 'n' denotes the total number of individuals measured for each plot type. Note the differences in scale on y-axis.

Multivariate analysis of community structure - For multivariate analysis, it was necessary to omit *P. elegans* from the community data. Since sampling was stratified, omitting *P. elegans* was necessary to avoid including this species as both a response variable and as a factor.

The 2-dimensional ordination plots from non-metric MDS of the community data from each of the 4 sampling occasions are given in Figures 8.6-8.9. The stress values were all 0.10 or below implying that the species matrices are well represented by their 2-dimensional MDS ordination plots (Warwick and Clarke, 1994). Therefore, dendrograms are not included. Lines separating patch and non-patch replicates are superimposed onto the MDS plots as carried out for those in Chapter 6.

The ordination plots clearly show that for each month during which patch and non-patch plots were sampled, distinctly different faunal communities were present in the *P. elegans* patches compared with non-patches and straight lines easily separate the two plot types on the MDS plots. Since the sampling was stratified into *P. elegans* patches and non-patch plots, replicate variability, i.e., spatial variation of the community, was greater in the latter, except perhaps during August 1997. Differences in the faunal communities between patches and non-patches were statistically analysed by the One-way ANOSIM tests. Table 8.3 gives the results of these tests for each of the 4 months. The test statistic R reflects the observed differences *between* sites contrasted with differences among replicates *within* sites. R assumes a value of 1 if all replicates within sites are more similar to each other than any replicates from different sites and a value of 0 for the contrary situation (Clarke, 1993). In each of the ANOSIM tests carried out, only one permuted statistic out of 462 permutations was greater than the sample statistic R, giving significant levels of R equal to 0.2% in each case, and therefore H_0 was rejected at a significance level of $p<0.2\%$ for each test. Although the significance levels were not adjusted for multiple testing and hence one must be cautious with these significance levels, significant differences were supported by the R values which were all above 0.5.

Month	Sample statistic (Global R)	No.statistics ≥ Global R	Significance level of sample statistic
April 1997	0.672	1	0.2%
August 1997	0.694	1	0.2%
December 1997	0.611	1	0.2%
August 1998	0.957	1	0.2%

Table 8.3: Results of One-way ANOSIM tests between patch and non-patch communities for April, August and December 1997 and August 1998. The total number of statistics permuted in each test was 462.

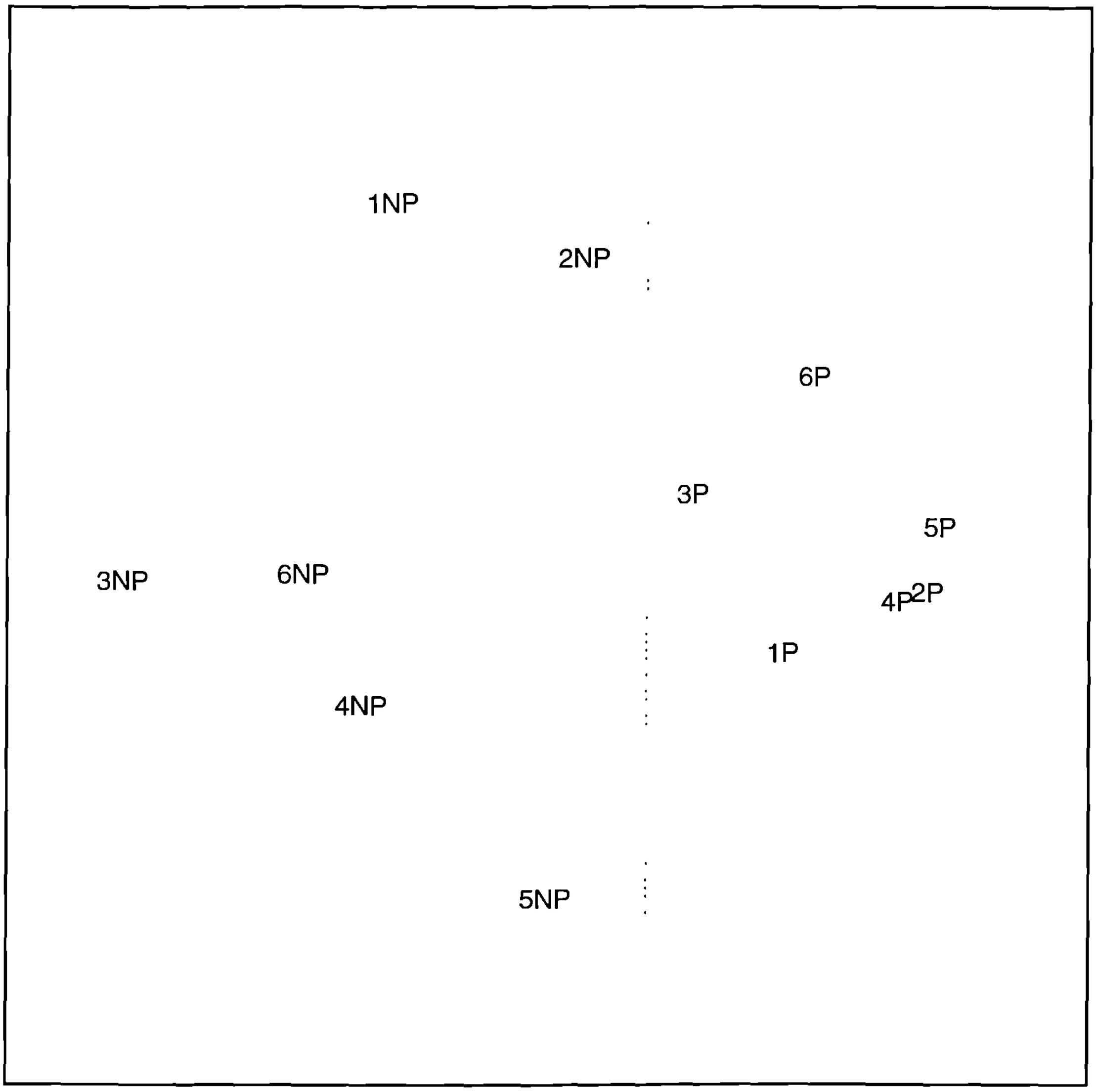


Figure 8.6: Two-dimensional MDS ordination of patch (P1-P6) and non-patch (NP1-NP6) replicates for April 1997. Dashed line separates patch from non-patch replicates. Stress = 0.10.

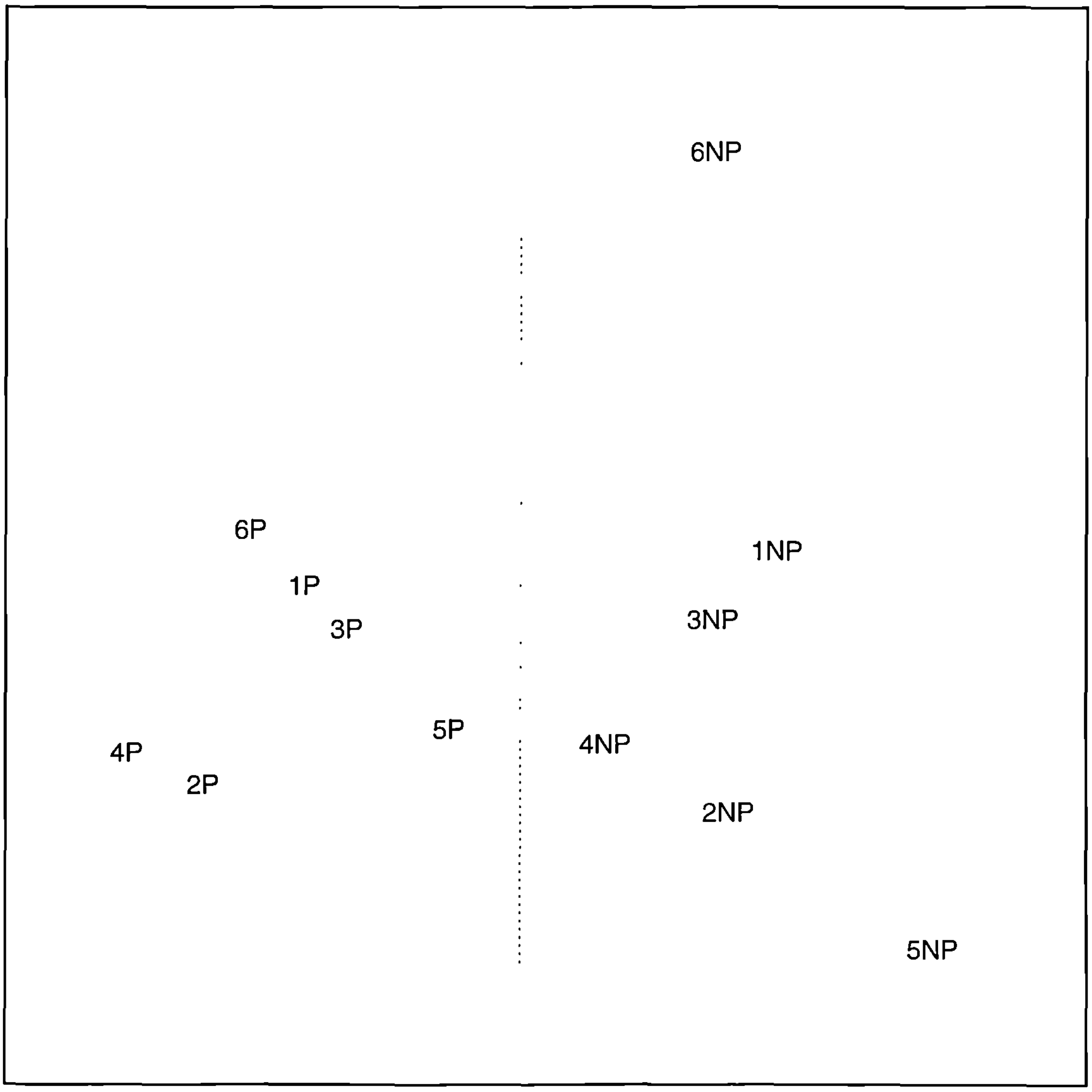


Figure 8.7: Two-dimensional MDS ordination of patch (P1-P6) and non-patch (NP1-NP6) replicates for August 1997. Dashed line separates patch from non-patch replicates. Stress = 0.07.

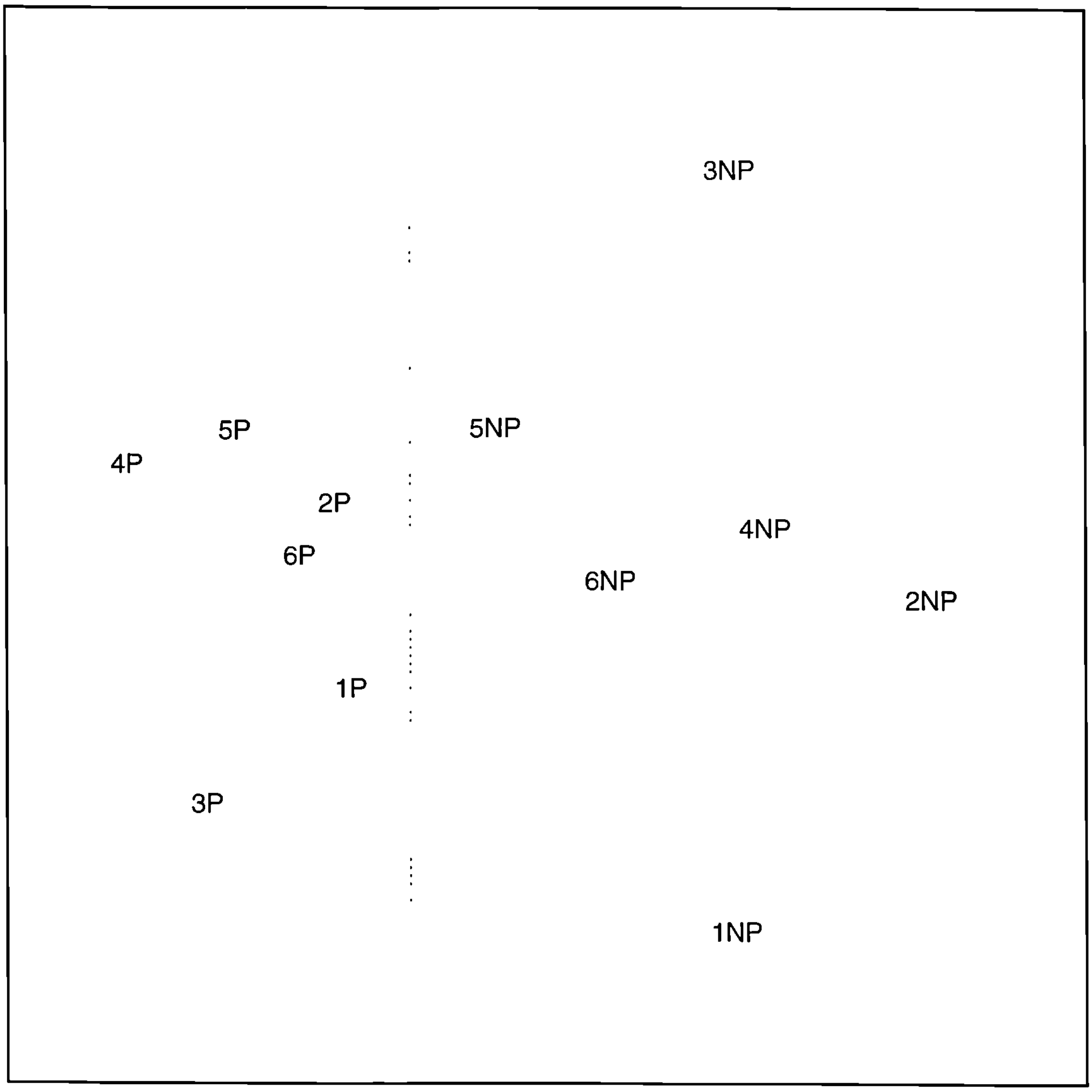


Figure 8.8: Two-dimensional MDS ordination of patch (P1-P6) and non-patch (NP1-NP6) replicates for December 1997. Dashed line separates patch from non-patch replicates. Stress = 0.09.

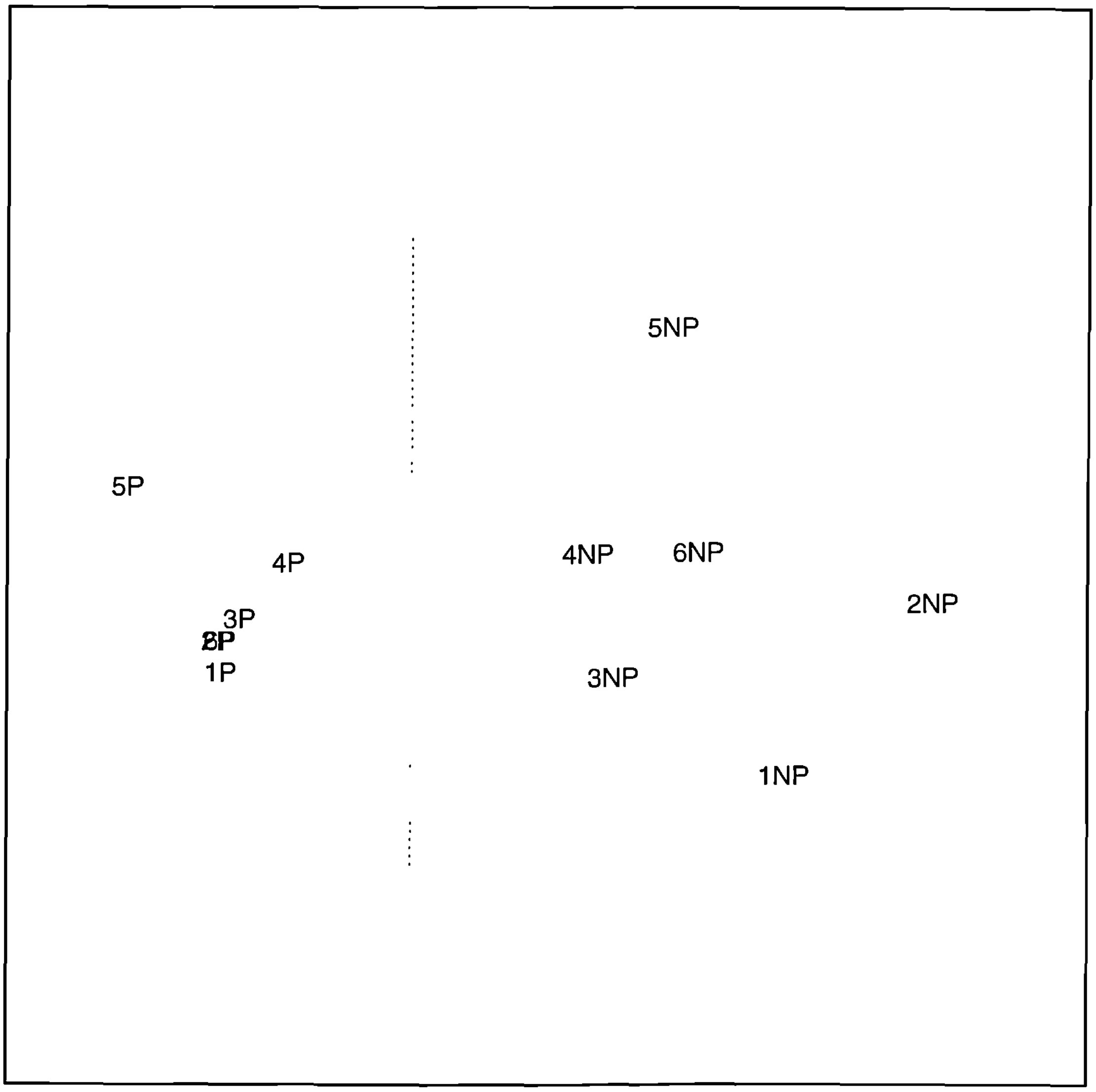


Figure 8.9: Two-dimensional MDS ordination of patch (P1-P6) and non-patch (NP1-NP6) replicates for August 1998. Dashed line separates patch from non-patch replicates. Stress = 0.02.

Figure 8.10 shows the dendrogram produced by hierarchical agglomerative clustering with group-average linking of all 48 samples, i.e., the 6 patch and 6 non-patch replicates for each of April, August and December 1997, and August 1998. The dendrogram shows that most replicates within sites cluster with greater similarities between each other than they do with replicates between sites. Additionally, the dendrogram suggests that the August 1998 communities were very dissimilar to those of the 3 previous sampling months. Figure 8.11 shows the 2-dimensional MDS ordination plot of this dendrogram, with groups formed by patch and non-patch replicates defined. Non-patch replicates are labelled as 'N' rather than 'NP' for this plot due to the large number of points. This plot allows an assessment of the temporal changes in both patch and non-patch community structures.

There is very little overlap between the patch and non-patch replicates in Figure 8.11 which implies that the community differences between these two plot types were large compared to temporal effects. However, temporal effects are noticeable. Although there was very little change in community structure from April to August 1997, replicates for December are positioned predominantly on the left of the MDS plot. The community change which occurred during August 1998 is also very apparent from the MDS and these replicates are located on the right of the plot with a clear separation from the others.

Table 8.4 presents the results from the SIMPER program on PRIMER. This program calculates the relative contribution of each species to the total dissimilarity between groups (patches and non-patches), the 3 species with the highest percentage dissimilarity each month are shown in Table 8.4. The main species responsible for the statistical differences in faunal communities between patch and non-patch areas were *C. edule*, *C. volutator* and *C. capitata*, with *P. cornuta*, *M. balthica* and oligochaetes (mainly tubificids) being influential at certain times of the year.

April 1997		August 1997		December 1997		August 1998	
Taxa	%	Taxa	%	Taxa	%	Taxa	%
C. edule	22.9	*C. edule*	22.2	*C. volutator*	19.1	*C. edule*	39.0
C. volutator	14.5	*C. volutator*	19.5	*C. capitata*	16.8	*M. balthica*	20.4
C. capitata	8.9	*P. cornuta*	10.7	oligochaete	11.8	*C. capitata*	10.5

Table 8.4: The 3 most influential taxa contributing to the dissimilarity between patch and non-patch communities from April 1997 to August 1998. Values (%) refer to the percentage each taxa contributes to the total dissimilarity between patch and non-patch communities.

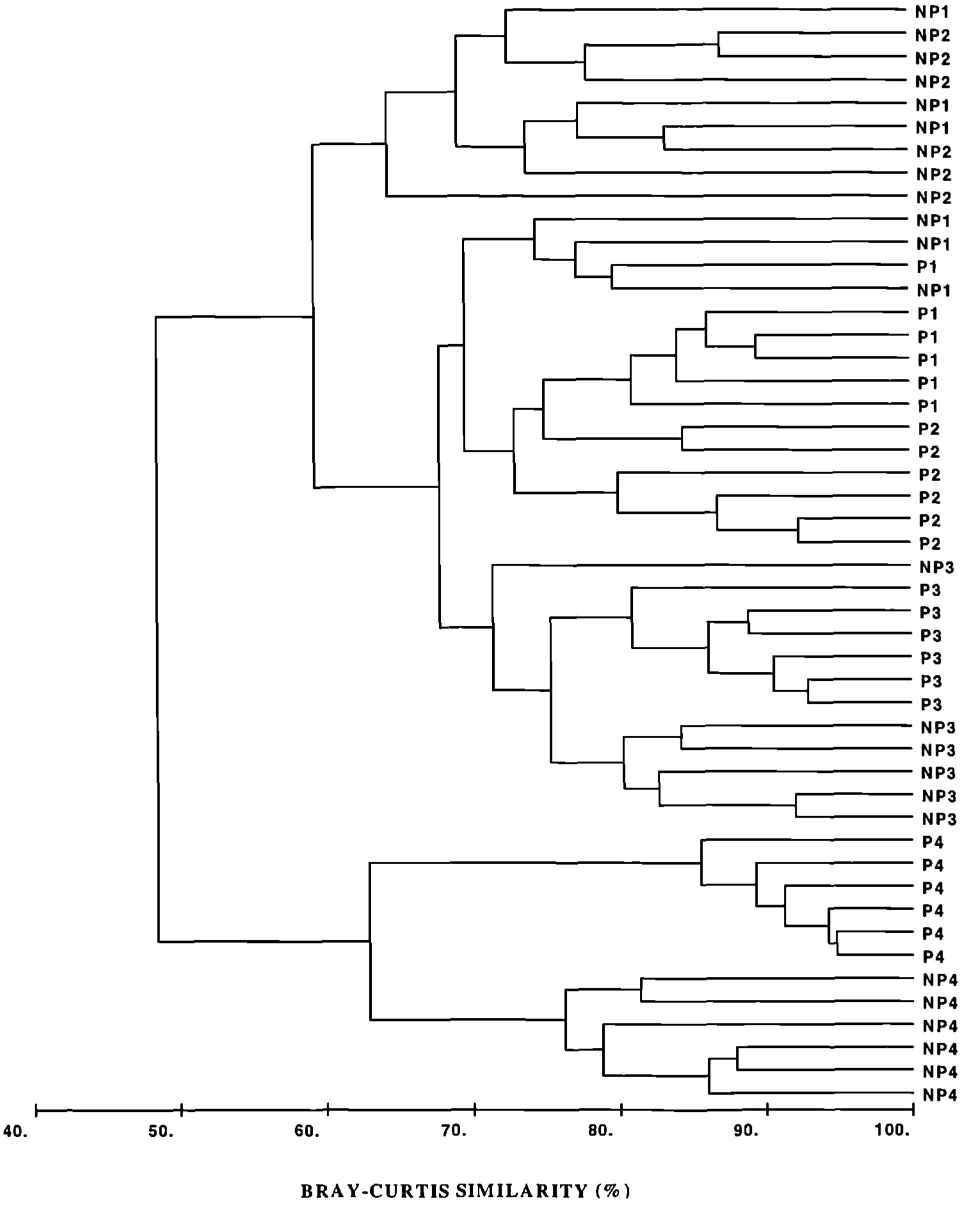


Figure 8.10: Dendrogram of all patch (P) and non-patch (NP) replicates, using group-average clustering from Bray Curtis similarities on √-transformed abundances. The months April, August and December 1997 and August 1998 are labelled as 1,2,3 and 4 respectively.

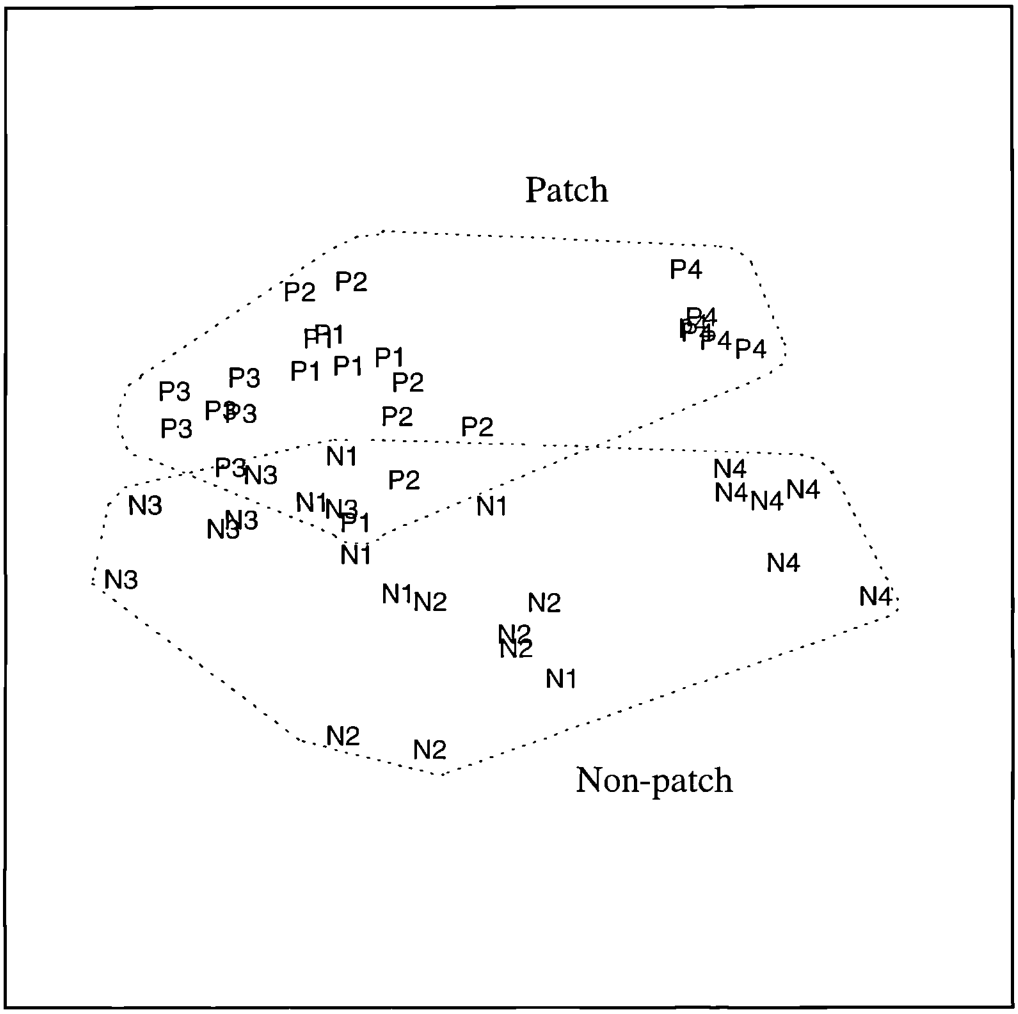
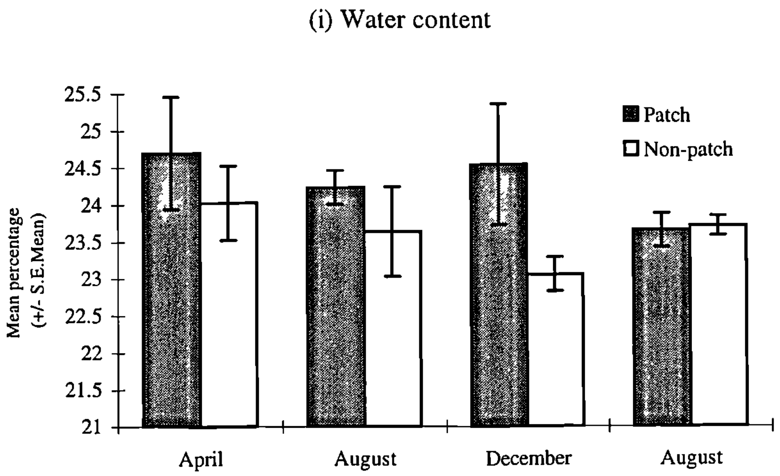
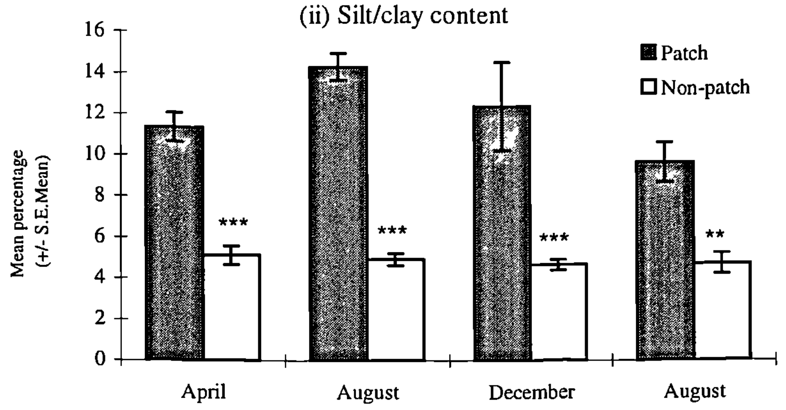


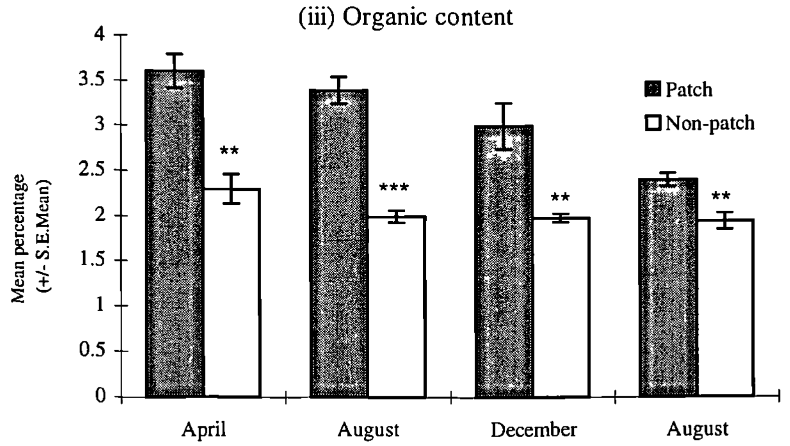
Figure 8.11: Two-dimensional ordination plot of all patch (P) and non-patch (N) replicates. The months April, August and December 1997 and August 1998 are labelled as 1,2,3 and 4 respectively. Dashed lines represent groups formed by patch and non-patch replicates. Stress = 0.14.

Sediment water, organic and silt/clay contents - There were no statistical differences between patches and non-patches for water content (Figure 8.12(i)), while for the % silt/clay and % organic contents, significantly higher values were found in *P. elegans* patches throughout the sampling period from April 1997 to August 1998 (Figures 8.12(ii-iii)). Silt/clay content remained at approximately 5% in non-patch samples while it rose to 14.2% ± 0.64% in August 1997 in patches, then slowly decreased to 9.58% ± 0.95% in August 1998. A decreasing trend was observed for the organic content in patches from 3.6% ± 0.19% at the start of the sampling period to 2.4% ± 0.08% in August 1998, although this was always significantly higher than in non-patch sediments, which was consistently around 2%.

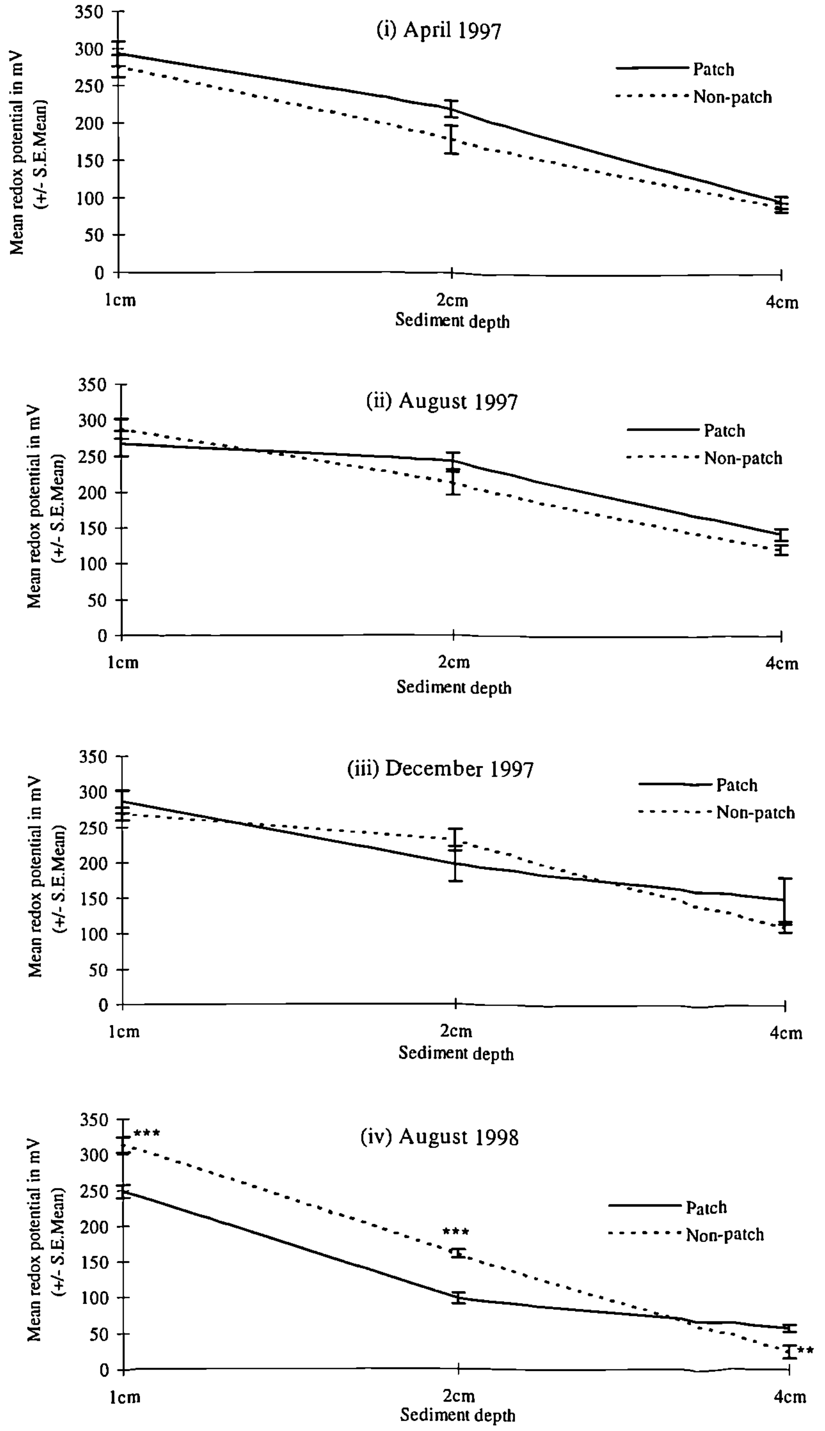
Redox potentials - Whilst sedimentary variables such as the silt/clay and organic contents showed clear differences between patch and non-patch sediments, the results of the redox measurements were more equivocal. Figures 8.13(i-iii) show that the redox profiles of the two plot types were very similar between April and December 1997. However, during August 1998, the sediments at 1cm and 2cm depths in *P. elegans* patches were significantly more reducing than those in non-patch areas, while at the 4cm depth, they were significantly less reducing than non-patch sediments (Figure 8.13(iv)).







Figures 8.12(i-iii) : Mean sediment results (±S.E.Mean, n=6) showing the results of statistical tests between patch and non-patch values. ** Denotes a statistical difference between patch and non-patch means using Two-sample t-test at 0.01 level of significance and *** at 0.001.



Figures 8.13(i-iv) : Mean redox potential results (±S.E.Mean, n=6) for each sampling month showing the results of Two-sample t-tests between patch and non-patch values. ** Denotes a statistical difference between patch and non-patch means at 0.01 level of significance and *** at 0.001.

DISCUSSION

This study monitored the faunal and sediment conditions of *P. elegans* patches and non-patch areas between April 1997 and August 1998. This discussion will firstly address the faunal differences observed between the two habitat types, and secondly, the differences observed in their sediment variables. Finally, since the results obtained at the end of this study revealed the demise of the *P. elegans* patches, this discussion will conclude with the faunal changes occurring within patches and the possible processes causing their decline on Drum Sands.

Faunal differences between *P. elegans* patches and non-patch areas.

The results indicated that many species showed significant differences in abundance between these two areas. *C. capitata* (April 1997), *C. edule* (April and August 1997, August 1998), *M. balthica* (December 1997 and August 1998) and *C. volutator* (April to December 1997) were all significantly more abundant in *P. elegans* patches compared with non-patch areas while no species were significantly more abundant in non-patch areas. The size distributions of certain species, i.e., *P. elegans* (April to December 1997) *and C. capitata* (December 1997), were also significantly different between the two habitat types. Multivariate analysis together with non-parametric ANOSIM tests revealed that the community compositions were always significantly different between the two habitat types and this was consistently due to several species such as *C. edule*, *C. capitata* and *C. volutator.*

The significant differences between the fauna of *P. elegans* patches compared with those of non-patch areas in this study support the results of previous studies. Fager (1964) noted that several species, the isopod *Munna ubiquita*, the pycnogonid *Oropallene heterodentata*, the hermit crab *Pagurus* sp. and the anemone *Zaolitus actius* were only found in the stabilised sediments within the dense *Owenia fusiformis* tube-beds in his study. Similarly, Sanders *et al.* (1962) found that the small amphipod *Listriella clymenella* was only found within the tube arrays of the maldanid *Clymenella torquata* in the intertidal flats of Barnstable Harbor, Massachusetts. Woodin (1981) experimentally demonstrated that increases in the density of *Diopatra cuprea* tubes resulted in increases in macroinvertebrate species richness and abundances. Within the spionids, Noji (1994) noted that areas with moderate abundances of *P. ciliata* had more diverse meiofaunal and macrofaunal communities compared with areas of low abundances, while Reise (1983b) found that the presence of dense assemblages of *P. elegans* promoted the abundance of small benthic organisms by approximately 40%. Morgan (1997), using a correlation approach, indicated that the majority of the most common taxa in the Baie de Somme, France, e.g., *Eteone longa*, *Hediste diversicolor* and *Cerastoderma edule*, were significantly positively correlated with *P. elegans* abundances.

Many studies endeavouring to elucidate the mechanism by which high numbers of tube-builders affect infaunal community structure have focused on the way in which recolonisation is effected (e.g., Gallagher *et al.*, 1983; Trueblood, 1991). Resident adults may influence colonists in many ways determined by their feeding mode and modifications to the sediments and hydrodynamics (Thrush *et al.*, 1992). However, experimental studies on such mechanisms have proved equivocal. Since recruitment is usually assayed some time after settlement and metamorphosis (Bachelet, 1990) the actual patterns of larval settlement are often obscured (Hadfield, 1986). Consequently, studies have failed to assess the mechanisms by which tube-builders affect recolonisation since it is inherently difficult to distinguish between differential settlement and differential mortality of larvae (Woodin, 1986).

Larvae of some marine benthic invertebrate species have been experimentally shown to actively select settlement sites using certain cues (Scheltema, 1974; Woodin, 1986; Butman *et al.*, 1988a; Pawlik and Butman, 1993; Hsieh, 1994). However, it is likely that in the field, water flow is greater than the swimming speeds of larvae and instead, larvae are transported as passive particles and deposited via passive entrainment (Hannan, 1984; Butman, 1987; Butman *et al.*, 1988b). Eckman (1983) predicted that velocity of near-bed flow through plastic straws (seagrass mimics) would be reduced to such an extent that suspended particles, such as larvae and meiofauna, would be passively deposited. His results supported this prediction although his experimental design was flawed by replication of only one of his treatments, his defaunated control. Later experiments have incorporated replication of the defaunated controls but the results have been inconclusive due to a number of factors including a plot size too small to allow the formation of a fully developed boundary layer (Kern and Taghon,

1986) and low level of replication resulting in too low a statistical power (Ragnarrson, 1996).

The present study was observational and not intended to determine the mechanisms responsible for any differences in abundances between patch and non-patch communities. However, the increased silt/clay fraction and higher meiofaunal abundances in patches may have been due to increased passive deposition due to the reduction in velocity of near-bed flow. In the same way, passive larval entrainment may be responsible for some of the observed differences in this study. This was observed even though tube-building spionids have been shown to ingest settling bivalve larvae (Breese and Phibbs, 1972; Daro and Polk, 1973). Once an individual of a species had colonised a *P. elegans* patch, the physico-chemical effects of the tubes possibly concurred to provide an increased food supply in the form of the flourishing microbial and meiofaunal communities observed in this study. Furthermore, the resistance to shearing forces provided by the beds may have allowed a dense community by virtue of individuals not being 'swept' away (Morgan, 1997). Increased abundances of meiofauna (43%) were observed by Reise (1983b) in *P. elegans* patches compared to areas lacking the spionid, whilst a similar increase has been documented for beds of another spionid, *Polydora ciliata*, by Noji (1994), who suggested that the meiofauna were utilising the worms faecal pellets as a food source.

The presence of *C. volutator* in patches, while almost completely absent outside patches, probably resulted from active habitat selection of adults to areas of increased silt/clay fraction and more stabilised sediments. This amphipod attains particularly high densities in muddy sediments with high numbers of diatoms (Lawrie, 1996). Its almost exclusive existence within patches suggests some sort of functional group interaction (*sensu* Woodin, 1976) for this tube-building, deposit-feeding amphipod. Similarly, Reise (1978) noticed *C. volutator* beds harbouring large numbers of *P. elegans* in the Wadden Sea.

Sediment differences between *P. elegans* patches and non-patch areas.

Sediment analyses indicated that although sediment water content was the same for patch and non-patch areas, the former consistently contained significantly increased levels of silt/clay and organics. Significant differences in sediment redox potential were only observed during August 1998 when the sediment of *P. elegans* patches were significantly more reducing at 1-2cm depth and less reducing at 4cm depth.

The lack of a significant difference between the water content of the patch and non-patch sediments during this study was contrary to the findings of other studies. The *P. elegans* tube-beds on Drum Sands and in other areas, e.g., the Baie de Somme, France (Morgan, 1997) and the Clyde estuary, Scotland (Tufail *et al.*, 1989), were raised above the mean sediment surface level and therefore were presumably better drained during periods of tidal emmersion. Furthermore, dense arrays of tube-builders have been shown to enhance sediment permeability (Sanders *et al.*, 1962; Morgan, 1997). It is possible that the increase in the silt/clay fraction of the sediments in *P. elegans* patches on Drum Sands retained water to such an extent that it counteracted the effect of the raised sediments to produce the non-significant differences in this study.

The increased levels of silt/clay and organic content within the *P. elegans* patches were consistent with the findings of other studies (e.g., Daro and Polk, 1973; Dupont, 1975; Eckman *et al.*, 1981; Frithsen and Doering, 1986; Noji, 1994; Morgan, 1997). The stabilised conditions within patches probably resulted in increased deposition of silt/clay particles and lower erosion rates, while the increased organic contents were possibly due to both the feeding of *P. elegans* and increased microbial and meiofaunal communities.

There were no significant differences between the patch and non-patch redox potential values recorded at 1, 2, and 4cm depths from April to December 1997. The effect of a tube-building species on the below-sediment surface redox potential depends on a number of factors including worm feeding mechanism and density. While some tube-builders such as *Clymenella torquata* feed from sediments below their tubes, drawing water down from the surface (Sanders *et al.*, 1962) and therefore oxygenating the sediments, *P. elegans* has been shown to reduce the sediments below the surface (Morgan, 1997). This is in contrast to the observations of Noji (1994) on *Polydora ciliata* beds and Featherstone and Risk (1977) on *Spiophanes* cf. *wigleyi.* Featherstone and Risk (1977) found a marked lowering of the anoxic zone in sediments containing large numbers of *S.* cf. *wigleyi*. The possible explanation for the lack of any measurable reduction in redox in patches during the present study is not certain, it may have been that the *P. elegans* densities were not high enough to produce any discernible effect on such a spatially mutable variable, or that deposit-feeding spionids have different effects on sediment redox potentials (*cf.* Featherstone and Risk, 1977; Noji, 1994; Morgan, 1997) in different environments. In August 1998, however, the sediments of *P. elegans* patches were significantly more reducing compared to non-patch sediments at 1 and 2cm depths. This result was very unexpected since the sediments of *P. elegans* patches at this time contained very high numbers of *C. edule* and *M. balthica*. These bivalves, especially the former (Reise, 1985; Flach, 1996), are bioturbators of surface sediments and their bioturbation activity oxygenates the top few centimetres of the sediment. Therefore, one would have expected that the patch sediments at this time would have been less reducing than non-patch sediments. Consequently, the reasons why patch sediments at 1cm and 2cm depths were more reducing during August 1998 remain unclear based on the information obtained from this study.

Demise of *P. elegans* patches on Drum Sands.

In the few weeks preceding the August 1998 sampling, it was noticeable that the visual appearance of the *P. elegans* patches at Drum Sands became less marked and it became more difficult to distinguish them from non-patch areas. The golden brown coloration due to diatoms was much less obvious and some of the patches had ripple-marks across them. The samples taken during August 1998 showed that although the numbers of *P. elegans* adults were still significantly higher in patch compared to non-patch areas, there was a large decline in their numbers from the previous December when an upward trend in *P. elegans* densities seemed to have been occurring throughout 1997. By August 1998, the numbers of *C. edule* had significantly increased. Although silt/clay fraction and the organic content of the sediments were still significantly higher than those of non-patch sediments, their levels appeared to start falling from December levels.

Populations of opportunistic species are unstable (Whitlatch and Zajac, 1985) and dense beds are generally replaced by subsequent colonisers (Grassle and Sanders, 1973; Noji and Noji, 1991). Competition for food and space, tidal scouring, bivalve bioturbation and predation by infauna, birds and fish are some factors that have been suggested as responsible for the demise of opportunistic populations (Daro and Polk, 1973; Whitlatch and Zajac, 1985; Noji and Noji, 1991; Flach, 1996). Many field observations (Smidt, 1944; Desprez *et al.*, 1992; Noyer, 1993, cited by Morgan, 1997) and field experiments (Reise, 1985; Flach, 1996) have suggested a negative interaction between *P. elegans* and *C. edule*. For example, in the Baie de Somme, *C. edule* densities decreased from several thousand per m^2 prior to 1982 to a few hundred per m^2 in subsequent years due to eutrophication (Desprez *et al.*, 1992). During the period of low *C. edule* densities, *P. elegans* greatly increased in numbers. The return of the *C. edule* in 1987 led to the almost complete disappearance of the spionid in less than one year. Although most of the literature reports an interaction between *P. elegans* and *C. edule*, the functionally similar *M. balthica* is likely to evoke a cognate interaction.

Cerastoderma edule populations are highly variable, mainly due to their sensitivity to low winter temperatures and variable recruitment (Smidt, 1944; Reise, 1985). It is not clear whether it is winter temperatures or adult densities which govern recruitment success (Flach, 1996). However, what is evident is that the spat-fall on Drum Sands during the spring of 1998 was particularly successful. It is possible that bivalve spat settlement was higher in patches than non-patches since, acting like passive particles, they were more likely to be deposited in such areas of slower net water flow. After settlement of the spat, it is possible that in *P. elegans* patches, post-settlement mortality and/or emigration of juvenile *C. edule* was low. Once established, *C. edule* individuals may have benefited from the indirect effects of the tubes slowing the water flow across the beds, promoting the *C. edule* feeding, and increased protection from erosion.

Competition, predation and sediment disturbance by *C. edule* and *M. balthica* have all been suggested as being responsible for their negative effect on *P. elegans*. *P. elegans* feeds on small surface deposits as well as on suspended particles (Fauchald and Jumars, 1979) and thus there is a niche overlap between the spionid and the two bivalves. Reise (1983c) observed *P. elegans* withdrawing into their tubes when touched by *M. balthica* siphons. *C. edule* has been shown to inhale settling *P. elegans* larvae (Noyer, 1993; cited by Morgan, 1997). Reise (1983c; 1985), Jensen (1985) and Flach (1996) have suggested that *C. edule* could affect other infaunal species by disturbing the upper sediment layer due to its crawling (ploughing) and 'shaking' (Flach, 1996) behaviour. In Flach's study, significant reductions in densities of most infaunal species, including *P. elegans*, were found even at the lowest *C. edule* density, i.e., 4-8% *C. edule* occupancy (area occupied by *C. edule*). The *C. edule* occupancy in *P. elegans* patches in August 1998 was calculated to be 9.5%, with an appreciably greater 'disturbance area' (i.e., total area disturbed) (Flach, 1996). Therefore, it is likely that *C. edule* was having a large negative effect on *P. elegans* within patches in August 1998 due to sediment disturbance.

Settling spionid larvae seem to be particularly prone to the disturbance and predation effects of *C. edule* and in most studies it is the juveniles which have suffered the greatest decrease in numbers. Size measurements taken of *P. elegans* from the August 1998 samples in this study showed that although the size-frequency distributions were not quite significantly different, the proportion of juveniles was greatly reduced in *P. elegans* patches compared with non-patches which had significantly lower bivalve populations. Therefore, the decrease in numbers of *P. elegans* in patches at this time was mainly due to the juveniles, suggesting that there was high larval mortality in patches during the peak settlement period earlier in the year. However, it is not possible to determine whether this was predominantly due to sediment disturbance or inhalation by the bivalves.

It could be envisaged that the numerical dominance of *C. edule*, and to a lesser extent *M. balthica*, were likely to cause further reductions in *P. elegans* densities from those of August 1998 because of their negative effects on spionids. The *C. edule* individuals sampled in August 1998 had reached a mean size of 2.5mm length and hence had already reached a size refuge from predation by infaunal predators such as *Nereis* spp. and epibenthic species such as *Crangon crangon*, 0-group *Carcinus maenas* and 0- and I-group *Pleuronectes* spp. (Reise, 1985). *C. maenas* and *C. crangon* have been shown to be important predators on juvenile *C. edule*, and *C. crangon*, found in moderate abundances during sampling at Drum Sands, has been shown to consume up to 68% of a 0-group *C. edule* population (Pihl and Rosenberg, 1984). Reise (1985) suggested that once *C. edule* have managed to escape their predators in their first summer, they are capable of establishing dense populations lasting about 5 years, unless they are killed by the next severe winter.

Chapter 3 has shown that the *P. elegans* population on Drum Sands did not produce benthic larvae nor reproduce asexually, but instead had a dispersal mode of reproduction with planktotrophic larvae. Consequently, this population was particularly susceptible to adult-juvenile interactions and therefore likely to be replaced by suspension-feeding bivalves. For example, Commito (1987) and Commito and Boncavage (1989) suggested that only those tube-building or deposit-feeding species which produce cocoons or benthic larvae that are too large for siphonal inhalation are relatively immune from adult-larval interactions with suspension-feeding bivalves.

It is not possible to suggest why 1998 saw the start of the interaction between the two species at Drum Sands and the onset of *P. elegans* patch decline. It was possibly due to a high *C. edule* spat-fall, low adult bivalve densities (facilitating successful juvenile *C. edule* settlement) or the relative timing of bivalve and spionid larval settlement. Since there were low adult *C. edule* densities at this time it is possible that adult densities may have been regulating *C. edule* recruitment. Successful *C. edule* spat settlement has been recorded during summers following severe winters which decimated adult populations (Smidt, 1944; Reise, 1985) and Kristensen (1957) concluded that high adult *C. edule* densities may prevent a successful settlement of larvae. *C. edule* has been shown to ingest its own larvae, in addition to other bivalve species (Jensen, 1985; Andre and Rosenberg, 1991). The almost complete absence of adult *C. edule* in *P. elegans* patches could have therefore been responsible for the increased number of juvenile *C. edule* observed in patches compared to non-patches in this study.

CHAPTER 9

GENERAL DISCUSSION

This study had 3 main aims, these were:

- To determine the spatial distribution of *P. elegans* on Drum Sands;
- To investigate the processes affecting *P. elegans* densities and the possible role of these processes in the formation and maintenance of small-scale patches;
- To assess the ecological importance of the spatial distribution of *P. elegans* on Drum Sands.

These 3 main aims have been successfully fulfilled by the surveys and controlled experiments performed on Drum Sands and are now discussed separately.

The spatial distribution of *P. elegans* on Drum Sands, Firth of Forth, Scotland.

Irrespective of the field of study, all marine ecologists are faced with the problem of establishing and quantifying patterns in nature since they are the building blocks of the models from which hypotheses are generated (Andrew and Mapstone, 1987). In the first part of the present study, the small-scale (metres) and meso-scale (tens of metres) spatial patterns of *P. elegans* were determined, followed by an investigation of the micro-scale (centimetres) spatial patterns. The small- and meso-scale patterns were considered in Chapter 2 and the micro-scale patterns in Chapter 7.

In Chapter 2 the presence of areas of smooth, raised sediments observed on Drum Sands were confirmed by spatial surveys to be areas of significantly higher densities of *P. elegans*. These 'patches' were found to be approximately 1-1.5m^2 and were randomly distributed. The detection of these patches was crucial to all later studies described within this thesis since these studies depended upon the presence of significantly increased numbers of *P. elegans* within patches compared with non-patch sediments.

In Chapter 7 the micro-scale spatial distribution of *P. elegans* within small-scale high density patches was investigated. Since the extent in this survey was relatively small, a contiguous sampling design was used. This study indicated that *P. elegans* was non-randomly distributed at this scale, forming patches mainly of less than 3cm^2, although patches of 3-12cm^2 were detected. The detection of micro-scale clumping of *P. elegans* within small-scale patches supported the proposition that most, if not all, marine invertebrate species are aggregated at many spatial scales (Andrew and Mapstone, 1987; Morrisey *et al.*, 1992; Hewitt *et al.*, 1996).

The multi-scale patchiness of marine benthic invertebrates, as has been shown to occur for *P. elegans* in this study, has both practical and statistical implications for most studies carried out within the soft-bottom environment. Most researchers have previously ignored the presence of spatial patterns in marine benthic invertebrates when carrying out surveys or experiments. Legendre and Trousellier (1988) and Legendre (1993) pointed out that where a species has a distribution which is spatially autocorrelated, the abundance of that species at any one location can be at least partly predicted by the abundances at neighbouring points. Therefore, these abundance values, or samples, are not statistically independent from one another. This affects the subsequent power of statistical comparisons since each replicate does not bring one whole degree of freedom (Legendre, 1993). Positive autocorrelation induces the same bias with all standard statistical tests: computed tests are too often declared significant under the null hypothesis. This should affect sampling design and numerical analyses used in monitoring studies. While it is formally possible to estimate the statistical bias of autocorrelation (Cliff and Ord, 1973; Legendre, 1993), a more sensible approach would be to have an idea of the scale of patchiness of the most abundant species or the species of particular interest before carrying out an experiment or survey. Inter-replicate distances can then be selected accordingly. For *P. elegans* on Drum Sands for example, inter-replicate distances should ideally be at least 1-1.5m apart for each replicate to be totally independent from each other. For subsurface species, this information can only be gained from spatial surveys, such as those described in Chapter 2.

There are many sample designs which can be employed to assess the spatial patterns of marine benthic populations and communities, each of them being more or less suitable for different habitats and different scales (Andrew and Mapstone, 1987). Contiguous sample designs give less equivocal assessments of spatial patterns since the abundances of all individuals within the extent of the survey are determined. When the extent of the survey is too large for contiguous sample designs, assessment of spatial patterns becomes more inexact.

McArdle and Blackwell (1989) proposed that a systematic (grid) sample design was the most suitable for the detection of spatial patterns. This design will usually provide the smallest estimate of the mean (Milne, 1959) and patterns can be detected and displayed easily. The present results suggest that when the lag is large relative to the average patch size, however, this design may lead to equivocal results. Grid sample designs were used in this study to determine the spatial patterns of *P. elegans* on Drum Sands. Using mapping and spatial autocorrelation analysis, the size and spatial distribution of *P. elegans* patches could only be determined using a survey in which the lag, or distance between samples, was less than the mean size of the patches and less than the average distance between patches. Consequently, the 1m survey provided important information about the size and spatial arrangement of small-scale *P. elegans* patches. The 8m and 40m surveys, however, revealed little information about the spatial distribution of *P. elegans* because the results obtained from these two surveys depended upon the actual spatial arrangement of the small-scale *P. elegans* patches. For example, if two neighbouring plots were located on separate *P. elegans* patches in either the 8m or the 40m surveys, mapping and spatial autocorrelation analysis may have erroneously indicated the presence of larger scale patches. This was revealed by the present study because *P. elegans* is a tube-building polychaete and, therefore, high-density areas were very visible on the sandflat. For subsurface invertebrate species, or species in which high-density areas are less readily observed, a grid-sample design can potentially lead to misleading results when patches smaller in size than the lag are present. For such species, a hierarchical sampling design may be more suitable since patchiness at a larger range of scales can be detected simultaneously (Morrisey *et al.*, 1992). This sample design lacks the resolving power of grid-sample designs and, therefore, does not give information about the exact size and positions of patches. Consequently, hierarchical sampling designs are ideal pilot surveys for field experiments and for more detailed investigations into spatial patterns (McArdle and Blackwell, 1989).

The detection of small-scale patches of increased numbers of *P. elegans* was invaluable for the present study since it provided unequivocal information as to the scale the processes generating increased numbers of *P. elegans* operated. Furthermore, their detection supported the observation that Drum Sands was a particularly good sandflat within which the processes affecting the spatial distribution of a tube-building polychaete could be investigated. Firstly, these patches occurred in high numbers. Secondly, these patches were all approximately the same size which suggested that the same process(es) were responsible for their generation. Thirdly, these patches appeared as areas of smooth, raised sediment within a moderately high-energy, wave-rippled sandflat, which implied that they had different hydrodynamic properties from surrounding sediments and that they represented distinct ecological habitats.

The processes affecting *P. elegans* densities and the possible role of these processes in the formation and maintenance of small-scale patches.

Chapters 3, 4, 5 and 6 investigated the roles of population dynamics and reproductive strategy (Chapter 3), macroalgal mat establishment (Chapters 4 and 5) and sediment disturbance (Chapter 6) in the generation of the small-scale patches of *P. elegans* on Drum Sands. Although sediment heterogeneity, sediment disturbance and life history characteristics have been proposed as being important in the formation of patches of increased spionid density (Noji and Noji, 1991; Zettler and Bick, 1996; Morgan, 1997), explicit investigations as to the processes creating them have not previously been carried out. Moreover, these investigations were conducted with a good understanding of the population dynamics and reproductive biology of the species under study.

Chapter 3 indicated that the *P. elegans* population on Drum Sands exhibited a planktonic mode of development with two main recruitment phases during the year, April/May and November/December. This life history provides a massive larval availability for patch foundation. No evidence for the production of benthic larvae and/or asexual proliferation was found. It is conceivable that the latter two methods of propagation could lead to patch formation since they are likely to produce localised areas of increased density. A planktonic mode of development, however, made *P. elegans* more suited to respond to large-scale disturbances (Levin, 1984a). The reliance on planktonic larval development for population maintenance suggested that several conditions must have occurred on Drum Sands for the generation of the small-scale patches of increased density present within this area. Firstly, patches must have initially been areas of increased larval recruitment. Macroalgal mat development and/or sediment disturbance are two factors which could have led to these high juvenile numbers. These were investigated in Chapter 4, 5 and 6. Since recruitment of this *P. elegans* population was very seasonal, the timing of these perturbations must coincide with a recruitment phase. Secondly, there must be increased adult and/or larval recruitment to these patches for patch maintenance. Although other factors may have initially been involved, such as localised areas of increased larval deposition due to eddy currents, these were not addressed in the present study.

The possibility that the establishment of macroalgal mats may have been responsible for the generation of increased numbers of *P. elegans* was firstly investigated in Chapter 4 by a controlled weed-implantation experiment. This study showed that *E. prolifera*, at a relatively low biomass compared to other experimental studies, had a negative effect on *P. elegans* numbers, both on adults and larval recruitment. The communities underneath *E. prolifera* mats became numerically dominated by *C. capitata*. These results suggested that *E. prolifera* mats may not have generated *P. elegans* patches. However, the possibility that *P. elegans* increased in numbers as a later successional species in areas dominated by *C. capitata* after *E. prolifera* decay could not be investigated due to mussel settlement on experimental plots.

Although controlled, experimental investigations into the ecological effects of macroalgal mats are potentially less equivocal than comparative surveys, their results tend to be less specific to a particular environment. This is because macroalgal manipulation experiments are likely to show different effects from surveys focusing upon mats which develop naturally unless all aspects of the implanted weed closely represent those found establishing in that environment. For this reason, a weed survey was carried out during 1997 to investigate the effects of *V. subsimplex* mats which established naturally on Drum Sands. The results from this survey indicated that *V. subsimplex*, at the biomass which naturally established, had an enriching effect on the faunal communities present. The numbers of *P. elegans* particularly increased mainly due to increased larval recruitment. The results of this survey suggested that natural weed establishment on Drum Sands was very important in structuring the benthic communities. *V. subsimplex*, although significantly increasing the numbers of *P. elegans*, did not lead to the formation of new *P. elegans* patches during 1997 since the accumulated sediments and increased numbers of *P. elegans* they created were washed away in the winter storms. However, this could potentially be attributed to the late development of *V. subsimplex* during the year of the study. The link between weed mats and patch formation was further supported by their matching spatial scales, *V. subsimplex* mats which developed during 1997 were approximately the same spatial scale as *P. elegans* patches. Although *V. subsimplex* led to increased *P. elegans* numbers during 1997, it is not known whether this species established at the same biomass during previous years. Therefore, the link between weed mat establishment and *P. elegans* patch formation cannot be proven.

Noji and Noji (1991) suggested that populations of spionid polychaetes have been commonly found to increase rapidly following disturbances to form high densities and display typical opportunistic life history patterns. They therefore implied that sediment disturbance was a precursor in the formation of patches. This was investigated in Chapter 6. Two aspects of the effects of sediment disturbance were investigated. Firstly, the response of *P. elegans* to small-scale sediment disturbance was investigated, and secondly, *P. elegans* larval and adult recruitment following a disturbance in established patches was compared with non-patches. While the first specifically relates to the possibility of a link between *P. elegans* patch formation and sediment disturbance, the latter pertains to the maintenance of established high-density patches.

The response of *P. elegans* to the simulated sediment disturbances was related to its reproductive behaviour. During periods of high larval availability, *P. elegans* was capable of numerically dominating the early stages of succession following sediment disturbance. Although the later stages of succession were not investigated in the present study, Noji and Noji (1991) suggested that spionids such as *P. elegans* are capable of persisting at very high densities for some time after numerically dominating the early stages of succession. Sediment disturbance is most likely on Drum Sands during the winter months and therefore it must coincide with the second recruitment period if patches are to be formed. Sediment disturbance during periods of low *P. elegans* larval availability results in an early community dominated by *C. capitata*, the later successional stages of which were not investigated. Although this study showed that *P. elegans* was capable of dominating after small-scale disturbances it did not show this on the same scale as *P. elegans* patches, i.e., 1-1.5m^2. Experiments in which the area of sediment disturbance was equivalent to the size of *P. elegans* patches, approximately 150-200 times larger than those in the present experiments, were not performed.

The absence of asexual proliferation and benthic larval production suggested that the maintenance of increased *P. elegans* densities within patches would have involved increased larval/adult recruitment to patches and/or decreased larval/adult emigration. Increased larval recruitment to defaunated sediments within patches compared to non-patches were shown by the present experiments during periods of high *P. elegans* larval availability. Without further studies it is not possible to suggest the mechanism of this, but in view of the hydrodynamics of established patches, it is likely that increased passive larval entrainment was an important factor. Similarly, adult colonisation of defaunated sediments within patches was shown to be higher than in non-patch areas. These results suggest that *P. elegans* patch maintenance was possible without asexual proliferation and benthic larval production.

This thesis concentrated on the processes responsible for the generation of the small-scale *P. elegans* patches and no explicit studies were carried out to investigate the processes responsible for the presence of micro-scale patches of *P. elegans*. This could form the basis of further research. A correlative approach, however, was used to investigate whether intraspecific interactions (adult-larval interactions), interspecific interactions or sediment heterogeneity were likely to affect *P. elegans* distribution at the micro-scale. Adult-larval interactions and sediment heterogeneity were implicated as being important processes in determining *P. elegans* distribution at this scale. However, inferring processes based on spatial co-occurrence is very ambiguous and controlled laboratory and/or field investigations would be required to support these predictions.

Trying to match observed patterns to particular processes is inherently difficult (Hewitt *et al.*, 1996). Heterogeneity results from a complex interaction of biotic and abiotic processes (Livingston, 1987; Caswell and Cohen, 1991) and, intuitively, it is likely that a given pattern may result from a combination of processes. The practical and conceptual difficulties associated with such an investigation were emphasised in this study. The small-scale patterns of *P. elegans* on Drum Sands were relatively distinct and were present at the tractable scale of experimental investigations. Factors previously proposed as being responsible for spionid patch formation were shown to lead to localised increases in *P. elegans* numbers, and, therefore, the second aim of this thesis was successfully achieved. However, the role of these processes in patch generation was not unequivocally shown. Consequently, further research should be carried out, including a more detailed investigation into the macroalgal mat establishment on Drum Sands (weed type, biomass and timing), a study of the localised hydrodynamics on Drum Sands and further studies on larval settlement of *P. elegans* (their responses to the presence of adult conspecifics, boundary flow and sediment heterogeneity).

The ecological importance of small-scale *P. elegans* patches on Drum Sands.

The final part of this study showed that *P. elegans* patches were discrete ecological habitats. It must be remembered that associating the changes in numbers of a species to changes in the structure of associated communities in the field is inherently dubious due to the inability to control environmental variables. Consequently, the use of controlled, manipulated experiments are advocated.

Within the *P. elegans* patches on Drum Sands, many invertebrate species, e.g., *C. capitata*, *C. edule*, *M. balthica* and *C. volutator*, exhibited significantly increased abundances compared to non-patch areas, and the population size structure of some species, e.g., *P. elegans* and *C. capitata*, were significantly different from those in non-patch areas. The structure of *P. elegans* patch communities were significantly different from those of non-patch areas. Additionally, the physical, chemical and physico-chemical properties of the sediments within these patches were significantly different from those of non-patch areas. These findings are very important as marked ecological differences within high densities of tube-builders have previously only been documented either for species with much larger tubes, e.g., *L. conchilega* (Carey, 1982; Ragnarrson, 1996) and *O. fusiformis* (Fager, 1964), or for *P. elegans* in much higher densities than those found in patches on Drum Sands (Dupont, 1975; Morgan, 1997). The present results suggest that tube-building polychaetes can significantly alter their environment at much lower densities than previously thought. Since Drum Sands is a moderately high-energy sandflat, it is possible that tube-building species have more marked effects in high-energy sandflats compared to those in more sheltered sandflats or mudflats.

The present study did not explicitly examine the actual processes responsible for the differences in the fauna and sediments between *P. elegans* patches and non-patch areas, this should form the basis for further research. The large numbers of tubes emerging above the sediment surface within patches have a hydrodynamic effect, reducing net flow and leading to sediment stabilisation (Nowell and Church, 1979; Eckman *et al.*, 1981). Evidence for this was given by the smooth appearance of the patch surfaces and the presence of a golden-brown colour, assumed to be due to high densities of diatoms. A tube-bed offers a refuge from erosion: increased sediment cohesiveness and stability allow residents to resist resuspension by strong localised hydrodynamic activity. Individuals of small species may otherwise have been unable to tolerate life in such physically disturbed areas.

The findings that *P. elegans* patches comprised of significantly different macrobenthic communities from surrounding sediments emphasise the importance of investigating the processes which generate areas of high tube-building polychaete densities. The importance of spionid tube-beds have been summarised by Noji and Noji (1991). Basically, such beds are important in the supply of colonists for rapid colonisation of disturbed sediments, they condition and improve sediments for future colonists and provide a rich food source for demersal fish. It is likely that all these apply to the *P. elegans* patches on Drum Sands. In addition, the results presented here suggest that tube-building species have a marked effect on the distributions of many invertebrate species. *C. volutator* was found to be present almost exclusively within *P. elegans* patches and, therefore, these tube-beds allow some species to occur on Drum Sands which would otherwise not survive. A change in the population fitness of *P. elegans* may result in the population fitness of other species. Consequently, elucidating the processes which affect the distributions of tube-building polychaetes (the second aim of this thesis) helps in the understanding of the processes spatially structuring the benthic communities in such areas. This is particularly important in areas where tube-beds occur on large scales, e.g., 150,000m^2 in Barnstable Harbour, Massachusetts (Sanders *et al.*, 1962). For this to be achieved, explicit studies addressing the reasons why many species exhibit significantly higher densities in tube-beds should also be conducted.

In conclusion, the approach adopted here of a combination of pattern documentation and manipulative experiments to test hypotheses about the underlying mechanisms is unusual in ecology. Only too often are *post hoc* explanations proposed to explain patterns without serious attempts to experimentally falsify such hypotheses. In this respect the present thesis makes, I believe, an important contribution to understanding the structure and dynamics of intertidal assemblages.

REFERENCES

Addicott J.F., Aho J.M., Antolin M.F., Padilla D.K., Richardson J.S. and Soluk D.A., 1987. Ecological neighbourhoods : Scaling environmental patterns. *Oikos* **49**:340-346.

Allen T.F.H. and Hoekstra T.W., 1991. The role of heterogeneity in scaling of ecological systems under analysis. In : *Ecological heterogeneity.* Kolassa J. and Pickett S.T.A.(eds.). Springer-Verlag. New York.

Ambrose W.G.Jr., 1984. Role of predatory infauna in structuring marine soft-bottom communities. *Mar. Ecol. Prog. Ser.* **17**:109-115.

Andre C. and Rosenberg R., 1991. Adult-larval interactions in the suspension-feeding bivalves *Cerastoderma edule* and *Mya arenaria. Mar. Ecol. Prog. Ser.* **71**:227-234.

Andrew N.L. and Mapstone B.D., 1987. Sampling design and the description of spatial pattern in marine ecology. *Oceanogr. Mar. Biol. Ann. Rev.* **25**:39-90.

Angel H.H. and Angel M.V., 1967. Distribution pattern in a marine benthic community. *Helgolander wiss. Meeres.* **15**:445-454.

Anger K., 1977. Benthic invertebrates as indicators of organic pollution in the Western Baltic Sea. *Int. Revue Ges. Hydrobiol.* **62**:245-254.

Anger K., Anger V. and Hagmeier E., 1986. Laboratory studies on the larval growth of *Polydora ligni*, *Polydora ciliata* and *Pygospio elegans* (Polychaeta, Spionidae). *Helgolander Meeres.* **40**:377-395.

Anger V., 1984. Reproduction in *Pygospio elegans* (Spionidae) in relation to its geographical origin and to environmental conditions: a preliminary report. *Fortsch. Zool.* **29**:45-51.

Armonies W., 1988. Active emergence of meiofauna from intertidal sediment. *Mar. Ecol. Prog. Ser.* **43**:151-159.

Armonies W., 1994. Drifting meio- and macrobenthic invertebrates on tidal flats in Konigshafen : a review. *Helgolander Meeres.* **48**:299-320.

Bachelet G., 1990. Recruitment of soft-sediment infaunal invertebrates: the importance of juvenile benthic stages. *La mer* **28**:199-210.

Boesch D.F., Diaz R.S. and Virnstein R.W., 1976. Effects of tropical storm Agnes on soft-bottom macrobenthic communities of the James and York estuaries and the lower Chesapeake Bay. *Chesapeake Sci.* **17**:246-259.

Bonsdorff E., 1989. Infaunal colonization and its dependence on environmental variation - experimental evidence from the northern Baltic Sea. In: *Reproduction, genetics and distributions of marine organisms.* (Fredensberg, Olsen and Olsen, eds.). pp.349-356.

Bonsdorff E., 1992. Drifting algae and zoobenthos - effects on settling and community structure. *Neth. J. Sea Res.* **30**:57-62.

Bonsdorff E. and Osterman C-S., 1984. The establishment, succession and dynamics of a zoobenthic community - an experimental study. In: *Proceedings of the 19th European marine biology symposium.* Gibb P.E. (ed.). Cambridge University Press, London. pp.287-297.

Breese W.P. and Phibbs F.D., 1972. Ingestion of bivalve Molluscan larvae by the polychaete annelid *Polydora ligni. Veliger* **14** **(3)**:274-275.

Brey T., 1991. Interactions in soft-bottom benthic communities: quantitative aspects of behaviour in the surface deposit feeders *Pygospio elegans* (Polychaeta) and *Macoma balthica* (Bivalvia). *Helgolander Meeres.* **45**:301-316.

Burgman M.A. and Williams M.R., 1995. An analysis of the spatial pattern of arthropod fauna of jarrah (*Eucalyptus marginata*) foliage using a Mantel correlogram. *Austral. J. Ecol.* **20**:455-457.

Burrough P.A., 1987. Spatial aspects of ecological data. In: *Data analysis in community and landscape ecology*. Jongman, Ter Braak and Van Tongeren (eds.). Pudoc. Wageningen, The Netherlands. pp.213-251.

Butman C.A., 1987. Larval settlement of soft-sediment invertebrates: the spatial scales of pattern explained by active habitat selection and the emerging role of hydrodynamic processes. *Oceanogr. Mar. Biol. Ann. Rev.* **25**:113-165.

Butman C.A., Grassle J.P. and Webb C.M., 1988a. Substrate choices made by marine larvae settling in still water and in a flume flow. *Nature* **333**:771-773.

Butman C.A., Grassle J.P. and Buskey E.J., 1988b. Horizontal swimming and gravitational sinking of *Capitella* sp.I (Annelida : Polychaeta) larvae: implications for settlement. *Ophelia* **29** (**1**):43-57.

Carey D.A., 1982. Sedimentalogical, ecological and hydrodynamic effects of a tube-building polychaete (*Lanice conchilega* Pallas). PhD. Dissertation, University of St. Andrews.

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

Caswell H. and Cohen J.E., 1991. Communities in patchy environments: a model of disturbance, competition and heterogeneity. In: *Ecological heterogeneity*. Kolassa J. and Pickett S.T.A. (eds.). Springer-Verlag, New York. pp.97-122.

Caudwell C.M. and Jones A.M., 1994. Montrose basin tidal flats: annual monitoring program, September 1993. Reports to Scottish Natural Heritage.

Cha M.W., in prep. Macroalgal mats and mudflats invertebrates: effects of mat removal.

Chia F.S., 1989. Differential larval settlement of marine invertebrates. In: *Reproduction, genetics, and distribution of marine organisms, 23rd European marine biology symposium.* Ryland J.S. and Tyler P.A. (eds.). pp.3-12.

Chia F.S., Gibson G. and Quian P.Y., 1996. Poecilogony as a reproductive strategy of marine invertebrates. *Oceanol. Acta* **19 (3-4)**:203-208.

Clarke K.R., 1993. Non-parametric multivariate analyses of changes in community structure. *Austral. J. Ecol.* **18**:117-143.

Cliff A.D. and Ord J.K., 1973. *Spatial autocorrelation.* Pion Ltd. London, 178pp.

Commito J.A., 1987. Adult-larval interactions: predictions, mussels and cocoons. *Estuar. Coast. Shelf Sci.* **25**:599-606.

Commito J.A. and Boncavage E.M., 1989. Suspension-feeders and coexisting infauna: an enhancement counterexample. *J. Exp. Mar. Biol. Ecol.* **125**:33-42.

Connell J.H., 1963. Territorial behaviour and dispersion in some marine invertebrates. *Res. Popul. Ecol.* **5**:87-101.

Connell J.H. and Slatyer R.O., 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *Amer. Natur.* **111**:1119-1144.

Covill R.W., 1972. The quality of the Forth Estuary. *Proc. Roy. Soc. Edin.* **12**:143-167.

Covill R.W., 1975. Bacteriological, biological and chemical parameters employed in the Forth Estuary. In: *Pollution criteria for estuaries.* (Hellawell, P.R., and Bossanyi, J., eds.). Unwin Brothers, Woking. pp.9.1-9.57.

Craig R.E., 1972. Water movements in the Firth of Forth. *Proc. Roy. Soc. Edin.* **10**:131-135.

Crisp D.J., 1974. Energy relations of marine invertebrate larvae. *Thalassia Jugoslavica* **10**:103-120.

Cummings V.J., Pridmore R.D., Thrush S.F. and Hewitt J.E., 1995. Post-settlement movement by intertidal benthic macroinvertebrates: do common New Zealand species drift in the water column?. *N. Zeal. J. Mar. Freshw. Res.* **29**:59-67.

Daro M.H. and Polk P., 1973. The autecology of *Polydora ciliata* along the Belgian coast. *Neth. J. Sea Res.* **6 (1-2)**:130-140.

Dauer D.M. and Simon J.L., 1976a. Repopulation of the polychaete fauna of an intertidal habitat following natural defaunation: species equilibrium. *Oecologia (Berl.)* **22**:99-117.

Dauer D.M., and Simon J.L., 1976b. Habitat expansion among polychaetous annelids repopulating a defaunated marine habitat. *Mar. Biol.* **37**:169-177.

Desprez M., Rybarczyk H., Wilson J.G., Ducrotoy J.P., Seuer F., Olivesi R. and Elkaim B., 1992. Biological impact of eutrophication in the Bay of Somme and the induction and impact of anoxia. *Neth. J. Sea Res.* **30**:149-159.

Diniz-Filho J.A. and Bini L.M., 1994. Space-free correlation between morphometric and climatic data: a multivariate analysis of Africanised honeybees (*Apis mellifera* L.) in Brazil. *Global Ecology and Biogeography Letters* **4**:195-202.

Dobbs F.C. and Vozarik J.M., 1983. Immediate effects of a storm on coastal fauna. *Mar. Ecol. Prog. Ser.* **11**:273-279.

Dorsett D.A., 1961. The reproduction and maintenance of *Polydora ciliata* (Johnst.) at Whitstable. *J. Mar. Biol. Ass. U.K.* **41**:383-396.

Downing J.A., 1979. Aggregation, transformation, and the design of benthos-sampling programs. *J. Fish. Res. Board Can.* **36**:1454-1463.

Dupont M.J-P., 1975. Presence de biolithosores a *Pygospio elegans* Claparede (Polychaetes sedentaires) dans la baie de Somme. *Sedimentologie* **280**:1773-1776.

Dutilleul P. and Legendre P., 1993. Spatial heterogeneity against heteroscedasticity: an ecological paradigm versus a statistical concept. *Oikos* **66** **(1)**:152-171.

Dyke P.P.G., 1987. Water circulation in the Firth of Forth, Scotland. *Proc. Roy. Soc. Edin.* **93B**:273-284.

Eagle R.A., 1973. Benthic studies in the south east Liverpool Bay. *Estuar. Coast. Shelf Sci.* **1**:285-299.

Eagle R.A., 1975. Natural fluctuations in a soft-bottom benthic community. *J. Mar. Biol. Assoc. U.K.* **55**:865-878.

Eckman J.E., 1979. Small-scale patterns and processes in a soft-substratum, intertidal community. *J. Mar. Res.* **37**:437-457.

Eckman J.E., 1983. Hydrodynamic processes affecting benthic recruitment. *Limnol. Oceanogr.* **28** **(2)**:241-257.

Eckman J.E., Nowell A.R.M. and Jumars P.A., 1981. Sediment destabilization by animal tubes. *J. Mar. Res.* **39** **(2)**:361-374.

Elliot J.M., 1977. *Methods for the analysis of samples of benthic invertebrates.* Freshwater Biological Association, Scient. Publ. No. 25, Ferry House, U.K. 160pp.

Everett R.A., 1991. Intertidal distribution of infauna in a California lagoon: the role of seasonal blooms of macroalgae. *J. Exp. Mar. Biol. Ecol.* **150**:223-247.

Everett R.A., 1994. Macroalgae in soft-sediment communities: effects on benthic faunal assemblages. *J. Exp. Mar. Biol. Ecol.* **175**:253-274.

F.R.P.B., 1988. F.R.P.B. Report TW20/88. Coastal waters of the Firth of Forth: Classification for SLS 4.

F.R.P.B., 1992. F.R.P.B. Report TW1/92. Coastal waters of the Firth of Forth: Classification for SLS 4.

F.R.P.B., 1993. F.R.P.B. Report TW1/93. Seasonal distribution of phytoplankton in the Firth of Forth, April-October 1992.

Fager E.W., 1964. Marine sediments: effects of a tube-building polychaete. *Science* **143**:356-358.

Fahy E., Goodwillie R., Rochford J. and Kelly D., 1975. Eutrophication of a partially enclosed estuarine mudflat. *Mar. Pollut. Bull.* **6** (**2**):29-31.

Fauchald K. and Jumars P.A., 1979. The diet of worms: a study of polychaete feeding guilds. *Oceanogr. Mar. Biol. Ann. Rev.* **17**:193-284.

Featherstone R.P. and Risk M.J., 1977. Effect of tube-building polychaetes on intertidal sediments of the Minas Basin, Bay of Fundy. *J. Sed. Petrol.* **47** (**1**):446-450.

Flach E.C., 1996. The influence of the cockle, *Cerastoderma edule*, on the macrobenthic community of the tidal flats in the Wadden Sea. *Mar. Ecol.* **17 (1-3)**:87-98.

Fowler J. and Cohen L., 1990. *Practical statistics for field biology.* John Wiley and Sons. 227pp.

Frid C.L.J., 1989. The role of recolonization processes in benthic communities, with special reference to the interpretation of predator-induced effects. *J. Exp. Mar. Biol. Ecol.* **126**:163-171.

Frithsen J.J. and Doering P.H., 1986. Active enhancement of particle removal from the water column by tentaculate benthic polychaetes. *Ophelia* **25 (3)**:169-182.

Frostick L.E. and McCave I.N., 1979. Seasonal shifts of sediment within an estuary mediated by algal growth. *Estuar. Coast. Mar. Sci.* **9**:569-576.

Gage J.D. and Geekie A.D., 1973. Community structure of the benthos in Scottish sea-lochs. II Spatial patterns. *Mar. Biol.* **19**:41-53.

Gage J.D. and Coghill G.G., 1977. Studies on the dispersion patterns of Scottish sea loch benthos from contiguous core transects. In: *Ecology of the marine benthos.* (Coull B.C., ed.). University of South Carolina Press. pp.319-337.

Gaines S.D. and Bertness M.D., 1992. Dispersal of juveniles and variable recruitment in sessile marine species. *Nature* **360**:579-580.

Gallagher E.D., Jumars P.A. and Trueblood D.D., 1983. Facilitation of soft-bottom benthic succession by tube builders. *Ecology* **64**:1200-1216.

Gayanilo F.C., Soriano M. and Pauly D., 1989. *A draft guide to the complete ELEFAN.* ICLARM Software, Manila.

Grant J., Bathmann U.V. and Mills E.L., 1986. The interaction between benthic diatom films and sediment transport. *Estuar. Coast. Shelf Sci.* **23**:225-238.

Grassle J.P., 1984. Speciation in the genus *Capitella* (Polychaeta, Capitellidae). In: *Polychaete reproduction*, Fortsschr der Zool Band 29 Fischer\ Pfannenstiel Hrsg: Polychaete reproduction. Gustaf Verlag, Stuttgart. pp.293-398.

Grassle J.F. and Sanders H.L., 1973. Life histories and the role of disturbance. *Deep-Sea Res.* **20**:643-659.

Grassle J.F. and Grassle J.P., 1974. Opportunistic life histories and genetic systems in marine benthic polychaetes. *J. Mar. Res.* **32** **(2)**:253-284.

Grassle J.P. and Butman C.A., 1989. Active habitat-selection by larvae of the polychaetes *Capitella* spp. I and II, in a laboratory flume. In: *Reproduction, genetics and distributions of marine organisms, 23rd European marine biology symposium.* Ryland J.S. and Tyler P.A. (eds.). Olsen and Olsen, Denmark. pp.107-114.

Greig-Smith P., 1952. The use of random and contiguous quadrats in the study of the structure of plant communities. *Ann. Bot.* **16**:293-316.

Griffiths A.H., 1987. Water quality of the Estuary and the Firth of Forth, Scotland. *Proc. Roy. Soc. Edin.* **93B**:303-314.

Gudmundsson H., 1985. Life history patterns of polychaete species of the family Spionidae. *J. Mar. Biol. Ass. U.K.* **65**:93-111.

Gunther C.P., 1992. Dispersal of intertidal invertebrates: a strategy to react to disturbances of different scales?. *Neth. J. Sea Res.* **30**:45-56.

Hadfield M.G., 1986. Settlement and recruitment of marine invertebrates: a perspective and some proposals. *Bull. Mar. Sci.* **39** **(2)**:418-425.

Hall S.J., Raffaelli D.G., Basford D.J. and Robertson M.R., 1990. The importance of flatfish predation and disturbance on marine benthos: an experiment with dab *Limanda limanda* (L.). *J. Exp. Mar. Biol. Ecol.* **136**:65-76.

Hall S.J., Basford D.J., Robertson M.R., Raffaelli D.G. and Tuck I., 1991. Patterns of recolonisation and the importance of pit-digging by the crab *Cancer pagurus* in a subtidal sand habitat. *Mar. Ecol. Prog. Ser.* **72**:93-102.

Hall S.J., Raffaelli D. and Thrush S.F., 1993. Patchiness and disturbance in shallow water benthic assemblages. In: *Aquatic ecology: Scale, pattern and processes.* Giller P.S., Hildrew A.G., and Raffaelli D. (eds.). Blackwell Scientific Publications. 649pp.

Hannan C.A., 1984. Planktonic larvae may act like passive particles in turbulent near-bottom flows. *Limnol. Oceanogr.* **29** **(5)**:1108-1116.

Hannerz L., 1956. Larval development of Spionidae. *Zoologiska Bidrag Fran Uppsala* **31**:3-194.

Hanski I., 1994. Spatial scale, patchiness and population dynamics on land. *Phil. Trans. R. Soc. Lond.*. **343B**:19-25.

Havenhand J.N., 1993. Egg to juvenile period, generation time, and the evolution of larval type in marine invertebrates. *Mar. Ecol. Prog. Ser.* **97**:247-260.

He F., Legendre P., Bellehumeur C. and LaFrankie J.V., 1994. Diversity pattern and spatial scale: a study of a tropical rainforest of Malaysia. *Env. Ecol. Stat.* **1**:265-286.

Hempel V.C., 1957. Uber den Rohrenbau und die Nahrungensaufnahme einiger Spioniden (Polychaeta sedentaria) der deutschen Kusten. *Helgolander Wiss. Meeres.* **6**:100-135.

Hsieh H.L., 1994. Habitat selection by settling larvae of the spionid *Pseudopolydora diopatrae*. *Memoires Du Museum National D'Histoire Naturelle* **162**:625.

Hubert L.J., Golledge R.G. and Costanzo C.M., 1981. Generalized procedures for evaluating spatial autocorrelation. *Geogr. Anal.* **13**:224-233.

Hull S.C., 1987. Macroalgal mats and species abundance: a field experiment. *Estuar. Coast. Shelf Sci.* **25**:519-532.

Hull S.C., 1988. The growth of macroalgal mats on the Ythan estuary, with respect to their effects on invertebrate abundance. PhD Thesis, University of Aberdeen.

Hurlbert S.H., 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* **54** **(2)**:187-211.

Hurlbert S.H., 1990. Spatial distribution of the Montane Unicorn. *Oikos* **58**:257-271.

Jensen K.T., 1985. The presence of the bivalve *Cerastoderma edule* affects migration, survival and reproduction of the amphipod *Corophium volutator*. *Mar. Ecol. Prog. Ser.* **25**:269-277.

Johnson R.G., 1970. Variations in diversity within benthic marine communities. *Amer. Natur.* **104**:285-300.

Jones J.E. and Jago C.F., 1993. In situ assessment of modification of sediment properties by burrowing invertebrates. *Mar. Biol.* **115**:133-142.

Jumars P.A., 1978. Spatial autocorrelation with RUM (Remote Underwater Manipulator): vertical and horizontal structure of a bathyal benthic community. *Deep-Sea Res.* **25**:589-604.

Jumars P.A., Thistle D. and Jones M.L., 1977. Detecting two-dimensional spatial structure in biological data. *Oecologia (Berl.)* **28**:109-123.

Keckler D., 1997. *Surfer for Windows, Version 6: Contouring and 3D surface mapping*. Golden Software Inc., Colorado, USA.

Kern J.C. and Taghon G.L., 1986. Can passive recruitment explain harpacticoid copepod distributions in relation to epibenthic structure?. *J. Exp. Mar. Biol. Ecol.* **101**:1-23.

Kotliar N.B. and Wiens J.A., 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* **59**:253-260.

Krebs C.J., 1989. *Ecological methodology*. Harper and Row, New York.

Kristensen I., 1957. Differences in density and growth in a cockle population in the Dutch Wadden Sea. *Archs. neerl. Zool.* **12**:351-453.

Lamont P.A., Gage J.D. and Tyler P.A., 1995. Deep-sea macrobenthic communities at contrasting sites off Portugal, preliminary results : II. Spatial dispersion. *Int. Revue Ges. Hydrobiol.* **80** **(2)**:251-265.

Lawrie S.M., 1996. Spatial pattern in the amphipod *Corophium volutator* in the Ythan Estuary. PhD Thesis. University of Aberdeen.

Leduc A., Drapeau P., Bergeron Y. and Legendre P., 1992. Study of the spatial components of forest cover using partial Mantel tests and path analysis. *J. Veget. Sci.* **3**:69-78.

Legendre P., 1990. Quantitative methods and biogeographic analysis. In: *Evolutionary biogeography of the marine algae of the North Atlantic.* NATO ASI Series, Vol. G22. Garbary D.J., and South G.R.,(eds.). Springer-Verlag. pp.9-34.

Legendre P., 1993. Spatial autocorrelation: trouble or a new paradigm?. *Ecology* **74** **(6)**:1659-1673.

Legendre P. and Troussellier M., 1988. Aquatic heterotrophic bacteria: modelling in the presence of spatial autocorrelation. *Limnol. Oceanogr.* **33** (**5**):1055-1067.

Legendre P. and Fortin M.J., 1989. Spatial pattern and ecological processes. *Vegetatio* **80**:107-138.

Legendre P. and Legendre L., 1997. *Numerical ecology.* Second edition. Elsevier Scientific Publ. Co., Amsterdam.

Legendre P., Thrush S.F., Cummings V.J., Dayton P.K., Grant J., Hewitt J.E., Hines A.H., McArdle B.H., Pridmore R.D., Schneider D.C., Turner S.J. and Whitlatch R.B., 1997. Spatial structure of bivalves in a sandflat: scales and regenerating processes. *J. Exp. Mar. Biol. Ecol.* **216**:99-128.

Levin L.A., 1981. Dispersion, feeding behaviour and competition in two spionid polychaetes. *J. Mar. Res.* **39** (**1**):99-117.

Levin L.A., 1982. Interference interactions among tube-dwelling polychaetes in a dense infaunal assemblage. *J. Exp. Mar. Biol. Ecol.* **65**:107-119.

Levin L.A., 1984a. Life history and dispersal patterns in a dense infaunal polychaete assemblage: community structure and response to disturbance. *Ecology* **65** (**4**):1185-1200.

Levin L.A., 1984b. Multiple patterns of development in *Streblospio benedicti* Webster (Spionidae) from three coasts of North America. *Biol. Bull.* **166**:494-508.

Levin L.A., 1987. Demographic consequences of larval development mode: planktotrophy vs. lecithotrophy in *Streblospio benedicti*. *Ecology* **68** (**6**):1877-1886.

Levin L.A. and Creed E.L., 1986. Effect of temperature and food availability on reproductive responses of *Streblospio benedicti* (Polychaeta : Spionidae) with planktotrophic or lecithotrophic development. *Mar. Biol.* **92**:103-113.

Levin L.A., Zhu J. and Creed E., 1991. The genetic basis of life history characters in a polychaete exhibiting planktotrophy and lecithotrophy. *Evolution* **45 (2)**:380-397.

Levin S.A., 1992. The problem of pattern and scale in ecology. *Ecology* **73 (6)**:1943-1967.

Lewin R., 1986. Supply-side ecology. *Science* **234**:25-27.

Lindegarth M., Andre C. and Jonsson P.R., 1995. Analysis of the spatial variability in abundance and age structure of two infaunal bivalves, *Cerastoderma edule and C. lamarcki,* using hierarchical sampling programs. *Mar. Ecol. Prog. Ser.* **116**:85-97.

Livingston R.J., 1987. Field sampling in estuaries: the relationship of scale to variability. *Estuaries* **10 (3)**:194-207.

Lowthian D., Soulsby P.G. and Houston M.C.M., 1985. Investigation of a eutrophic tidal basin. I. Factors affecting the distribution and biomass of macroalgae. *Mar. Env. Res.* **15**:262-284.

Ludwig J.A. and Reynolds J.F., 1988. *Statistical ecology : A primer on methods and computing.* John Wiley and Sons.

Lukenbach M.W., 1986. Sediment stability around animal tubes: the roles of hydrodynamic processes and biotic activity. *Limnol. Oceanogr.* **31 (4)**:779-787.

Lukenbach M.W., 1987. Effects of adult infauna on new recruits: implications for the role of biogenic refuges. *J. Exp. Mar. Biol. Ecol.* **105**:197-206.

Mardia K.V., Kent J.T. and Bibby J.M., 1979. *Multivariate analysis.* Academic Press. London.

Mathieson S. and Atkins S.M., 1995. A review of nutrient enrichment in the estuaries of Scotland: implications for the natural heritage. *Neth. J. Aquat. Ecol.* **29 (3-4)**:437-448.

McArdle B.H. and Blackwell R.G., 1989. Measurement of density variability in the bivalve *Chione stutchburyi* using spatial autocorrelation. *Mar. Ecol. Prog. Ser.* **52**:245-252.

McArdle B.H., Gaston K.J. and Lawton J.H., 1990. Variation in the size of animal populations: patterns, problems and artefacts. *J. Anim. Ecol.* **59**:439-454.

McArdle B.H., Hewitt J.E. and Thrush S.F., 1997. Pattern from process: it is not as easy as it looks. *J. Exp. Mar. Biol. Ecol.* **216**:229-242.

Meadows P.S. and Tufail A., 1986. Bioturbation, microbial activity and sediment properties *in an estuarine* ecosystem. *Proc. Roy. Soc. Edin.* **90B**:129-142.

Meadows P.S. and Hariri M.S.B., 1991. Effects of two infaunal polychaetes on sediment shear strength and permeability: an experimental approach. *Symp. Zool. Soc. Lond.* **63**:313-316.

Meire P.M., Dereu J.P.J., van der Meer J. and Develter D.W.G., 1989. Aggregation of littoral macrobenthic species: some theoretical and practical considerations. *Hydrobiologia* **175**:137-148.

Mendez N., Romero J. and Flos J., 1997. Population dynamics and production of the polychaete *Capitella capitata* in the littoral zone of Barcelona (Spain, NW Mediterranean). *J. Exp. Mar. Biol. Ecol.* **218**:263-284.

Mileikovsky S.A., 1971. Types of larval development in marine bottom invertebrates, their distribution and ecological significance: a re-evaluation. *Mar. Biol.* **10**:193-213.

Milne A., 1959. The centric systematic area-sample treated as a random sample. *Biometrics* **15**:270-295.

Morgan T.S., 1997. The formation and dynamics of *Pygospio elegans* tube-beds in the Somme Bay, France. PhD Thesis, Southampton University.

Morisita M., 1962. I_0-Index, a measure of dispersion of individuals. *Res. Popul. Ecol.* **4**:1-7.

Morris H.M., 1955. A new concept of flow in rough conduits. *Trans. Amer. Soc. Civil Eng.* **120**:373-398.

Morrisey D.J., Howitt L., Underwood A.J. and Stark J.S., 1992. Spatial variation in soft-sediment benthos. *Mar. Ecol. Prog. Ser.* **81**:197-204.

Muus B.J., 1967. The fauna of Danish estuaries and lagoons. Distribution and ecology of dominating species in the shallow reaches of the mesohaline zone. *Medd. Danm. Fisk. Havunders* **5**:3-316.

Myers A.A. and Giller P.S., 1988. Process, pattern and scale in biogeography. In: *Analytical biogeography: An integrated approach to the study of animal and plant distributions.* Myers A.A. and Giller P.S. (eds.). Chapman and Hall. New York and London.

Myers J.H., 1978. Selecting a method of dispersion. *Environ. Entomol.* **7** (**5**):619-621.

Nicholls D.J., Tubbs C.R. and Haynes F.N., 1981. The effect of green algal mats on intertidal macrobenthic communities and their predators. *Kieler. Meeresforsch. Sonderh.* **5**:511-520.

Noji C.I-M., 1994. Influence of the tube-building spionid polychaete *Polydora ciliata* on benthic parameters, associated fauna and transport processes. *Memoires Du Museum National D'Histoire Naturelle* **162**:493-502.

Noji C.I-M. and Noji T.T., 1991. Tube lawns of spionid ploychaetes and their significance for recolonization of disturbed benthic substrates. *Meeresforsch.* **33**:235-246.

Nowell A.R.M. and Church M., 1979. Turbulent flow in a depth-limited boundary layer. *J. Geophys. Res.* **84**:4816-4824.

Nowell A.R.M., Jumars P.A. and Eckman J.E., 1981. Effects of biological activity on the entrainment of marine sediments. *Mar. Geol.* **42**:133-153.

Oden N.L., 1984. Assessing the significance of a spatial autocorrelogram. *Geogr. Anal.* **16**:1-16.

Oden N.L. and Sokal R.R., 1986. Directional autocorrelation: an extension of spatial correlograms to two dimensions. *Syst. Zool.* **35** **(4)**:608-617.

Olafsson E.B., 1988. Inhibition of larval settlement to a soft-bottom benthic community by drifting algal mats: an experimental test. *Mar. Biol.* **97**:571-574.

Olafsson E.B., Peterson C.H. and Ambrose W.G.Jr., 1994. Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft sediments: the relative significance of pre- and post-settlement processes. *Oceanogr. Mar. Biol. Ann. Rev.* **32**:65-109.

Oliver J.S., Kvilek R.G. and Slattery P.N., 1985. Walrus feeding disturbance: scavenging habits and recolonization of the Bering Sea benthos. *J. Exp. Mar. Biol. Eco*l. **91**:233-246.

Ong B. and Krishnan S., 1995. Changes in the macrobenthos community of a sandflat after erosion. *Estuar. Coast. Shelf Sci.* **40**:21-33.

Owens N.J.P. and Stewart W.D.P., 1983. *Enteromorpha* and the cycling of nitrogen in a small estuary. *Estuar. Coast. Shelf Sci.* **17**:287-296.

Paterson D.M., 1994. Microbiological mediation of sediment structure and behaviour. In: *Microbial mats.* NATO ASI Series vol. G35 (Lucas S.J. and Caumette P., eds.). Springer-Verlag, Berlin. pp.97-109.

Pauly D. and David N., 1981. ELEFAN I, a basic program for the objective extraction of growth parameters from length-frequency data. *Meeresforsch.* **28**:205-211.

Pawlik J.R. and Butman C.A., 1993. Settlement of a marine tube worm as a function of current velocity: interacting effects of hydrodynamics and behaviour. *Limnol. Oceanogr.* **38** (**8**):1730-1740.

Pawlik J.R., Butman C.A. and Starczak V.R., 1991. Hydrodynamic facilitation of gregarious settlement of a reef-building tube-worm. *Science* **251**:421-424.

Pearson T.H. and Rosenberg R., 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanogr. Mar. Biol. Ann. Rev.* **16**:229-311.

Pearson T.H. and Stanley S.O., 1979. Comparative measurement of the redox potential of marine sediments as a rapid means of assessing the effect of organic pollution. *Mar. Biol.* **53**:371-379.

Perkins E.J. and Abbott O.J., 1972. Nutrient enrichment and sandflat fauna. *Mar. Pollut. Bull.* **3**:70-72.

Peterson J.H. and DeAngelis D.L., 1996. Prey patchiness and predator foraging behaviour: predation on migrating juvenile salmon in the Columbia River. Draft.

Pianka E.R., 1994. *Evolutionary ecology.* Fifth Edition. Harper Collins College Publishers, New York, USA. 486pp.

Pielou E.C., 1969. *An introduction to mathematical ecology.* Wiley, New York, USA. 286pp.

Pihl L. and Rosenberg R., 1984. Food selection and consumption of the shrimp *Crangon crangon* in some shallow marine areas in western Sweden. *Mar. Ecol. Prog. Ser.* **15**:159-168.

Platt T. and Sathyendranath S., 1992. Scale, patterns and processes in marine ecosystems. In: *Aquatic ecology: Scale, pattern and processes.* Giller P.S., Hildrew A.G. and Raffaelli D.G. (eds.). Blackwell Scientific Publications. 649pp.

Pleijel F. and Dales R.P., 1991. *Polychaetes: British Phyllodocoideans, Typhloscolecoideans and Tomopterideans.* Synopsis of the British Fauna (New Series). Kermack D.M. and Barnes R.S.K. (eds.). 202pp.

Prescott G.W., 1970. *How to know the freshwater algae.* 2nd edition. W.M.C. Brown Co. Publishers, Dubuque, Iowa.

Price L.H. and Hylleberg J., 1982. Algal-faunal interactions in a mat of *Ulva fenestrata* in False Bay, Washington. *Ophelia* **21 (1)**:75-88.

Probert P.K., 1984. Disturbance, sediment stability, and trophic structure of soft-bottom communities. *J. Mar. Res.* **42**:893-921.

Raffaelli D., Limia J., Hull H. and Pont S., 1991. Interactions between the amphipod *Corophium volutator* and macroalgal mats on estuarine mudflats. *J. Mar. Biol. Ass. U.K.* **71**:899-908.

Raffaelli D.G., Hildrew A.G. and Giller P.S., 1993. Scale, pattern and processes: Concluding remarks. In: *Aquatic ecology: Scale, pattern and processes.* Giller P.S., Hildrew A.G. and Raffaelli D.G., (eds.). Blackwell Scientific Publications. 649pp.

Raffaelli D., Raven J. and Poole L., 1999. Ecological impact of green macroalgal blooms. *Aquatic Conservation: Marine and Freshwater Ecosystems* **9**:219-236.

Ragnarsson S.A., 1996. Successional patterns and biotic interactions in intertidal sediments. PhD Thesis. University of Aberdeen.

Ramus J. and Venable M., 1987. Temporal ammonium patchiness and the growth rate in *Codium* and *Ulva* (Ulvaceae). *J. Phycol.* **23**:518-523.

Rasmussen E., 1953. Asexual reproduction in *Pygospio elegans* Claparede (Polychaeta Sedentaria). *Nature* **171**:1161-1162.

Rasmussen E., 1973. Systematics and ecology of the Isefjord fauna, Denmark. *Ophelia* **11**:1-493.

Rees E.I.S., Nicholaidou A. and Laskaridou P., 1977. The effects of storms on the dynamics of shallow water association. In: *Biology of benthic organisms.* Keegan B.F., Ceidigh P.O. and Boaden P.J.S.(eds.). Pergamon, New York. USA. pp.465-474.

Reise K., 1978. Experiments on epibenthic predation in the Wadden Sea. *Helgolander Wiss. Meeres.* **31**:55-101.

Reise K., 1979. Spatial configurations generated by motile benthic polychaetes. *Helgolander Wiss. Meeres.* **32**:55-72.

Reise K., 1983a. Sewage, green algal mats anchored by lugworms, and the effects on Turbellaria and small Polychaeta. *Helgolander Meeres.* **36**:151-162.

Reise K., 1983b. Experimental removal of lugworms from marine sand affects small benthos. *Mar. Biol.* **74**:327-332.

Reise K., 1983c. Biotic enrichment of intertidal sediments by experimental aggregates of the deposit-feeding bivalve *Macoma balthica. Mar. Ecol. Prog. Ser.* **12**:229-236.

Reise K., 1985. *Tidal flat ecology: An experimental approach to species interaction.* Ecological studies, Vol. 61. Springer-Verlag. 191pp.

Renshaw E. and Ford E.D., 1984. The description of spatial pattern using two-dimensional spectral analysis. *Vegetatio* **56**:75-85.

Rhoads D.C. and Young D.K., 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. *J. Mar. Res.* **28** (**2**):150-178.

Rosenberg R., 1973. Succession in benthic macroinfauna in a Swedish fjord subsequent to the closure of a sulphite pulp mill. *Oikos* **24**:244-258.

Sanders H.L., Goudsmit E.M., Mills E.L. and Hampson G.E., 1962. A study of the intertidal fauna of Barnstable Harbor, Massachusetts. *Limnol. Oceanogr.* **7**:63-79.

Santos S.L. and Simon J.L., 1980a. Response of soft-bottom benthos to annual catastrophic disturbance in a South Florida estuary. *Mar. Ecol. Prog. Ser.* **3**:347-355.

Santos S.L. and Simon J.L., 1980b. Marine soft-bottom community establishment following annual defaunation: larval or adult recruitment?. *Mar. Ecol. Prog. Ser.* **2**:235-241.

Savidge W.B. and Taghon G.L., 1988. Passive and active components of colonization following two types of disturbance on intertidal sandflats. *J. Exp. Mar. Biol. Ecol.* **115**:137-155.

Scheltema R.S., 1974. Biological interactions determining larval settlement of marine invertebrates. *Thalassia Jugoslavica* **10 (1/2)**:263-296.

Schlotzer-Schrehardt U., 1987. Ultrastructural investigation of the nuchal organs of *Pygospio elegans* (Polychaeta). II. Adult nuchal and dorsal organs. *Zoomorphology* **107**:169-179.

Schlotzer-Schrehardt U., 1991. Ultrastructural differentiation of nuchal and dorsal organs during postembryonic and sexual development of *Pygospio elegans* Claparede (Polychaeta : Spionidae). *Ophelia Suppl.* **5**:633-640.

Schories D. and Reise K., 1993. Germination and anchorage of *Enteromorpha* spp. in sediments of the Wadden Sea. *Helgolander Meeres.* **47**:275-285.

Shull D.H., 1997. Mechanisms of infaunal polychaete dispersal and colonization in an intertidal sandflat. *J. Mar. Res.* **55 (1)**:153-179.

Simard Y., Legendre P., Lavoie G. and Marcotte D., 1992. Mapping, estimating biomass and optimizing sampling programs for spatially autocorrelated data: case study of the Northern Shrimp (*Pandulas borealis*). *Can. J. Fish. Aquat. Sci.* **49**:32-45.

Smidt E.L.B., 1944. The effects of ice winters on marine littoral faunas. *Folio Geographica Danica* **2**:1-36.

Smidt E.L.B., 1951. Animal production in the Danish Wadden Sea. *Medd. Komm. Danm. Fisk. Havunders.* **11 (6)**:1-151.

Smirnov N., 1948. Tables for estimating the goodness of fit of empirical distributions. *Ann. Math. Stat.* **19**:280-281.

Smith C.R. and Brumsickle S.J., 1989. The effects of patch size and substrate isolation on colonization modes and rates in an intertidal sediment. *Limnol. Oceanogr.* **34** (**7**):1263-1277.

Snelgrove P.V.R., Butman C.A. and Grassle J.P., 1993. Hydrodynamic enhancement of larval settlement in the bivalve *Mulina lateralis* (Say) and the polychaete *Capitella* sp.I in microdepositional environments. *J. Exp. Mar. Biol. Ecol.* **168**:71-109.

Sokal R.R., 1979. Ecological parameters inferred from spatial correlograms. In: *Contemporary quantitative ecology and related econometrics.* (Patil G.P. and Rosenzweig M., eds.). International Co-operative Publishing House, Fairland, Maryland. pp.167-196.

Sokal R.R., 1986. Spatial data analysis and historical processes. In: *Data analysis and informatics, IV.* Diday E., *et al.* (eds.). Elsevier Science Publishers, Amsterdam, North Holland. pp.29-43.

Sokal R.R. and Oden N.L., 1978. Spatial autocorrelation in biology. 2. Some biological implications and four applications of evolutionary and ecological interest. *Biol. J. Linn. Soc.* **10**:229-249.

Sokal R.R. and Wartenberg D.E., 1981. Space and population structure. In: *Dynamic spatial models* (Griffith and Mackinnon, eds.). Alpher Van Der Rijn, Netherlands. pp.186-213.

Sokal R.R. and Thomson J.D., 1987. Applications of spatial autocorrelation in ecology. In: *Developments in numerical ecology.* NATO ASI Series, Vol. G14. Legendre P. and Legendre L., (eds.). Springer-Verlag, Berlin. pp.431-465.

Soulsby P.G., Lowthion D. and Houston M., 1982. Effects of macroalgal mats on the ecology of intertidal mudflats. *Mar. Pollut. Bull.* **13** (**5**):162-166.

Soulsby P.G., Lowthion D., Houston M. and Montgomery H.A.C., 1985. The role of sewage effluent in the accumulation of macroalgal mats on intertidal mudflats in two basins in southern England. *Neth. J. Sea Res.* **19** **(3/4)**:257-263.

Stephen A.C., 1929. Studies on the Scottish marine fauna: the fauna of the sandy and muddy areas of the tidal zone. *Trans. Roy. Soc. Edin.* **56**:291-306.

Strathmann R.R., 1985. Feeding and non-feeding larval development and life-history evolution in marine invertebrates. *Ann. Rev. Ecol. Syst.* **16**:339-361.

Strathmann R.R., 1986. What controls the type of larval development?. Summary statement for the evolution session. *Bull. Mar. Sci.* **39** **(2)**:616-622.

Sundback K., Jonsson B., Nilsson P. and Lindstrom I., 1990. Impact of accumulating drifting macroalgae on a shallow-water sediment system: an experimental study. *Mar. Ecol. Prog. Ser.* **58**:261-274.

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., 1985. Inhibition of larval recruitment of *Armandia* sp. (Polychaeta : Opheliidae) by established adults of *Pseudopolydora paucibranchiata* (Okuda) (Polychaeta : Spionidae) on an intertidal sandflat. *J. Exp. Mar. Biol. Ecol.* **87**:67-82.

Taylor L.R., 1984. Assessing and interpreting the spatial distributions of insect populations. *Ann. Rev. Entomol.* **29**:321-357.

Ter Braak C.J., 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* **67** **(5)**:1167-1179.

Thistle D., 1981. Natural physical disturbances and communities of marine soft bottoms. *Mar. Ecol. Prog. Ser.* **6**:223-228.

Thistle D., Reidenauer J.A., Robert R.F. and Waldo R., 1984. An experimental investigation of enhanced harpacticoid (Copepoda) abundances around isolated seagrass shoots. *Oecologia* **63**:295-299.

Thorson G., 1946. Reproduction and larval development of Danish marine bottom invertebrates with special reference to the planktonic larvae of the Sound. *Med. Komm. Danm. Kisk. Havunders* **4**:1-523.

Thorson G., 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev.* **25**:1-45.

Thrush S.F., 1986a. The sublittoral macrobenthic community structure of an Irish sea-lough: effect of decomposing accumulations of seaweed. *J. Exp. Mar. Biol. Ecol.* **96**:199-212.

Thrush S.F., 1986b. Spatial heterogeneity in subtidal gravel generated by the pit-digging activities of *Cancer pagurus*. *Mar. Ecol. Prog. Ser.* **30**:221-227.

Thrush S.F., 1988. The comparison of macrobenthic recolonization patterns near and away from crab burrows on a sublittoral sandflat. *J. Mar. Res.* **46**:669-681.

Thrush S.F., 1991. Spatial pattern in soft-bottom communities. *TREE* **6** (**3**):75-79.

Thrush S.F., Hewitt J.E. and Pridmore R.D., 1989. Patterns in the spatial arrangement of polychaetes and bivalves in intertidal sandflats. *Mar. Biol.* **102**:529-535.

Thrush S.F., Pridmore R.D., Hewitt J.E. and Cummings V.J., 1992. Adult infauna as facilitators of colonisation on intertidal sandflats. *J. Exp. Mar. Biol. Ecol.* **159**:253-265.

Thrush S.F., Pridmore R.D., Bell R.G., Cummings V.J., Dayton P.K., Ford R., Grant J., Green M.O., Hewitt J.E., Hines A.H., Hume T.M., Lawrie S.M., Legendre P., McArdle B.H., Morrisey D., Schneider D.C., Turner S.J., Walters R., Whitlatch R.B. and Wilkinson M.R., 1997a. The sandflat habitat: scaling from experiments to conclusions. *J. Exp. Mar. Biol. Ecol.* **216**:1-9.

Thrush S.F., Cummings V.J., Dayton P.K., Ford R., Grant J., Hewitt J.E., Hines A.H., Lawrie S.M., Legendre P., McArdle B.H., Pridmore R.D., Schneider D.C., Turner S.J., Whitlatch R.B. and Wilkinson M.R., 1997b. Matching the outcome of small-scale density manipulation experiments with larger scale patterns: an example of bivalve adult/juvenile interactions. *J. Exp. Mar. Biol. Ecol.* **216**:153-169.

Thrush S.F., Schneider D.C., Legendre P., Whitlatch R.B., Dayton P.K., Hewitt J.E., Hines A.H., Cummings V.J., Lawrie S.M., Grant J., Pridmore R.D., Turner S.J. and McArdle B.H., 1997c. Scaling-up from experiments to complex ecological systems: where to next?. *J. Exp. Mar. Biol. Ecol.* **216**:243-254.

Trueblood D.D., 1991. Spatial and temporal effects of terebellid polychaete tubes on soft-bottom community structure in Phosphorescent Bay, Puerto Rico. *J. Exp. Mar. Biol. Ecol.* **149**:139-159.

Tubbs C.R. and Tubbs J.M., 1983. Macroalgal mats in Langstone Harbour, Hampshire, England. *Mar. Pollut. Bull.* **14** (**4**):148-149.

Tufail A., Meadows P.S. and McLaughlin P., 1989. Meso- and micro-scale heterogeneity in benthic community structure and the sedimentary environment on an intertidal muddy-sand beach. *Scientifica Marina* **53**:319-327.

Turner S.J., Grant J., Pridmore R.D., Hewitt J.E., Wilkinson M.R., Hume T.M. and Morrisey D.J., 1997. Bedload and water-column transport and colonization processes by post-settlement benthic macrofauna: does infaunal density matter?. *J. Exp. Mar. Biol. Ecol.* **216**:51-75.

Upton G. and Fingleton B., 1985. *Spatial data analysis by example, Vol. 1.* Wiley series in probability and mathematical statistics. John Wiley and Sons, Ltd.

Valiela I., 1984. Marine ecological processes. In: *Spatial heterogeneity : Structure over space.* Chapter 13. Springer-Verlag, New York.

Vance R.R., 1973. On reproductive strategies in marine benthic invertebrates. *Amer. Natur.* **107**:339-352.

Volckaert F., 1987. Spatial pattern of soft-bottom polychaeta off Nova Scotia, Canada. *Mar. Biol.* **93**:627-639.

Warren L.M., 1976. A population study of the polychaete *Capitella capitata* at Plymouth. *Mar. Biol.* **38**:209-216.

Wartenberg D., 1985. Multivariate spatial correlation: a new method for explanatory geographical analysis. *Geogr. Anal.* **17**:263-283.

Wartenberg D., 1989. *SAAP - A Spatial Autocorrelation Analysis Program.*

Warwick R.M. and Clarke K.R., 1994. *Change in marine communities: An approach to statistical analysis and interpretation.* Natural Environment Research Council, U.K., 144pp.

Warwick R.M., Davey J.T., Gee J.M. and George C.L., 1982. Faunistic control of *Enteromorpha* blooms: a field experiment. *J. Exp. Mar. Biol. Ecol.* **56**:23-31.

Webb A.J. and Metcalfe A.P., 1987. Physical aspects, water movements and modelling studies of the Forth Estuary, Scotland. *Proc. Roy. Soc. Edin.* **93B**:259-272.

Weinberg J.R., 1979. Ecological determinants of spionid distributions within dense patches of deposit-feeding polychaete *Axiothella rubrocincta. Mar. Ecol. Prog. Ser.* **1**:301-314.

Wharfe J.R., 1977. An ecological survey of the benthic invertebrate macrofauna of the lower Medway Estuary, Kent. *J. Anim. Ecol.* **46**:93-113.

Whitlatch R.B. and Zajac R.N., 1985. Biotic interactions among estuarine infaunal opportunistic species. *Mar. Ecol. Prog. Ser.* **21**:299-311.

Wiens J.A., 1989. Spatial scaling in ecology. *Functional Ecology* **3**:385-397.

Wilson D.P., 1958. Some problems in larval ecology related to the localized distribution of bottom animals. In: *Perspectives in marine biology* (Buzzati-Traverso A.A., ed.). pp.87-103.

Wilson W.H.Jr., 1983. The role of density dependence in a marine infaunal community. *Ecology* **64** **(2)**:295-306.

Wilson W.H.Jr., 1985. Food limitation of asexual reproduction in a spionid polychaete. *Int. J. Invert. Reprod. Dev.* **8**:61-65.

Wilson W.H.Jr., 1992. Dispersal of adult infaunal organisms: lateral or vertical migration?. *Ann. Meet. Am. Soc. Zool. Can. Soc. Zool.* **32** **(5)**:121.

Wilson W.H.Jr., 1994. Dispersal of soft-bottom benthos: migration through the water column or through the sediment?. In: *Dispersal of benthic infauna. Symposium of reproduction and development of marine invertebrates.* (Wilson W.H., Stricker S.A. and Shinn G.L., eds.). pp.302-312.

Wiltse W., Foreman K., Valiela I. and Teal J., 1981. Regulation of benthic invertebrates in salt marsh creeks. *Estuaries* **4**:254.

Woodin S.A., 1976. Adult-larval interactions in dense infaunal assemblages: patterns of abundance. *J. Mar. Res.* **34**:25-41.

Woodin S.A., 1977. Algal 'gardening' behaviour by nereid polychaetes: effects on soft-bottom community structure. *Mar. Biol.* **44**:39-42.

Woodin S.A., 1978. Refuges, disturbance and community structure: a marine soft-bottom example. *Ecology* **59** (**2**):274-284.

Woodin S.A., 1981. Disturbance and community structure in a shallow water sandflat. *Ecology* **62** (**4**):1052-1066.

Woodin S.A., 1982. Browsing: important in marine sedimentary environments?. Spionid polychaete examples. *J. Exp. Mar. Biol. Ecol.* **60**:35-45.

Woodin S.A., 1984. Effect of browsing predators: activity changes in infauna following tissue loss. *Biol. Bull.* **166**:558-573.

Woodin S.A., 1985. Effects of defecation by arenicolid polychaete adults on spionid polychaete juveniles in field experiments: selective settlement or differential mortality?. *J. Exp. Mar. Biol. Ecol.* **87**:119-132.

Woodin S.A., 1986. Settlement of infauna: larval choice?. *Bull. Mar. Sci.* **39** (**2**):401-407.

Yokoyama H., 1990. Life history and population structure of the spionid polychaete *Paraprionospio* sp. (form A). *J. Exp. Mar. Biol. Ecol.* **144**:125-143.

Zajac R. N., 1991. Population ecology of *Polydora ligni* (Polychaeta: Spionidae). I. Seasonal variation in population characteristics and reproductive activity. *Mar. Ecol. Prog. Ser.* **77**:197-206.

Zajac R.N. and Whitlatch R.B., 1982a. Responses of estuarine infauna to disturbance. I. Spatial and temporal variation of initial recolonization. *Mar. Ecol. Prog. Ser.* **10**:1-14.

Zajac R.N. and Whitlatch R.B., 1982b. Responses of estuarine infauna to disturbance. II. Spatial and temporal variation of succession. *Mar. Ecol. Prog. Ser.* **10**:15-27.

Zar J.H., 1984. *Biostatistical analysis.* 2nd edition. Prentice Hall, New Jersey, USA.

Zettler M.L. and Bick A., 1996. The analysis of small- and meso-scale dispersion patterns of *Marenzelleria viridis* (Polychaeta : Spionidae) in a coastal water area of the southern Baltic. *Helgolander Meeres.* **50**:265-286.

Zobell C.E., 1946. Studies on redox potential of marine sediments. *Bull. Am. Assoc. Petrol. Geol.* **30**:477-511.

APPENDIX 1.1 : SPECIES ABUNDANCES FROM 1M SURVEY, PLOTS 1-64.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
NEMERTEA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	0
Polynoidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eteone cf *flava*	0	0	0	1	6	3	3	0	1	2	0	1	4	1	2	3	0	2	2	1	0	1	1	1	7	1	0	0	1	3	1	0
Phyllodoce mucosa	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Glycera tridactyla	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	1	0	0	0	0	0	0
Neanthes virens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nephtys hombergii	2	3	5	4	2	3	4	3	2	3	4	5	6	3	8	3	3	3	6	6	4	5	7	6	2	2	3	3	2	6	7	9
Scoloplos armiger	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0
Aricidea catherinae	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0
Pygospio elegans	18	14	13	6	26	26	23	5	11	19	19	21	200	154	15	25	9	24	24	22	15	22	23	36	27	24	20	20	17	190	143	30
Spio martinensis	5	1	0	1	4	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0	1	0	0	0	0	0
Spiophanes bombyx	0	0	0	1	1	7	0	0	4	0	0	1	1	1	1	1	1	0	3	1	3	0	5	2	4	1	2	0	1	0	0	1
Streblospio benedicti	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Magelona sp.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Capitella capitata	0	2	1	3	0	0	0	0	1	0	0	0	0	0	4	0	0	1	0	0	7	0	0	0	0	0	1	0	1	0	0	2
Arenicola marina	2	5	2	7	5	3	4	0	2	3	4	6	3	3	3	6	9	6	2	2	5	5	4	3	1	4	2	3	5	7	3	5
Lanice conchilega	0	0	1	0	2	2	2	2	0	0	3	6	4	3	0	1	0	1	1	1	18	27	7	2	1	1	0	7	3	10	11	1
OLIGOCHAETA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Praunus flexuosus	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Urothoe brevicornis	0	0	0	0	0	1	0	0	0	0	3	0	0	2	1	1	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Bathyporeia sarsi	11	2	2	3	17	12	2	2	1	2	5	1	4	3	3	1	1	1	1	0	1	0	0	0	1	0	3	0	0	0	0	1
Gammarus duebeni	0	2	2	0	0	0	0	0	0	2	7	2	1	3	0	1	8	4	14	6	5	3	0	6	0	3	4	1	7	3	0	0
Corophium volutator	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
TANAIDACEA	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cumopsis goodsiri	3	1	1	0	1	0	0	1	3	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Crangon crangon	0	2	1	2	3	0	0	3	5	4	1	1	0	0	1	3	1	2	7	1	0	4	0	1	3	4	1	0	2	0	0	0
Cerastoderma edule	5	6	6	7	6	4	6	8	5	3	6	6	4	6	1	4	10	6	6	10	7	6	10	7	6	3	8	4	6	5	6	10
Angulus tenuis	0	0	0	0	0	0	0	1	0	0	0	0	0	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fabulina fabula	0	0	0	3	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0
Macoma balthica	4	4	8	3	10	6	10	1	3	5	6	5	7	17	9	10	6	15	5	18	10	17	8	6	4	5	4	10	13	11	4	10
Mya arenaria	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Taxon	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64
NEMERTEA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	1	0	0	0	1	1
Polynoidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Eteone cf *flava*	2	1	10	1	1	4	0	1	1	2	3	3	2	1	1	7	1	2	1	1	1	0	0	3	2	0	0	4	2	0	2	2
Phyllodoce mucosa	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
Glycera tridactyla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	2	0	0	0	0	1	1	1	1	0
Neanthes virens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Nephtys hombergii	4	9	6	9	3	8	2	6	6	11	4	5	5	4	3	6	5	9	4	3	6	2	2	7	5	6	3	2	3	1	3	3
Scoloplos armiger	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Aricidea catherinae	1	0	0	0	0	0	1	2	1	0	2	1	0	0	1	1	1	1	2	1	1	0	0	4	0	1	1	0	1	1	2	2
Pygospio elegans	22	6	37	15	42	50	27	154	12	49	16	37	16	6	29	163	27	48	14	15	22	2	21	16	132	9	11	32	13	19	9	159
Spio martinensis	0	2	0	0	1	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Spiophanes bombyx	0	0	2	1	1	1	0	1	0	1	2	2	0	0	1	0	0	1	0	0	0	0	0	1	0	1	0	0	0	1	2	0
Streblospio benedicti	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Magelona sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Capitella capitata	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	3	0	0	6	0	0	0	0	1	0	4	4	0	0
Arenicola marina	9	5	2	1	2	4	1	0	3	2	1	0	2	3	3	6	6	4	2	4	2	6	2	2	0	6	3	5	9	6	1	0
Lanice conchilega	2	0	0	21	20	4	16	0	17	0	2	2	2	0	0	0	1	8	6	4	4	0	0	4	4	10	15	1	1	6	0	0
OLIGOCHAETA	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0
Praunus flexuosus	0	0	1	0	0	0	0	0	2	0	0	2	3	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	1	1	0
Urothoe brevicornis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	3	0	0	0	0	1	0	1	0	0	3	0	0
Bathyporeia sarsi	2	0	0	2	0	0	2	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	1	0	7	0	0	1	1	0	0
Gammarus duebeni	6	2	1	2	0	2	1	1	0	0	5	0	1	1	2	1	0	0	0	0	0	0	1	1	1	0	2	3	2	15	2	2
Corophium volutator	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0
TANAIDACEA	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cumopsis goodsiri	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Crangon crangon	1	0	1	3	2	0	0	0	0	1	4	2	1	0	3	0	1	0	5	0	0	1	3	2	0	2	1	1	0	2	2	0
Cerastoderma edule	6	9	9	3	4	6	11	10	7	12	9	3	10	7	10	4	10	4	5	5	6	4	4	10	7	6	8	9	3	7	9	10
Angulus tenuis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fabulina fabula	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0
Macoma balthica	10	6	16	8	13	10	9	5	5	6	5	9	19	23	2	2	3	15	11	14	24	7	3	8	39	5	3	11	6	10	4	18
Mya arenaria	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

APPENDIX 1.2 : SPECIES ABUNDANCES FROM 8M SURVEY, PLOTS 1-64.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
Eteone cf *flava*	3	3	1	3	2	5	3	0	3	5	4	2	0	2	7	3	4	5	3	3	3	3	5	0	7	0	0	2	1	7	6	2	7
Phyllodoce mucosa	0	0	0	1	1	0	2	1	0	1	0	1	0	0	0	2	0	1	1	1	0	0	1	0	0	0	1	0	0	0	1	2	0
Glycera tridactyla	0	0	0	2	0	1	0	1	0	1	0	0	0	0	2	0	0	1	0	0	3	0	1	0	0	0	2	1	0	0	0	0	0
Goniada maculata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Nephtys caeca	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nephtys hombergii	3	7	8	3	5	5	5	0	6	6	4	5	3	4	1	7	4	3	4	2	8	6	1	3	4	7	4	1	4	4	4	3	0
Scoloplos armiger	0	1	1	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	1
Aricidea catherinae	2	0	0	1	3	1	2	0	1	1	2	0	0	1	0	0	0	0	0	0	2	3	1	0	1	0	0	0	0	0	1	1	0
Polydora cornuta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Pygospio elegans	91	9	14	53	17	114	12	10	31	9	19	12	3	12	21	14	76	10	17	109	28	18	41	26	88	26	81	14	142	90	19	40	8
Spio filicornis	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Spio martinensis	0	5	4	1	6	0	9	0	6	2	0	3	1	6	14	10	2	6	3	2	3	4	8	7	0	5	0	2	1	10	18	1	14
Spiophanes bombyx	1	3	3	1	3	3	1	3	2	4	1	1	1	2	1	1	2	4	1	4	0	0	1	1	0	2	0	1	2	0	1	0	0
Streblospio benedicti	1	0	0	1	0	0	0	0	3	0	1	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0
Magelona sp.	0	1	1	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0
Chaetozone sp.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Capitella capitata	0	8	50	4	23	2	0	0	5	43	0	2	0	0	0	4	5	1	1	4	108	10	0	5	7	3	0	12	6	0	2	6	3
Arenicola marina	2	6	6	6	8	1	3	4	2	6	1	3	3	3	0	9	4	9	4	3	2	4	4	4	5	5	5	6	2	2	6	4	2
Lanice conchilega	0	2	4	1	4	4	1	3	2	2	1	0	8	3	5	0	0	0	1	1	24	20	22	0	4	1	2	21	18	17	2	3	2
Praunus flexuosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Urothoe brevicornis	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bathyporeia sarsi	0	0	0	0	2	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0
Gammarus duebeni	0	0	0	0	9	0	0	0	5	21	0	0	0	0	1	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0	0	1	0
Corophium volutator	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cumopsis goodsiri	0	0	0	0	1	0	0	0	1	1	1	0	0	2	1	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Crangon crangon	0	2	3	1	4	0	0	2	4	3	0	2	11	7	4	2	0	2	2	0	0	6	2	2	0	0	0	1	0	2	4	4	8
Cerastoderma edule	32	25	27	22	29	30	27	24	56	60	25	24	14	21	22	24	36	14	33	69	31	48	42	24	42	59	23	65	53	59	65	39	45
Angulus tenuis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
Fabulina fabula	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0
Macoma balthica	10	2	2	4	3	11	0	3	11	5	1	2	3	1	3	0	3	1	1	13	3	0	3	3	19	5	0	5	10	14	3	4	6
Mya arenaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0

Taxon	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64
Eteone cf *flava*	1	3	1	4	6	12	2	0	7	3	3	7	4	1	5	2	6	2	4	1	8	4	6	8	2	4	4	2	5	2	6
Phyllodoce mucosa	2	0	1	0	3	0	2	1	1	2	0	0	2	0	0	1	0	2	1	1	0	0	1	4	0	1	1	2	0	1	1
Glycera tridactyla	0	0	1	0	0	0	1	0	0	2	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1
Goniada maculata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nephtys caeca	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0
Nephtys hombergii	8	5	7	4	7	2	0	4	3	5	4	4	3	4	6	7	2	6	4	0	3	1	5	6	2	2	3	3	5	8	5
Scoloplos armiger	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	1	2	0	0	1	1	0	0	1
Aricidea catherinae	2	1	0	1	0	0	0	0	0	1	1	0	0	0	1	0	1	0	2	0	0	0	0	4	0	0	1	0	0	1	1
Polydora cornuta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Pygospio elegans	11	36	22	12	49	27	19	14	30	29	35	199	52	22	95	28	94	112	30	27	30	19	15	149	157	38	75	24	88	93	132
Spio filicornis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spio martinensis	13	9	28	13	2	6	4	6	10	8	16	5	1	0	4	5	2	1	5	0	4	7	0	1	0	6	0	0	1	0	1
Spiophanes bombyx	1	2	2	1	1	0	1	0	1	2	0	1	2	1	0	0	1	1	1	1	0	0	0	0	0	3	1	0	1	0	0
Streblospio benedicti	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Magelona sp.	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Chaetozone sp.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Capitella capitata	5	10	3	4	0	0	0	8	3	9	0	0	1	0	0	3	0	0	0	0	0	2	0	2	0	0	0	0	0	0	0
Arenicola marina	3	6	3	4	1	2	6	6	3	2	3	2	2	4	3	2	3	0	2	6	3	7	6	0	0	4	2	4	3	1	1
Lanice conchilega	8	4	1	0	0	3	2	1	0	16	1	3	5	0	11	0	2	2	0	1	0	0	0	0	0	24	17	4	3	4	3
Praunus flexuosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	3
Urothoe brevicornis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bathyporeia sarsi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
Gammarus duebeni	0	0	3	0	0	2	0	0	0	0	0	0	0	0	1	2	4	1	0	0	0	0	1	2	2	0	2	3	0	0	0
Corophium volutator	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4	0	0	1	0	0	0
Cumopsis goodsiri	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Crangon crangon	3	0	12	1	0	2	2	2	1	2	0	1	0	5	0	1	3	0	1	7	0	5	6	7	2	3	4	8	4	3	3
Cerastoderma edule	49	51	44	57	42	80	53	74	64	76	107	108	23	75	98	101	72	39	61	72	14	43	63	181	51	100	143	151	192	53	40
Angulus tenuis	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fabulina fabula	0	0	0	0	0	1	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Macoma balthica	6	7	3	1	6	7	2	4	6	9	10	34	8	2	26	17	12	7	13	6	1	2	5	71	21	13	46	20	22	9	9
Mya arenaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0

APPENDIX 1.3 : SPECIES ABUNDANCES FROM 40M SURVEY, PLOTS 1-63.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
NEMERTEA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	2	0	0	0	1	0	0	0
Eteone cf *flava*	3	1	1	1	2	0	1	0	0	0	4	2	1	0	1	5	2	2	1	2	0	2	8	6	4	7	1	3	5	1	5	9
Phyllodoce mucosa	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	2	0	3	0	0
Glycera tridactyla	1	0	2	1	0	0	1	0	1	1	2	0	0	0	1	0	0	0	1	0	0	1	1	1	1	0	0	0	0	2	2	0
Goniada emerita	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nephtys hombergii	1	1	3	0	0	4	2	3	5	3	2	3	6	3	0	3	8	6	1	4	0	6	3	5	6	4	2	2	7	1	1	3
Scoloplos armiger	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	3	0
Aricidea catherinae	0	0	1	0	1	2	0	2	1	6	3	0	2	0	0	0	1	1	2	0	2	1	1	1	0	0	0	0	5	2	1	11
Polydora cornuta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pygospio elegans	14	16	31	4	15	4	12	10	13	16	22	3	11	7	5	23	29	24	54	7	31	10	29	16	160	49	15	58	231	57	24	221
Spio martinensis	0	1	1	2	6	10	6	2	18	1	6	4	10	0	1	8	4	3	1	2	0	0	2	0	0	3	2	1	0	1	1	0
Spiophanes bombyx	0	0	0	0	0	1	0	0	0	1	2	1	2	0	1	4	2	2	3	1	2	1	0	0	2	0	1	0	0	2	0	0
Streblospio benedicti	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Magelona sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Chaetozone sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Capitella capitata	6	0	0	0	0	1	2	1	0	2	0	0	0	0	0	3	3	0	4	1	3	0	5	0	1	0	4	0	2	3	6	3
Arenicola marina	2	4	4	15	2	4	1	2	1	9	4	5	3	4	6	2	2	3	9	11	4	7	2	4	4	3	4	5	6	4	7	1
Ophelia sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Lanice conchilega	0	2	0	0	0	0	11	30	15	0	4	0	0	2	6	4	12	2	3	1	0	10	13	4	0	0	0	2	0	15	14	1
OLIGOCHAETA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0
Praunus flexuosus	0	0	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Urothoe brevicornis	0	0	0	0	0	0	0	0	2	1	0	0	0	1	6	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	1	0
Bathyporeia sarsi	4	11	7	8	40	24	17	14	11	1	0	5	4	4	5	2	1	2	0	0	0	1	0	0	0	3	0	0	0	0	0	1
Gammarus duebeni	0	0	6	0	1	1	3	10	0	1	1	0	0	11	2	5	6	0	3	1	0	2	1	1	6	8	3	1	2	0	0	0
Corophium volutator	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	1
TANAIDACEA	0	1	0	2	2	2	0	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cumopsis goodsiri	5	1	3	1	0	2	2	0	0	0	3	1	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Crangon crangon	1	2	2	1	0	1	4	2	1	0	1	0	0	2	3	0	0	0	0	9	1	4	0	0	0	3	0	1	0	0	1	0
Cerastoderma edule	15	6	8	14	16	11	8	8	9	22	13	19	24	16	12	13	20	14	16	17	24	28	25	8	18	10	5	12	29	34	13	37
Angulus tenuis	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Fabulina fabula	0	0	0	2	0	0	0	0	0	0	2	0	0	0	0	1	1	0	0	1	0	0	0	0	0	1	4	0	0	0	0	0
Macoma balthica	6	1	1	3	0	0	1	0	0	7	3	2	1	2	2	1	6	16	8	1	19	4	10	8	29	6	2	15	97	34	13	53
Mya arenaria	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	1	3	0	0	1	0	0	0	0	2	0	0

Taxon	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63
NEMERTEA	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eteone cf *flava*	3	13	8	3	4	8	1	1	1	6	1	0	4	2	4	1	2	1	11	6	3	1	1	4	2	2	2	4	6	5	0
Phyllodoce mucosa	0	0	0	1	0	3	0	0	1	0	0	5	0	0	0	2	0	1	5	0	3	1	1	2	0	0	0	0	1	2	2
Glycera tridactyla	1	0	0	0	0	2	1	0	1	0	1	1	0	1	0	2	0	0	2	0	0	0	0	0	1	0	1	1	0	0	0
Goniada emerita	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Nephtys hombergii	2	9	5	5	2	3	4	1	6	1	2	1	7	3	2	1	5	2	1	3	3	4	1	4	2	4	2	1	3	6	3
Scoloplos armiger	0	0	1	0	0	0	0	0	1	0	1	1	0	0	0	0	0	1	3	7	0	2	0	0	0	1	0	1	2	0	10
Aricidea catherinae	0	1	0	1	0	2	2	0	1	1	4	4	0	1	0	2	1	0	1	5	2	2	0	0	0	0	0	0	0	3	0
Polydora cornuta	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Pygospio elegans	14	207	14	20	170	70	12	28	200	80	38	30	44	33	65	37	51	88	187	88	170	42	46	131	52	33	40	64	50	150	35
Spio martinensis	0	0	0	0	0	5	0	0	0	0	2	1	0	2	1	6	0	2	0	1	0	1	0	0	0	3	0	0	0	0	0
Spiophanes bombyx	0	1	2	1	0	1	0	1	1	1	0	1	1	0	0	2	0	1	4	4	2	0	1	1	1	1	0	2	1	0	0
Streblospio benedicti	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Magelona sp.	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Chaetozone sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Capitella capitata	0	1	9	0	11	5	3	1	7	1	0	4	1	4	0	4	2	3	1	2	5	6	4	0	1	7	2	3	0	8	12
Arenicola marina	7	2	6	2	6	6	5	5	3	7	5	0	2	7	2	7	6	4	7	3	4	4	13	3	2	10	2	4	4	6	5
Ophelia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lanice conchilega	7	1	13	6	2	0	6	7	3	3	1	66	16	4	11	4	5	2	18	64	10	94	2	0	7	1	7	9	2	3	66
OLIGOCHAETA	0	1	0	0	0	1	1	4	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	1	2	0	0	0
Praunus flexuosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Urothoe brevicornis	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Bathyporeia sarsi	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0
Gammarus duebeni	3	1	4	1	1	3	1	2	1	2	29	0	1	5	5	4	5	1	20	12	7	16	0	8	1	2	1	1	1	9	44
Corophium volutator	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0
TANAIDACEA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cumopsis goodsiri	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Crangon crangon	5	0	0	1	0	0	0	0	1	0	1	7	0	1	3	11	1	1	3	1	1	0	0	2	1	3	0	11	0	0	0
Cerastoderma edule	11	19	22	21	28	12	32	57	22	12	4	6	37	17	38	14	20	30	30	12	9	6	10	10	11	13	12	36	19	20	12
Angulus tenuis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fabulina fabula	0	0	2	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Macoma balthica	10	17	25	32	44	8	41	85	48	114	7	15	39	19	56	27	28	75	15	15	43	5	22	56	102	9	52	12	70	26	7
Mya arenaria	0	0	1	0	0	1	3	0	0	0	0	0	0	0	6	1	1	6	1	0	0	0	1	0	0	1	1	1	0	0	1

APPENDIX 2 : SPECIES ABUNDANCES FROM MICRO-SCALE SURVEY.

This Appendix contains raw data from the survey used for both Chapter 3 and Chapter 7. Numbers of *P. elegans* adults per core for the 3 replicates are given for each month, together with the numbers of *P. elegans* tubes containing embryos or larvae, number of *P. elegans* new recruits and the numbers of other species.

SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Pygospio elegans (adults)	0	0	2	1	2	3	1	1	6	3	2	3	3	2	9	6	2	1	1	2	4	3	8	3	9	1	7	1	4	0	2	4
with embryos																																
with hunchback larvae																																
with mature larvae																																
P elegans (new recruits)																																
Eteone cf flava			1								1							1									1					1
Anaitides mucosa									1																							
Glycera tridactyla																																
Hediste diversicolor																																
Nephtys hombergii	1																															
Polydora cornuta																																
Spio martinensis																																
Spiophanes bombyx																						1										
Streblospio benedicti							1																									
Chaetozone sp.																																
Capitella capitata		1		3	2	1	1	4		1		1	1	1	1				3	2	3	7	1	1	5	7	6	1		4	3	1
OLIGOCHAETA													1																			
Corophium volutator																								1								
Cerastoderma edule	2			1				1	3	2	2	1	1	1	1	1	1	1		2			1	3	1	3	4	2	1	1	1	1
Macoma balthica	1		1	1	1				2	1						2	1				1		2		1	1	1	1	1			
Venus sp.																																

SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Pygospio elegans (adults)	7	7	6	4	9	6	0	5	4	2	1	5	5	6	2	0	0	5	3	8	6	3	4	4	1	4	4	7	4	1	3	10
with embryos	1	1	3		3	2		1						1					1	2	1	2	1			2		1				2
with hunchback larvae																																
with mature larvae	1				1				1																		1					2
P elegans (new recruits)	1																															
Eteone cf flava											1			1									1		1							
Anaitides mucosa				1																												
Glycera tridactyla																																
Hediste diversicolor						1																										
Nephtys hombergii																																
Polydora cornuta																																
Spio martinensis																													1			
Spiophanes bombyx																																
Streblospio benedicti											1		1						1							1						
Chaetozone sp																																
Capitella capitata	6	2	6			4	2	1	3	3	2	7			1	6	1	3	2	1			1	1	6	1	2	2	1	1	1	3
OLIGOCHAETA							1	2																								
Corophium volutator								1		2										1			1	2	2	1	2	1		1	1	2
Cerastoderma edule	4	5	9	3	1	7	1	5	3	5	6	3	5	3	4	2	1	6	2	8		6	3	4		4	1	2	5	2	3	2
Macoma balthica					1	1	2	2	1	1					1		1	2			1	1	1	1			1			1	2	
Venus sp.																										1	1					

SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Pygospio elegans (adults)	7	8	7	6	1	2	7	4	4	6	1	3	0	2	3	1	0	3	9	4	6	3	4	3	5	1	2	4	1	1	2	8
with embryos		1					1	1										1	1		1					1						
with hunchback larvae																																
with mature larvae																			1					1	1				1			
P elegans (new recruits)												1		1	2			1	1				1	1	1			1		1	1	
Eteone cf flava							1													1											1	
Anaitides mucosa																			1													
Glycera tridactyla															1																	
Hediste diversicolor																																
Nephtys hombergii																																
Polydora cornuta																																
Spio martinensis																																
Spiophanes bombyx																																
Streblospio benedicti													2					1					1							1		
Chaetozone sp									1																							
Capitella capitata					1	1	2	2	1	3		1	1		1			1		1			1	2			2				2	
OLIGOCHAETA																										1						
Corophium volutator								1										1														
Cerastoderma edule	3	2		2	1	2	1	3		1	2	1		1	4	2	2	1		3	5		3	6	5	1	1	2		2	3	1
Macoma balthica											2		1		1						1	1	1									1
Venus sp.																																

March 1997,
replicates1-3.

SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Pygospio elegans (adults)	3	5	5	5	5	3	3	6	3	7	7	10	4	7	3	2	4	4	2	2	0	3	2	8	1	3	4	4	2	5	4	6
with embryos		1	1	1	1		1	1			1	1		1			2	1				1	1	1			1			1		1
with hunchback larvae																																
with mature larvae									1	1	2	1			1																1	
P elegans (new recruits)				1								1			1										1	1				1		2
Eteone cf flava				1			1			1																				1		
Anaitides mucosa							1				1																					
Glycera tridactyla																																
Hediste diversicolor																																
Nephtys hombergii																																
Polydora cornuta																																
Spio martinensis																																
Spiophanes bombyx																																
Streblospio benedicti																																
Chaetozone sp																						1										
Capitella capitata		3	2		1	1		4	1		3	2	1	1			2		1	1		2	1		2		5	1	3	1	2	2
OLIGOCHAETA																																
Corophium volutator			1																													
Cerastoderma edule	1	1	1	6	2	1	3	1	3	2	2	4	2	4	2		1	2	2	2	1	2	1	5	6		2	1			1	1
Macoma balthica			1	1		1			1		1					1		1	1				1								2	3
Venus sp.																																

SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Pygospio elegans (adults)	5	2	10	5	3	1	2	0	4	5	2	3	2	4	6	7	9	7	3	2	1	1	1	7	5	2	0	2	5	0	4	2
with embryos		1	2	2			1					1	1				2	1	1									1	1			
with hunchback larvae																																
with mature larvae																					1			2	1							
P elegans (new recruits)																											1				1	
Eteone cf flava		1			1		1			1											1		1			2						
Anaitides mucosa																																
Glycera tridactyla																																
Hediste diversicolor																																
Nephtys hombergii	1											1																				
Polydora cornuta																																
Spio martinensis																																
Spiophanes bombyx																																
Streblospio benedicti							1	1				1				2						1			1			1	1			
Chaetozone sp.																																
Capitella capitata	1	3	1	4	1			2	4	4	2				2	10	4		2	2		3			3	3	3	13	4	1	3	
OLIGOCHAETA																												1				
Corophium volutator											1	1	1																			
Cerastoderma edule	3	3	2	7	8	4	5	6	4	3	5	1		1	1	2	4		3	1	2		1	4		3	3	1	5	1	3	4
Macoma balthica				2	1		2	1	2	1				1	1		1			2			1	1	1				1			2
Venus sp.																																

SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Pygospio elegans (adults)	6	4	5	9	5	12	2	3	3	3	7	5	12	6	4	2	5	6	5	5	2	2	5	4	9	1	8	3	6	6	12	3
with embryos		1		2		1	1					1	1	1	1		2	1	1	2				1	2				1	1	1	1
with hunchback larvae																																
with mature larvae				1		2		1				1	1	1					1				2						1		1	
P elegans (new recruits)						1		1	1	1	1	1	1	1				1	1							1					1	1
Eteone cf flava	1			1	1																1											1
Anaitides mucosa	1			1									1	1												1					1	
Glycera tridactyla																																
Hediste diversicolor																																
Nephtys hombergii								1				1											1									
Polydora cornuta						3									1	1																
Spio martinensis	1				1										1																	
Spiophanes bombyx																																
Streblospio benedicti													1		1			1							1						1	
Chaetozone sp																																
Capitella capitata	1	3		1	3	1	1			5			2	1			2	2				2	1	1		2	1				2	
OLIGOCHAETA		1												2	1			1														1
Corophium volutator																																
Cerastoderma edule	3	3	1	1		1	4	4	2	5	1	4	4	2	3	4	1		1	5	2	1	4	3	5	9	9	4	7	6	4	1
Macoma balthica	1			1	1	1	1	2	3			1			1			1			1	1		1	1	1	1	1	2	3		
Venus sp																																

April 1997,
replicates 1-3

SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Pygospio elegans (adults)	14	1	6	6	1	1	4	5	1	3	8	13	12	8	5	3	1	7	2	6	2	4	4	18	6	6	9	7	7	6	8	3
with embryos	1		1			1		1	1		1		2	2						1		1		2	1	3	2	3	1	1	2	
with hunchback larvae																																
with mature larvae	1											1	1											1								1
P elegans (new recruits)	15	15	12	10	15	9	13	9	11	5	5	11	14	5	5	7	8	19	8	13	10	11	9	12	16	18	8	18	15	17	10	11
Eteone cf flava				1								1														1					1	
Anaitides mucosa														1																		
Glycera tridactyla																													1			
Hediste diversicolor																																
Nephtys hombergii																																
Polydora cornuta	2	2	2	1	2	1	1	1	2	2	2		1	1		1	1	3	1	1	3	2	1	1	2		1	2	1	2	1	2
Spio martinensis																																
Spiophanes bombyx																																
Streblospio benedicti	1											2		1								1				1						
Chaetozone sp.																																
Capitella capitata	1		1	2			1	1		2		3	1						2	1	2	1	1					1	2		2	2
OLIGOCHAETA			1								1						1				1								1			1
Corophium volutator			7			1											1	1			1		3		7	2						
Cerastoderma edule	9	6	7	4	3	1	5	3		2	7	4	7	6	2	4	6	2	2	1	6	1	2	2	8	4	2	2	1	3	3	5
Macoma balthica			1		1	1				1	1				1		2	1	3	1	2	1			1		1		1			1
Venus sp.													1							1										1		

SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Pygospio elegans (adults)	1	3	6	4	4	5	3	3	2	3	5	6	1	2	3	3	6	11	4	4	5	8	4	6	8	4	6	13	3	7	3	2
with embryos	1		2		1		1	1	1	1	1	2		1				1	1		1	1	1		1	1	1	3	1	1	1	
with hunchback larvae																																
with mature larvae																								1			1	2				
P. elegans (new recruits)	16	4	9	8	5	8	9	8	8	8	3	4	5	10	9	13	10	9	3	6	1	13	1	11	6	1	12	10	10	13	8	6
Eteone cf flava			1	1												1			1													
Anaitides mucosa																					1	1	1				1					
Glycera tridactyla																																
Hediste diversicolor																																
Nephtys hombergii																																
Polydora cornuta		1				1		1						2							1		1	1	1	1	2	1	1			
Spio martinensis																																
Spiophanes bombyx																																
Streblospio benedicti		1	1	1						1																				1		
Chaetozone sp																																
Capitella capitata		1	3	3	1		2	9		1					1		1	1				1		1	1	3			1		2	
OLIGOCHAETA	1		1																								1			1		
Corophium volutator					1		2						1	2		1	1	1	1	4	1		2	8	1			4		1	1	
Cerastoderma edule	1	6	3	4	4	2	4		5	8	4	3	5	6	1	2	2	4	6	3	9	6	3	6	7	1	6	4	3	3	2	1
Macoma balthica			2			1	1	3	2	3	1		1	2	2		1		2		1				1					1	1	
Venus sp																										1						

SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Pygospio elegans (adults)	6	8	5	3	4	1	1	1	6	2	4	1	5	3	0	2	0	5	3	5	3		4	1	6	2	2	1	3	1	1	5
with embryos	1	2	1	1	2		1		1	1	1		1	1		1				1					1					1		2
with hunchback larvae																																
with mature larvae																					1											1
P elegans (new recruits)	7	4	7	6	5	9	6	9	8	8	3	7	6	7	9	4	7	7	5	9	4		5	2	5	4	6	5	2	4	4	9
Eteone cf flava			1										1		1					1										1		
Anaitides mucosa																																
Glycera tridactyla																																
Hediste diversicolor																																
Nephtys hombergii	2																							1								
Polydora cornuta	1			1	2	1		1	2			2	1	1			1			1	2		1	1						1		1
Spio martinensis																																
Spiophanes bombyx																																
Streblospio benedicti					1	1						1				1																
Chaetozone sp.																																
Capitella capitata	1				1						1				1	5		2										2	1			
OLIGOCHAETA						1				1	1				1		1															
Corophium volutator	1		1		1					1			2	2			1							1	4		1					
Cerastoderma edule	4	4		5	4		1	3	6	5	4	3	5	1	3	3	2	2	2	5	6		1	5	1	1	4	2	1	3	3	6
Macoma balthica		1		1		2	1		1			3		1	3	3							1		2					2	2	
Venus sp																							1									

May 1997,
replicates 1-3

SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Pygospio elegans (adults)	5	5	1	7	3	25	5	2	2	6	4	9	1	3	8	7	2	2	0	2	12	1	5	7	5	13	9	4	5	2	4	0
with embryos				1	1	2	1		1		1		1			2	1				1			1			1	1				
with hunchback larvae																																
with mature larvae						2						1		1							1				1	2	1					
P elegans (new recruits)	7	7	8	2	3	11	1		5	6	5	7	1	5	2	5	1	4	2	2	7	6	1	20	2	13	7	11		3	2	4
Eteone cf flava		1				3			1	1	1	2	1					1	1						1	1	2	1				1
Anaitides mucosa																																
Glycera tridactyla																																
Hediste diversicolor																																
Nephtys hombergii																																
Polydora cornuta		2		1		1	2	1					1					2						1		1		1		1		
Spio martinensis																																
Spiophanes bombyx																																
Streblospio benedicti						2								1				1							1							1
Chaetozone sp.																																
Capitella capitata	1					4	1		1		1					1			1						3							
OLIGOCHAETA					1		1	1			1			1					1													
Corophium volutator	1	3	20	2	8	4	1		1	1	1	1	1	3	1		1					28					3	20	15	1		1
Cerastoderma edule		1		1	2	3	1	1	2	3		1	2	7	1	3	2	1	2	1		2		2	3	6	2			1	2	1
Macoma balthica	1																	1	1	1												
Venus sp																																

SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Pygospio elegans (adults)	1	2	3	4	7	8	8	3	7	5	10	5	3	1	4	12	8	2	13	11	6	4	10	15	36	13	6	5	9	8	8	3
with embryos					1	1			1	1	1	1	1	1	1		2		1	2	1	1	1	2	2	1	1	1			1	
with hunchback larvae																																
with mature larvae			1	1													1		2		1			1	1	1	1			1		
P. elegans (new recruits)	1	9	5	7	5	11	10	10	1	4	5	5	3	4	7	2	10	6	12	7	5	5	2	10	14	7	12	8	2	4	2	
Eteone cf flava		1		1			1		1	1		1		1	1												1			1		1
Anaitides mucosa																										1						
Glycera tridactyla																																
Hediste diversicolor																																
Nephtys hombergii																																
Polydora cornuta				2	2		3		1	1	1	1						1	1			2	1	4	4		2	1	1	1	5	
Spio martinensis																																
Spiophanes bombyx																																
Streblospio benedicti	1			1			1	1									1													1	1	
Chaetozone sp.																																
Capitella capitata			1		2		1	1		1					1	1	1		2				1	1		1			1			
OLIGOCHAETA															1													1				
Corophium volutator	35	6	11	15	60		4	1	4	6					1		3					1				1	4	2	1	5		1
Cerastoderma edule	1	1	3	1	1		4	8		4	7	4	2	3	3	5	5	6	1	4	4	6	5	5	7	4	6	1	1	1	1	
Macoma balthica														1			1		1	1	2			2						1		
Venus sp																																

SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Pygospio elegans (adults)	3	2	5	3	3	5	5	3	10	6	6	4	1	2	4	5	1		3	9	6	12	9	10	8	4	5	6	2	3	9	4
with embryos			1	1	1	2			1		2	1	1		1				1	1	1		2	1	1			1	1	1	1	
with hunchback larvae																																
with mature larvae										1													1									
P elegans (new recruits)		3	1	13	10	7	17	6	8	3	3	2	2	5	1	4	3	3	4	6	16	10	3	25	3	4	8	4	14	2	21	11
Eteone cf flava										2										1		1										
Anaitides mucosa																											1					
Glycera tridactyla																																
Hediste diversicolor																																
Nephtys hombergii							1		2																							
Polydora cornuta					1		1				1				1	1	1		1	1						1				1	1	1
Spio martinensis																																
Spiophanes bombyx																																
Streblospio benedicti	2	1						1	1						1					3				1								
Chaetozone sp																																
Capitella capitata															1							1										
OLIGOCHAETA				1																						1						
Corophium volutator	7		1	3		2	10	3	1	1	27	6	4				3	3	3	2	8		1	1	4	10	6	6	5	10	2	1
Cerastoderma edule	3	2	2	3	7	4	9	2	3	3	3	1	3	1		2	2	2	3	4	2	6	1	4	1	5	1	2		1	3	3
Macoma balthica	1			1		1					1	2		1			1			1							1	2				
Venus sp																																

June 1997,
replicates 1-3

SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Pygospio elegans (adults)	3	1	9	14	6	4	16	15	2	7	13	3	0	2	3	2	9	10	5	6	6	6	2	2	2	8	6	2	11	2	9	9
with embryos	1		1												1						1								1		1	
with hunchback larvae																																
with mature larvae											1	1															1					
P elegans (new recruits)		2	2		1				2	4		2	1		5	1			2	3	1	6	1	1		3		1	1	3	4	4
Eteone cf flava					1	1	1				1	1								1		1		2					2		2	
Anaitides mucosa										1																						
Glycera tridactyla																																
Hediste diversicolor																																
Nephtys hombergii																																1
Polydora cornuta	1	2		2	1	3						2			2		1	2				3		2	1							1
Spio martinensis																																
Spiophanes bombyx			1																													
Streblospio benedicti																																
Chaetozone sp.																																
Capitella capitata				1	1																											
OLIGOCHAETA	2															1		1		1					2	1					1	
Corophium volutator																							1			3	5					
Cerastoderma edule		1	1	1	1	3	3	1	1		1	2	3	2		1		2	1		1	1	5	1	1	3	2	2	1	2	2	1
Macoma balthica		2			1	1											1	1					2		1			1				
Venus sp																																

SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Pygospio elegans (adults)	3	7	4	2	2	7	7	4	1	8	7	3	3	1	0	2	4	2	5	8	6	2	4	6	4	3	12	5	6	9	9	13
with embryos					1		2				1		1						1	1	1			2								1
with hunchback larvae																																
with mature larvae						1										1													2			
P elegans (new recruits)	1	5	4	2		1	1	3	4	3	1	1	1	3	2	2	1	4	7	3	3	1	1		1	3	2	2	2	4	3	5
Eteone cf flava					1			1		1	1		1		1				1	2	2										1	
Anaitides mucosa																																
Glycera tridactyla																																
Hediste diversicolor																												1				1
Nephtys hombergii								1																								
Polydora cornuta		2	3	1	1	1				1					1									1			1					1
Spio martinensis																																
Spiophanes bombyx																																
Streblospio benedicti																			1													
Chaetozone sp.																																
Capitella capitata									1						1													1		1		
OLIGOCHAETA									1		1																					
Corophium volutator			1	1			2		1				3		1						1			1	1		1			1	2	12
Cerastoderma edule	1		2		1	1	2	4	1	1	2	1	2	1	1	2	2	3	1	1	1	2	2	3		1		5	1	4	5	2
Macoma balthica	1								1	1																				1		
Venus sp.																																

SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Pygospio elegans (adults)	7	20	22	7	7	7	9	16	11	8	10	4	5	3	13	2	6	6	4	2	13	17	6	12	6	6	5	3	4	6	2	3
with embryos		1				1		1													1	2		1			1					
with hunchback larvae																																
with mature larvae						1		1	1			1			3												1				1	
P. elegans (new recruits)	1		10	1	2	2	1	2	2	2	3			4	3	5	1	1	1	1	6	10	2	2	2		1		1	1	3	2
Eteone cf flava			3	2	2	1						1	1	1									1	1	1						1	
Anaitides mucosa								1																								
Glycera tridactyla																																
Hediste diversicolor																																
Nephtys hombergii																																
Polydora cornuta				2	2		1	1	1				1		2						2	1				1	3		1			
Spio martinensis																							1									
Spiophanes bombyx																																
Streblospio benedicti																										1			1			
Chaetozone sp																																
Capitella capitata			1	2	1																											
OLIGOCHAETA									1									1							1						1	
Corophium volutator	2	1		1			1	4		1	5	1	1			1				1	2								2			
Cerastoderma edule	1	3	6	1	5	2	3	2		1		2		4	4	1	1	2	2	3	3	5	2	1		3	2	2		2	1	1
Macoma balthica				2								1			2	1		1		1				1				1				
Venus sp																																

July 1997,
replicates 1-3

SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Pygospio elegans (adults)	11	6	2	11	9	4	8	2	10	13	10	9	9	3	5	3	10	8	6	6	5	8	7	3	4	2	1	1	1	0	5	1
with embryos				1	1					1	1																					
with hunchback larvae																																
with mature larvae																																
P elegans (new recruits)	1		3			2	1				5	1	1	1	2		2		6	2			4	1		1	1	1		2		
Eteone cf flava	1	1	1	1			3						2		1	2	2	2					1			1		1				1
Anaitides mucosa																																
Glycera tridactyla																																
Hediste diversicolor																																
Nephtys hombergii													1		1																	
Polydora cornuta									1																							
Spio martinensis																						1						1		1		
Spiophanes bombyx																																
Streblospio benedicti																																
Chaetozone sp																																
Capitella capitata								4																				2				
OLIGOCHAETA											1																					
Corophium volutator																																
Cerastoderma edule	3				1				2	1	2	1			2		1	1		2	1				2				1	3	1	1
Macoma balthica				1																										1	1	
Venus sp.																																

SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Pygospio elegans (adults)	0	3	5	3	5	5	5	6	2	4	3	6	7	14	11	8	8	7	9	6	6	9	4	4	2	3	7	6	3	4	3	4
with embryos							1								1				1	1								1				
with hunchback larvae																																
with mature larvae														2																		
P elegans (new recruits)		3	1		1	1	2	1	3		1	2	2	1	1		1	2			3	2	3									1
Eteone cf flava				1						1			1			2	1	1	1	1												
Anaitides mucosa																																
Glycera tridactyla																																
Hediste diversicolor																																
Nephtys hombergii														1											1							
Polydora cornuta														2			2		4			1		1		1	2					1
Spio martinensis																																
Spiophanes bombyx																																
Streblospio benedicti		1																														
Chaetozone sp																																
Capitella capitata													1	1						1							1					
OLIGOCHAETA												1										1										
Corophium volutator		1									1										1	2	2	3		1					1	
Cerastoderma edule	2	2	1			1	2		2	3	2	5	3	7	3	2	3	1	1	1	1	1			2		1			4		1
Macoma balthica								1		1	1						3													1		
Venus sp.																																

SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Pygospio elegans (adults)	10	6	3	5	3	4	8	5	7	12	7	8	4	4	3	2	1	7	10	7	14	6	2	2	5	6	7	3	11	13	3	4
with embryos	1									1								1	1	1	2						1					
with hunchback larvae																																
with mature larvae							1										1															
P elegans (new recruits)	2		1	1	1	4	2	1	2	3	2	2	3	2	1	1		1		3	1	2	1	1	1	1	3	1	2	2		4
Eteone cf flava									1				2			1	1	1	1		1									1		
Anaitides mucosa																																
Glycera tridactyla																																
Hediste diversicolor																																
Nephtys hombergii																					1											
Polydora cornuta	1	2	1																1		1		1		1		1	1		2		
Spio martinensis																																
Spiophanes bombyx																																
Streblospio benedicti																																
Chaetozone sp																																
Capitella capitata																	1		1									1				
OLIGOCHAETA			2		1				1		1				1							1		1	1	1						
Corophium volutator		3	2		1						1		1	2	1	2			1	1	1							1		1		
Cerastoderma edule			1				1		1	3	2	1	1	1		1	3	2	3	3	2	3		3		1				1	1	2
Macoma balthica									1						2						1											
Venus sp.																																

August 1997,
replicates 1-3

SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Pygospio elegans (adults)	9	5	5	10	8	6	7	6	8	6	7	6	3	4	3	3	2	5	10	10	5	0	5	6	6	9	7	5	6	7	11	12
with embryos	1		1			1																										
with hunchback larvae																																
with mature larvae																																
P elegans (new recruits)	2	3	4	1		4	2	3	3	1	3	2		1	1	3		2		3			4		2	2	3				2	
Eteone cf flava	1		1				1				2	1													1	1				2		
Anaitides mucosa											1																					
Glycera tridactyla																																
Hediste diversicolor																																
Nephtys hombergii			1		1				1								1	1														
Polydora cornuta																																
Spio martinensis																																
Spiophanes bombyx																								1								
Streblospio benedicti										1							1	1		1		1							1			
Chaetozone sp.																																
Capitella capitata		2	3	2	2	2	6	3	1		1	5	5	2	3	1	1	1	1	2		3	4	4	2				2	5		
OLIGOCHAETA	3		1		1	1				2		1		2	1	1				1		2		1				1		1		
Corophium volutator																																
Cerastoderma edule															1						2											
Macoma balthica	1		1											2			1	1			1			1				1				
Venus sp																																

SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Pygospio elegans (adults)	8	0	6	1	7	2	6	7	8	9	10	5	4	3	7	7	6	9	2	9	5	2	9	6	3	5	4	7	7	6	7	7
with embryos																																
with hunchback larvae																																
with mature larvae																																
P elegans (new recruits)	5	1	2	3	5		3	2		1	3	4	1	4		2	4	8	1	1	1	3	3	2			2		3	1		4
Eteone cf flava					1							1		1			1	1					2				1	2				
Anaitides mucosa																																
Glycera tridactyla																																
Hediste diversicolor																																
Nephtys hombergii													1																			
Polydora cornuta	2	2			1		2		1				1					1	1	1			1	2				1		1		
Spio martinensis																																
Spiophanes bombyx																																
Streblospio benedicti							1			2																						1
Chaetozone sp																																
Capitella capitata	19	10	5	5	7	9	2					1			4	1							1		1	2			3	1	1	
OLIGOCHAETA		1				1																										1
Corophium volutator	1	1		1			1					2			4	1	3	1	1	3	4	1	3	5	2	5		1	2	2	1	4
Cerastoderma edule										1	1						1			2						1		2				
Macoma balthica	2				1	1		1		1	1		2	2	2		1										1			1		
Venus sp.																																

SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Pygospio elegans (adults)	3	5	6	5	3	2	3	3	2	3	3	0	4	4	7	2	4	3	3	2	6	9	3	4	2	2	6	1	2	11	5	3
with embryos																																
with hunchback larvae																																
with mature larvae																																
P elegans (new recruits)		2	1		1		2	1	1	1	1		2		2				1	1	4	1		1		3	2	2	2	7	7	
Eteone cf flava		2																1				1	1				1	1				1
Anaitides mucosa																																
Glycera tridactyla														1																		
Hediste diversicolor																																
Nephtys hombergii																													1			
Polydora cornuta					1									1			1						2		1		1			1		
Spio martinensis																																
Spiophanes bombyx																																
Streblospio benedicti		1														1						1							1			
Chaetozone sp																																
Capitella capitata		3	1	2				1		2		1	5	1	2	1		3	1			1	1	1			1	1	1	1	1	
OLIGOCHAETA	1			2					1						1						1	2										
Corophium volutator	1	1	3		1					3	5	1	4	10	2				1		2	5										
Cerastoderma edule	3		1	2	1	2	2		2		2	2		1		2		1		2	1	2			2	1	1	2	2	2	2	1
Macoma balthica	1											1					2		1					2		1		1		1		3
Venus sp																																

October 1997,
replicates 1-3

SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Pygospio elegans (adults)	12	5	6	21	9	9	5	10	7	14	13	9	8	11	5	5	7	5	9	12	6	9	2	1	9	10	10	7	9	6	5	5
with embryos		2		3			1	1					2							1		1			1		1		2			
with hunchback larvae																																
with mature larvae																																
P elegans (new recruits)	2	5	4	10	[illegible]	8	1	6	6	5	4	4	1	3	6	5	6	6	7	4	3	9	8	1	10	6	9	7	8	6	4	3
Eteone cf flava				1							1					1	1		1				1	1	1							
Anaitides mucosa	1				1																											
Glycera tridactyla																																
Hediste diversicolor																																
Nephtys hombergii															1									1								
Polydora cornuta	1	1												1					2											1		
Spio martinensis																																
Spiophanes bombyx														1																		
Streblospio benedicti									1					1				1									1					
Chaetozone sp																																
Capitella capitata	1	3	2		3	3		3	5	2		3		4	2	1	1	4	4	2	4	1	1	4	2	1	4	2	1		5	10
OLIGOCHAETA		1				1			1					2	3		1						2									
Corophium volutator											1						1															2
Cerastoderma edule										2																				2	1	
Macoma balthica		1	2	1	1			1															1		1					1		
Venus sp.																																

SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Pygospio elegans (adults)	8	10	7	7	6	6	13	8	12	5	4	10	5	8	12	4	8	13	17	10	24	12	7	11	7	5	6	5	6	12	12	5
with embryos		1			1	1		1	2		1						1	1	1		1	1	3		1							
with hunchback larvae																																
with mature larvae																																
P. elegans (new recruits)	3	4	1	6	3	1	3	8	1	4	3	5	2	4	3	1	3	1	4	4	1	3	2	7	3	2	1	2	1	5	4	7
Eteone cf flava		1	1		1	1		1		1		1						1	1	1					1		2		1			
Anaitides mucosa																																
Glycera tridactyla																																
Hediste diversicolor																																
Nephtys hombergii													1																			
Polydora cornuta	1	1	1						1		1		2	1			1	1	3	1	1	3								1	3	
Spio martinensis																																
Spiophanes bombyx																																
Streblospio benedicti		1						1						1																1	1	
Chaetozone sp.																																
Capitella capitata	4	5	2	1	1	3	1	3	1	1	5	1	2	3	1	4	1	2		1	1	4		2	7	4	2	1	2		6	4
OLIGOCHAETA				1											1															1		
Corophium volutator		2	4	2	1	2	2	2	1	5	3	4	2		1		1	2	2	3	1	5	1	1	1	2	4	3	3	1		
Cerastoderma edule											1	1		2			1		2	4	1	2	2			1		1	2		1	1
Macoma balthica	3		2		1				2				1			1	1	1		1	4	1	1		1	3		1	1			
Venus sp.																																

SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Pygospio elegans (adults)	2	5	9	12	11	6	2	5	5	2	7	10	1	9	6	9	4	10	5	14	7	4	8	10	5	8	10	9	6	10	8	6
with embryos	1		2	1	1				1				1	1													1	1				
with hunchback larvae																																
with mature larvae																																
P elegans (new recruits)	4	7	5	2	2	3	2	2	5	5	7	5	2	3	4	9	9	1	1	10	6	5	5	8	12	3	3	9	4	2		1
Eteone cf flava	1		1															1		1		1	2		1	1		1				1
Anaitides mucosa			1	2																												
Glycera tridactyla																																
Hediste diversicolor																																
Nephtys hombergii														1						1												
Polydora cornuta													1																			1
Spio martinensis																																
Spiophanes bombyx			1																											1		
Streblospio benedicti						1											1															
Chaetozone sp																																
Capitella capitata	3	2		5			1	11	3	5	3	1	1	1		2	5	1	3	7	4	3	3	4	3	5	2	3	6	2	3	
OLIGOCHAETA	1														1			1	1	2	1							1				
Corophium volutator								1									1															
Cerastoderma edule	3	2	2			1					1										2	1	1							1		
Macoma balthica				1	1	1							1				2		1					1				1				
Venus sp																																

December 1997,
replicates 1-3

SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Pygospio elegans (adults)	5	4	8	4	9	10	9	8	5	8	14	3	5	7	14	15	8	6	7	6	5	9	5	8	12	2	4	11	14	13	10	13
with embryos	2	1	1	3	1	6	1	1	4	3		3	1	3	2	3	1	1	2		1			1	3	1	1	2	7	2	1	3
with hunchback larvae																																
with mature larvae	3		2		3		1	1	1	2	1	2		1	2	1		2				2		1			1	1		3	1	3
P elegans (new recruits)	3	6	4	3	5	7	4	4	5	5	6	6	4	3	1	7	2	1	14	8	7	2	5	2	3	2	3	3	3	6	5	6
Eteone cf flava		1			1									1							1							1				1
Anaitides mucosa												1				1			1													
Glycera tridactyla																																
Hediste diversicolor																																
Nephtys hombergii					1				1																							
Polydora cornuta																												1				1
Spio martinensis																																
Spiophanes bombyx																														1		
Streblospio benedicti	1																1			1						1	1					
Chaetozone sp.																																
Capitella capitata	4	1	2	7	6	10	3	1	3		1	4	1	2	3	1	2	1	1	5		2	2		2	2	6	14	2	6		10
OLIGOCHAETA		1								1		1																				
Corophium volutator							3			1	3				2							1		1	1			1		1	4	
Cerastoderma edule				1		1			2		2			1		1		2		1			1									
Macoma balthica							1										1		2								1				1	
Venus sp																																

SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Pygospio elegans (adults)	5	7	3	4	10	9	3	6	13	11	7	7	11	5	4	6	0	13	15	7	5	8	11	12	7	14	3	6	7	11	12	25
with embryos	2	1	1	1	2	2	1	2	3	4	1	3	3	2	3	1		2	3	2	1	2	3		3	4	1	3	1	4	2	2
with hunchback larvae																																
with mature larvae			1		2		1		1	1	1	1	3	1	2	2		2	1	2		2	3		1			1	1	1	1	2
P elegans (new recruits)	2	4	2	3	5	4	4	5	3	8	1	1	2	5	4	2		2	3	4	3	4	6	1	4		9	3	3	4	2	6
Eteone cf flava											1					1	1					1			1	1		1	1	1		
Anaitides mucosa									1			1		1												1			1			
Glycera tridactyla																																
Hediste diversicolor																																
Nephtys hombergii		1							1												1											
Polydora cornuta																						1										
Spio martinensis																																
Spiophanes bombyx																																
Streblospio benedicti		1					1																									
Chaetozone sp.																																
Capitella capitata	11	10	5	6	5	7	11	9	7	7	13	7	11	8	5	3	1	3	2	12	3	7	7	3	2	10	14	13	4	7	10	
OLIGOCHAETA	1	1								1				2			1							1				1				
Corophium volutator											1			1	1	1										1					1	
Cerastoderma edule					1							1		1		1		1				1		1								
Macoma balthica	1	1					1							1		1							1	2				1	1			
Venus sp.																																

SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Pygospio elegans (adults)	5	7	10	11	14	11	9	12	13	13	10	8	7	5	8	17	14	11	13	6	10	4	11	13	9	6	7	10	5	10	14	20
with embryos	2	1	3		3		2	3	4	4	1	2		1	2	2	2	2	1		2	1		3	2	1	2	1		1	2	2
with hunchback larvae																																
with mature larvae	2		1			2	1		1					2	1	1	2	1	1	1	1		2					1		1	1	2
P elegans (new recruits)	3	5	9	6	5	2	1	1	3	4	3	7	7	1	2	3	8	1	15	8	3		8	9	3	5	4	5	5	4	3	8
Eteone cf flava					2		2								2			1														
Anaitides mucosa																																1
Glycera tridactyla																																
Hediste diversicolor																																
Nephtys hombergii																																
Polydora cornuta		1			1				1		1	1			2				1	1									1	3		1
Spio martinensis																																
Spiophanes bombyx																																
Streblospio benedicti											1		1	1				1	1	1	1					2				3	1	1
Chaetozone sp																																
Capitella capitata	1	8	4	5	4	1	5	2	2	4	5	6	1	4		1	5	2	7	12	2	5	5	7	5	1	10	10	1	8	11	4
OLIGOCHAETA															1																1	
Corophium volutator						1	1							1				1					1	1	4				1			
Cerastoderma edule								2		1							1		1			1							1	1		1
Macoma balthica	1	2	2	1	3		2	2	2	1	3	1		2	1	2	3	3	1		1				3	2	1	1	2		3	2
Venus sp.																																

February 1998,
replicates 1-3