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Predicting recovery of soft sediment communities following physical disturbance

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Predicting recovery of soft sediment communities following physical disturbance

A thesis presented to the University of Wales for the degree of Doctor of Philosophy

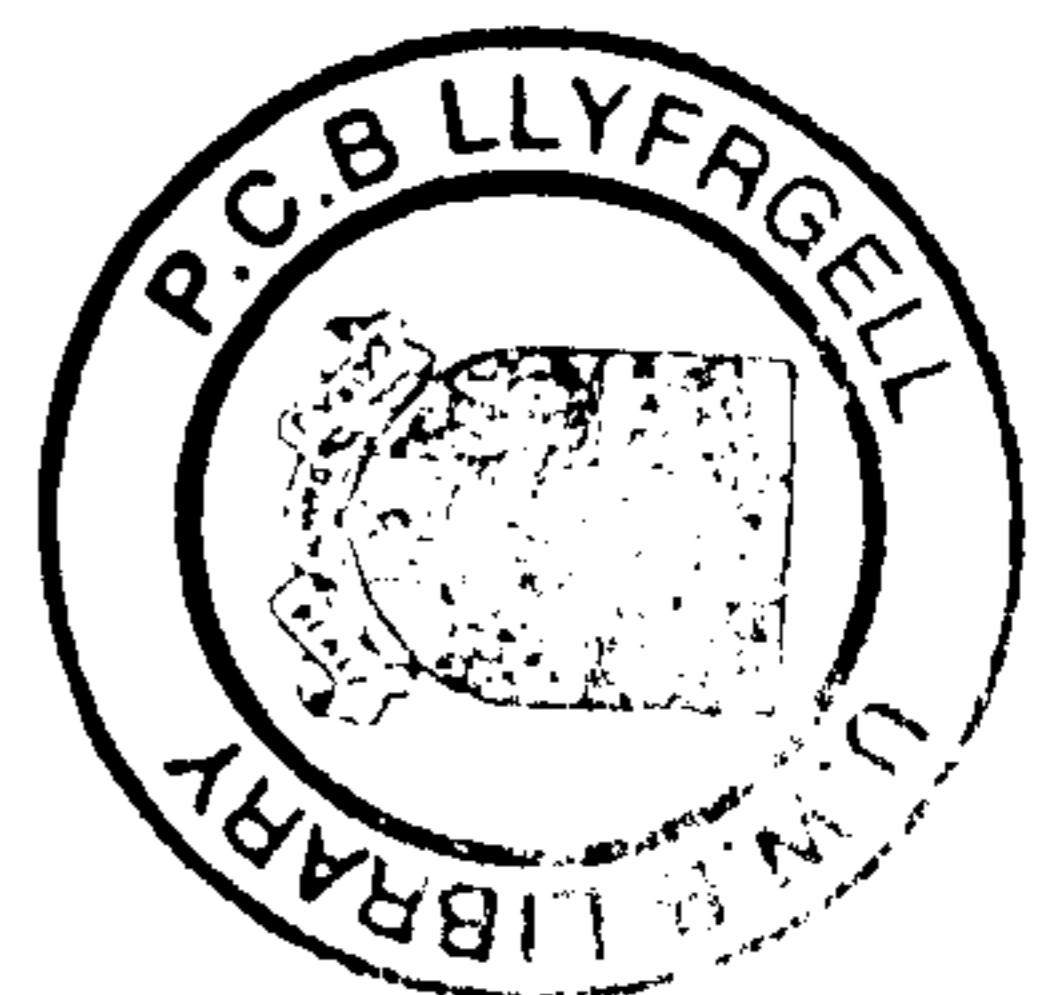
by

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May 2003



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SUMMARY

This study investigated the effects of physical disturbance on intertidal benthic habitats and communities. The aim of the work was to examine the use of physical habitat characteristics as a surrogate for biological recovery as an aid to the management of shallow water marine habitats.

The first field experiment investigated the effects of two intensities of a disturbance treatment on a sandflat habitat and community. Community recovery from the lower intensity treatment was complete after 63 days whereas recovery following from the higher intensity disturbance took at least twice as long. There were no effects of the disturbance detected for any of the measured sediment parameters. Depth of disturbed pits gradually decreased over time and was correlated to benthic community structure.

A comparison of macrofaunal and meiofaunal recovery as part of the same experiment revealed that significant differences existed in disturbed meiofaunal communities 32 days following the disturbance event.

A second field experiment investigated the recovery rates of benthic communities from a range of soft sediment habitats following the application of a uniform disturbance treatment. Communities from clean sand sediments were less negatively impacted and recovered more rapidly following disturbance than muddy sediment communities. No effects of the disturbance treatment were detected for any of the measured sediment parameters. However, the rate of infilling of the disturbed plots could be used to predict the recovery rate of the associated community.

An in situ device for the measurement of sediment properties used in this study is described and its potential for use in ecological studies is discussed.

Measuring the rate of habitat restoration could be an rapid and amenable method for predicting the recovery of intertidal benthic communities from a range of anthropogenic activities that impact upon intertidal areas.

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Chapter 1

Introduction

1. General Introduction

1.1 The importance of soft sediment habitats and communities

The world's oceans cover approximately 70% of the earth's surface and almost 90% of the seabed consists of sediment habitats that range from cohesive clays and muds to coarse gravel beds. Thus, marine soft sediment habitats occupy a higher surface area of the planet than any other habitat. The focus of the research within this thesis is the soft sediment habitats and communities of intertidal areas, which provide an important ecological and socio-economic resource (Costanza et al., 1997) and play a key role in flood defence, maintenance of seawater quality and the support of coastal and marine food chains (Crooks and Turner, 1999). Intertidal soft sediment habitats are an important source of invertebrate food for birds and fish (Ferns et al., 2000; Raffaelli and Milne, 1987) and additionally provide juvenile fish habitat (Jackson et al., 2001). These areas are also an important site for human activities including collection of shellfish species (e.g. Kaiser et al., 2001), aquaculture (e.g. Spencer et al., 1997) and recreation (May, 1996).

The significance of physical disturbance

Physical disturbance is an important process that determines temporal and spatial heterogeneity in both animal and plant communities (Sousa, 1984). In an ecological context, a disturbance has been defined as 'any discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substratum availability, or the physical environment' (Pickett and White, 1985). Some organisms actually depend on disturbance to complete their life cycles and this has been well demonstrated in certain forest ecosystems where the extreme temperatures of forest fires are required for the successful germination of the seeds of some species (e.g. Vogl, 1973). Barry (1989) suggested an analogy in the marine environment for a species of sabellid worm that forms dense aggregations in soft sediments. This worm exhibits a spawning response to damage after the occurrence of storms that directly impinge upon reefs of this species. This adaptation allows the worm to maximise reproductive effort when adult mortality is high and therefore there is a greater probability of the successful recruitment of juveniles as a result of reduced intra-specific competition.

The intermediate disturbance hypothesis (Connell, 1978; Horn, 1975; Wilkinson, 1999) indicates the importance of disturbance in maintaining species diversity by the prevention of competitive exclusion by dominant species within an assemblage. Fig. 1.1 illustrates the intermediate disturbance hypothesis concept where an increase in

diversity can occur with both decreasing and increasing levels of disturbance, such that communities subject to very high levels of disturbance will exhibit an increase in diversity when disturbance decreases, whilst communities subject to very low levels of disturbance will also exhibit an increase in diversity where disturbance increases sufficiently to prevent competitive exclusion of certain taxa by more dominant species. Thus an understanding of the background levels of disturbance to which the assemblage is usually subject will allow the prediction of the likely effects on diversity of a subsequent change in disturbance regime.

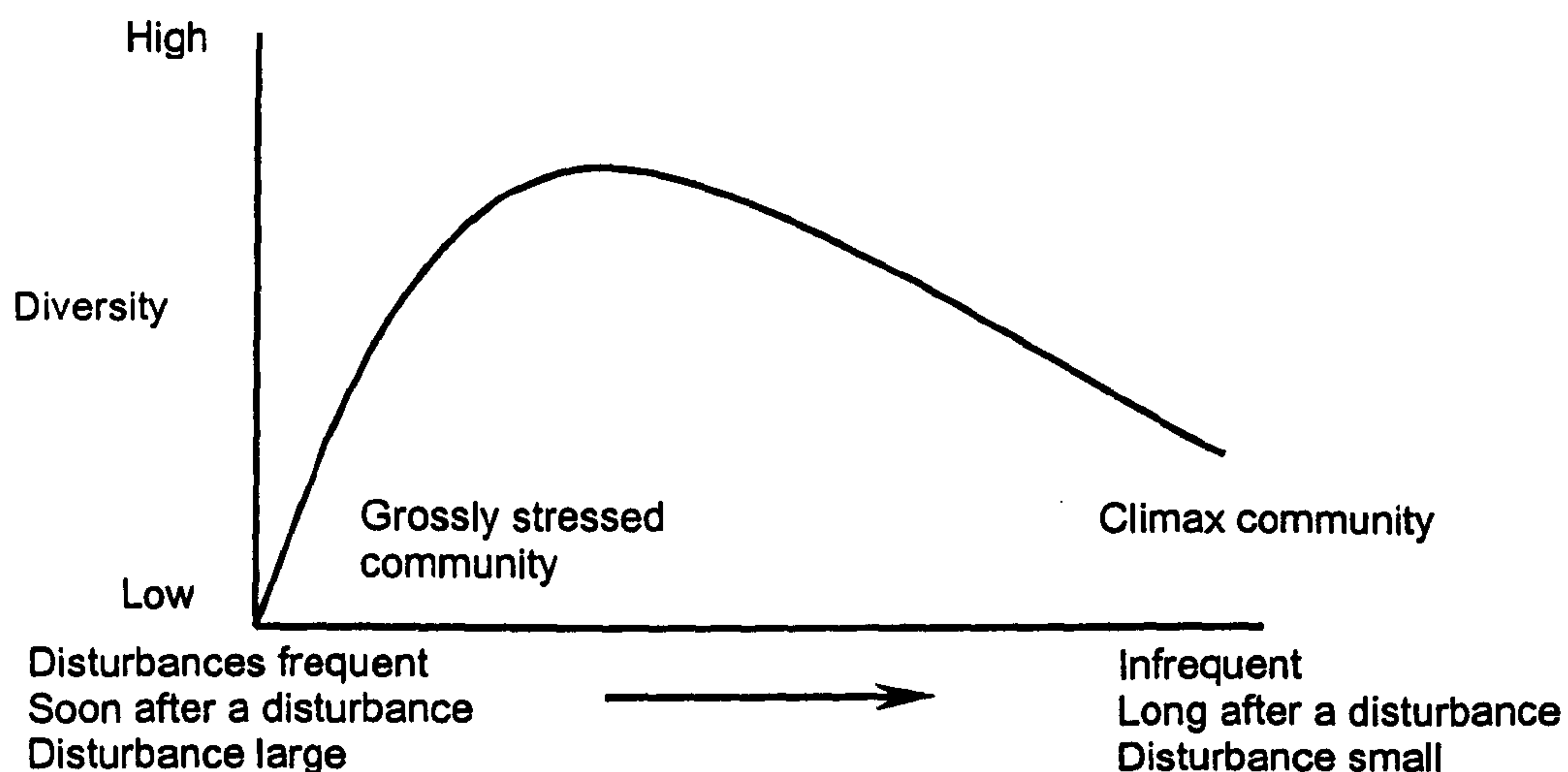


Figure 1.1: The intermediate disturbance hypothesis. Assemblages subject to very high levels of disturbance exhibit a low diversity due to persistent disruption and mortality of the community. As disturbance decreases community diversity increases to a peak at intermediate disturbance levels. Following this point, decrease in disturbance levels allows the competitive exclusion of certain taxa by more dominant species within the assemblage thus decreasing overall diversity. (adapted from various sources).

Spatial and temporal heterogeneity in the disturbance regime results in a mosaic of patches within a habitat, where communities are at different stages of succession (Grassle and Sanders, 1973). Thus, physical disturbance is a key factor controlling the spatial and temporal composition of marine soft sediment communities (Hall, 1994; Hall et al., 1994; Probert, 1984; Thrush et al., 1996), which are subject to a range of natural and anthropogenic perturbations. Natural abiotic agents of disturbance include storms (e.g. Dobbs and Vosarik, 1983; Posey et al., 1996), wave disturbance (Grant, 1983; Oliver et al., 1980), glacial scouring (Gordon and

Desplanques, 1983; Peck et al., 1999); anthropogenic sources of physical disturbance include bottom fishing with towed fishing gear (Hall and Harding, 1997; Kaiser, 1998), bait harvesting (e.g. Brown and Wilson, 1997; McClusky et al., 1983), hydrocarbon exploration, beach recharge or nourishment (Gorzelay and Nelson, 1987), pipe and cable laying (e.g. Knott et al., 1997), dumping of waste material (e.g. Boyd et al., 2000), and aggregate extraction (e.g. Kenny and Rees, 1996). In addition, biological disturbances occur as a result of processes such as foraging by predators (Hall et al., 1991; Oliver and Slattery, 1985), bioturbation (Grant, 1983; Rhoads, 1967; Widdicombe et al., 2000) and other biotic interactions that cause changes to habitat properties such as sediment stability and permeability, and communities (Jones and Jago, 1993; Thrush et al., 1996).

1.3 The effects of physical disturbance

1.3.1 Infauna

The effects of physical disturbance in marine soft sediment environments are usually manifested as the partial or sometimes complete defaunation of disturbed patches through direct mortality and physical damage, as well as through the displacement of species to nearby unfavourable habitats and an increased vulnerability to predation (Hall, 1994; Ramsay et al., 1998). In addition, the resuspension and subsequent deposition of fine sediments to the sea bed following a disturbance can lead to smothering of adjacent habitats (McCall, 1977), which may lead to further mortality in areas not directly impacted by the original disturbance (Theil and Schriever, 1990). Positive effects of disturbance have also been described, including the exposure of buried organic matter and increasing food availability for deposit feeders (Miller et al., 1984; Grant et al., 1990).

The impacts on, and subsequent response of infaunal communities to physical disturbance events is currently the focus of research in terms of the management of anthropogenic activities in the marine environment. The key requirement for management is to understand what levels of human disturbance are sustainable. To achieve this goal it is necessary to understand the processes that affect infaunal community recovery. For the purposes of this thesis, recovery is defined as having occurred when the community structure of the disturbed assemblage is not significantly different to that of an adjacent, undisturbed community. Following a perturbation, and assuming that the original habitat has not been entirely altered (e.g. the removal of a reef structure), the benthic community will undergo a period of recovery. The time scale of this recovery is dependent on a number of factors

including, for example, the scale of the disturbance. Small disturbed areas will tend to recover relatively quickly whilst larger areas will take longer to recover (see Fig. 1.2). Additionally, the frequency, intensity and the time of year of impact will influence recovery and different components of the biota may recover at different rates. For example, microbial biomass has been shown to recover to ambient levels only 8 hours following a physical disturbance treatment (Findlay et al., 1990) whilst studies of meiofaunal and macrofaunal communities indicate that recovery may take anything between a few days (Schratzberger and Warwick, 1998; Hall et al., 1990) to several years (Collie et al., 2000; Hall-Spencer and Moore, 2000; Peterson et al., 1987). The length of time taken for the benthic assemblage to achieve recovery may be linked closely to the physical, chemical and biological structure of the associated sediment habitat. Since communities that inhabit different sediment types will be adapted to very different physical regimes, it is generally assumed that communities found in dynamic sandy habitats will recover more quickly following physical disturbance than those found in less energetic muddy environments (Ferns et al., 2000; Kaiser, 1998; Oliver et al., 1980). This seems to be supported by microcosm studies (e.g. Schratzberger and Warwick, 1998) and a meta-analysis of fishing disturbance data indicated a similar pattern of increasing recovery time for communities inhabiting increasingly stable sediments (Collie et al., 2000).

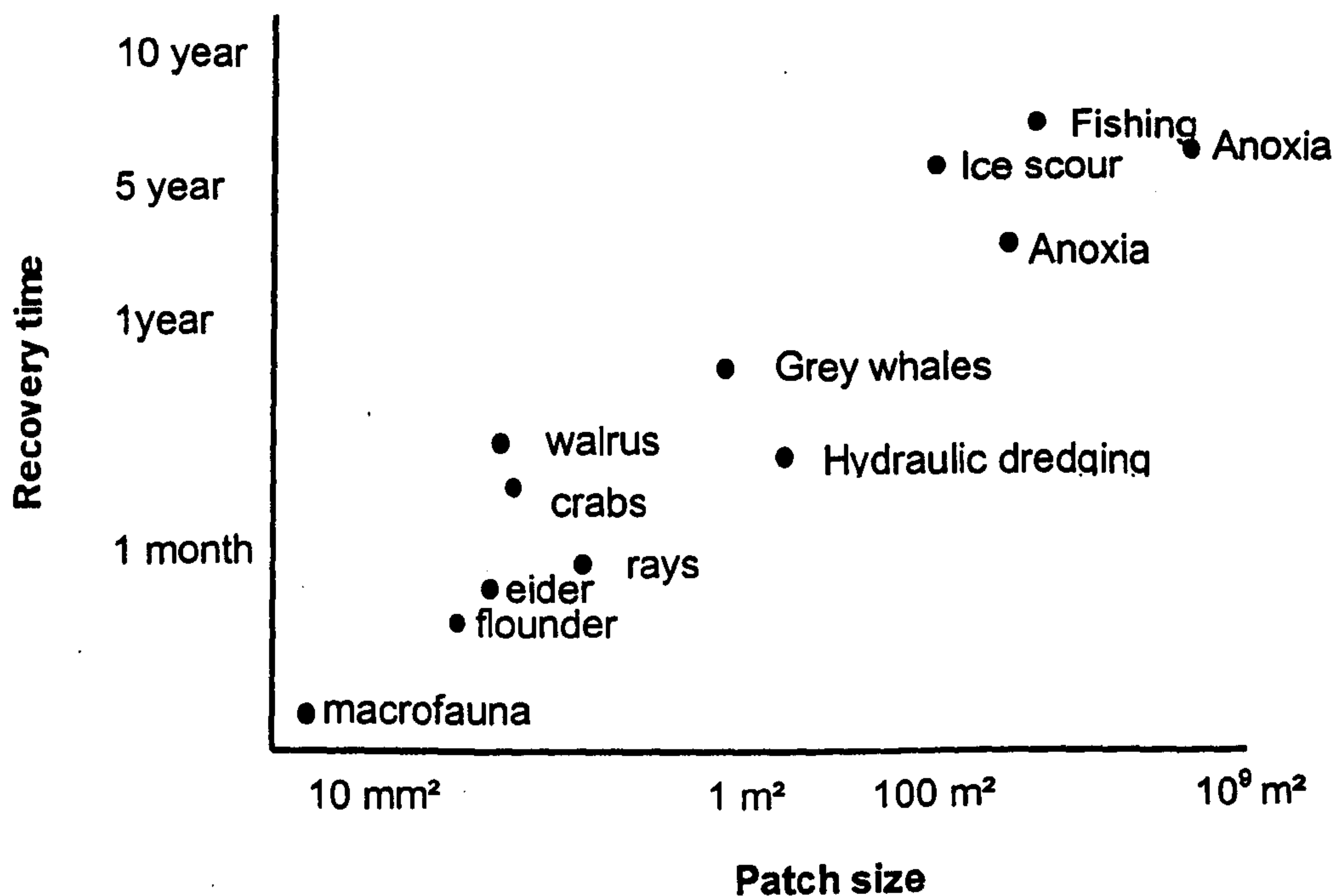


Figure 1.2: Graph summarising recovery times for benthic assemblages following a variety of disturbances over a range of patch sizes illustrating the importance of scale to the recovery rate of benthic communities (adapted from Hall et al., 1994).

Despite the plethora of studies that have investigated the recovery of benthic communities following physical disturbance impacts, drawing general conclusions from such studies is problematic due to the variation between different studies with respect to, for example, habitat type, geographic location, spatial extent of the disturbance, and the time of year of the impact (Collie et al., 2000). Therefore, there is a need for a new approach that would permit a detailed comparison of the effects of a uniform physical disturbance on communities across a range of habitats in order to understand the role of habitat structure in the community recovery process and to facilitate the interpretation of observations from other studies.

1.3.2 Habitats

Physical disturbance results in the homogenisation and resuspension of surface sediments (Schwinghamer et al., 1996; Palanques et al., 2001). In addition, disturbance can change surface roughness and microtopographic relief of the seabed (Auster et al., 1996; Jennings et al., 2001; Smith et al., 2003) and cause larger topographical changes (i.e. the formation of pits and furrows) that can alter near bed hydrodynamics (Probert, 1984) and affect the deposition of particles, such as organic matter and benthic invertebrate larvae (Thrush et al., 1992). When fine particulate material is deposited within disturbed pits and furrows, different sediment characteristics to those of the adjacent substrate may arise within these areas as they infill over time (van der Veer et al., 1985). Severe physical disturbances (e.g. aggregate extraction) may remove surface sediments to uncover substrata that are unfavourable for the settlement of the larvae of the original assemblage of organisms (e.g. Kenny and Rees, 1994).

The mechanical properties of the sediment matrix may be altered following a physical disturbance event. For example, a recent study undertaken by Hauton and Paterson (2003) reported a significant reduction in the shear strength of sediments within the tracks created by a hydraulic suction device commonly used for the collection of shellfish. Disturbance can also result in the disruption of the redox potential discontinuity layer (Nilsson and Rosenberg, 2003; Rosenberg et al., 2003) and can lead to changes to sediment chemistry including the release of ammonium and decreased oxygen concentrations, which have been shown to deter the settlement of invertebrate larvae (Marinelli and Woodin, 2002; Woodin et al., 1998).

1.4 Animal-sediment relationships

The relationship between sediment characteristics and the distribution of infaunal invertebrates has been studied since the beginning of the last century when Petersen (1913) noted that the composition of benthic communities differed among different seabed habitats. Further research led to the suggestion that the substratum was a key factor in determining community distribution when Thorson (1957) put forward his 'parallel level-bottom communities' concept. This concept has lost favour as more recent studies indicate a much greater variability in the animal associations that occur within different sediments which suggests that a number of factors are involved in determining the distribution patterns of benthic infauna (e.g. Snelgrove and Butman, 1994). Nevertheless, at large scales (> 100 m) empirical evidence suggests that clear associations do exist between community structure and abiotic environmental variables (Warwick et al., 1991; Warwick and Uncles, 1980). Yates et al. (1993) found that the close association of sediment characteristics with the densities of invertebrate prey allowed the prediction of densities invertebrate feeding shorebirds in the Wash, east England, based on sediment particle size distribution alone.

In addition to the influence of the physical environment on benthic assemblage structure, physical and chemical properties of soft sediment habitats are strongly influenced by the associated biota (e.g. Daborn et al., 1993). Burrowing organisms may cause an increase in the depth of the Redox Potential Discontinuity (RPD) layer by facilitating the passage of oxygen into deeper sediments. Particle size selection by deposit feeders alters the vertical structure of the sediment and can result in a biogenically graded bed where organism densities are sufficiently high (Rhoads and Stanley, 1965). The overall stability of marine sediments is at least partially related to the presence of meio- and microfauna, many of which produce extracellular polymeric substances (EPS) that bind sediments together (Hoagland, 1993; Krumbein et al., 1994) and thus can strongly influence the erodability and stability of surface sediments (Daborn et al., 1993; Underwood and Paterson, 1993). For example, Grant and Gust (1987) found that mats of purple sulphur bacteria increased the erosion threshold of sediment cores up to 5 times that of sterile control cores.

The different behaviours and life styles of infaunal organisms may have contrasting effects on sediment properties. Jones and Jago (1993) reported an increase in bed rigidity within dense beds of the sedentary worm, *Lanice conchilega*, which constructs stiff tubes made of sand grains, whilst the presence of the actively

burrowing deposit feeders *Arenicola marina* and *Corophium arenarium* reduced bed rigidity. Tubicolous and sedentary organisms may increase sediment stability (e.g. Thrush et al., 1996) whilst high densities of deposit feeding organisms rework sediments and may increase sediment water content and loosen the sedimentary fabric (e.g. Widdows et al., 2000).

1.5 Aims of the current study

Traditional methods for studying the post-disturbance recovery of soft sediment ecosystems involve analyses of large numbers of samples of macrofaunal and meiofaunal assemblages. Such work is time consuming and labour intensive (Olsgard and Somerfield, 2000) and requires identification skills that are often lacking (Maurer, 2000). In addition the effort required for this type of study may mean that important aspects such as replication and therefore experimental power, or the assessment of different community attributes, are not considered in sufficient detail (Elliott, 1993). A more amenable metric for assessing the longevity of the effects of disturbances would therefore be a very useful management tool. The latter could be achieved if the proposed metric provided a predictive basis for the assessment of biological recovery (as defined in 1.3.1).

The aims of the current study were to quantify the impacts of physical disturbance on soft sediment habitats and intertidal infaunal communities and test whether any habitat parameters could be used as a surrogate metric that related adequately to the recovery process of the infaunal assemblage. The work detailed within this thesis may be divided into two major experimental components. All experimental work was undertaken within the Menai Strait, North Wales (53°11'.3N, 4°12'.9W), which provided sufficient soft-sediment habitat diversity for the purposes of this study (Figure 1.3). Initially an investigation of the response of the macrofaunal community at one site (a sheltered sandflat) to two intensities of a physical disturbance treatment was carried out, which focused on the differences in the responses of the habitat and biota to different intensities of disturbance, and the degree to which changes in physical parameters could be used as a surrogate for biological recovery (Chapter 2). An analysis of the response of the macrofaunal and meiofaunal components of this sand flat community was also performed (Chapter 3) to determine the relative importance of physical disturbance to different components of a benthic assemblage. Although numerous studies have investigated the responses of one of these components (e.g. Schratzberger and Warwick, 1998; Hall and Harding, 1997), few

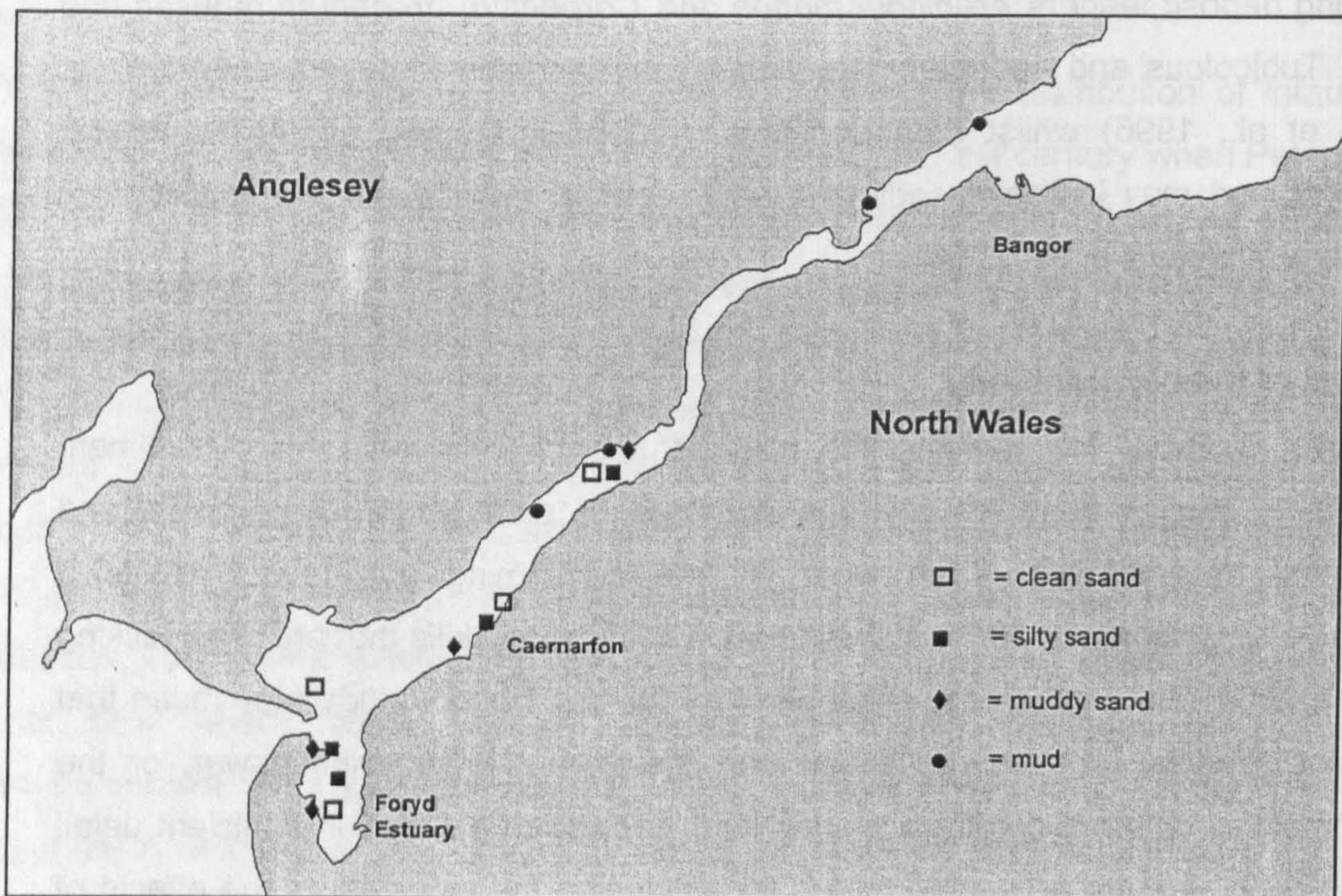


Figure 1.3: The position, and basic sediment description, of all experimental sites along the Menai Strait.

have directly compared the two simultaneously, although it is generally assumed that meiofaunal recovery will be quicker than macrofaunal recovery (Schratzberger and Jennings, 2002). Having investigated the impacts of the application of two intensities of disturbance within one habitat, the second major experimental component consisted of an investigation of the responses of benthic communities from a range of different soft-sediment types to a uniform physical disturbance treatment. A device to measure sediment properties *in situ* was designed for use in this experiment, and its utility in the measurement of appropriate sediment parameters and relationship to community metrics is investigated in Chapter 4. The relationship between the response of the habitat and the concomitant response of the biological components to the physical disturbance treatment is investigated in Chapter 5 with the aim of predicting the recovery rates of the benthic community using aspects of the physical environment. Chapter 6 includes a detailed analysis of the biological response of single species and functional groups of the disturbed assemblages from the different sediment types. This chapter focuses on the relative importance of biological factors (adaptations/behaviours of the community) and abiotic factors (local hydrodynamic regime) in determining the rate of recovery of the disturbed community. The general

discussion (Chapter 7) summarises the findings of this thesis and provides suggestions for future work.

This thesis is presented in the form of papers prepared for scientific publication. As such, while every effort has been made to avoid repetition between the chapters, some overlap is inevitable when common methodologies or the same experimental plots have been used for different components of the study.

The following chapters have been published or submitted for publication:

Chapter 2 : Dernie, K. M., Kaiser, M. J., Richardson, E. A. and Warwick, R. M. (2003). Recovery of soft sediment habitats and communities following physical disturbance. *Journal of Experimental Biology and Ecology* **285-286**: 415-434.

Chapter 3: Submitted to the Journal of Experimental Marine Biology and Ecology.

Chapter 4: Submitted to the Journal of Experimental Marine Biology and Ecology.

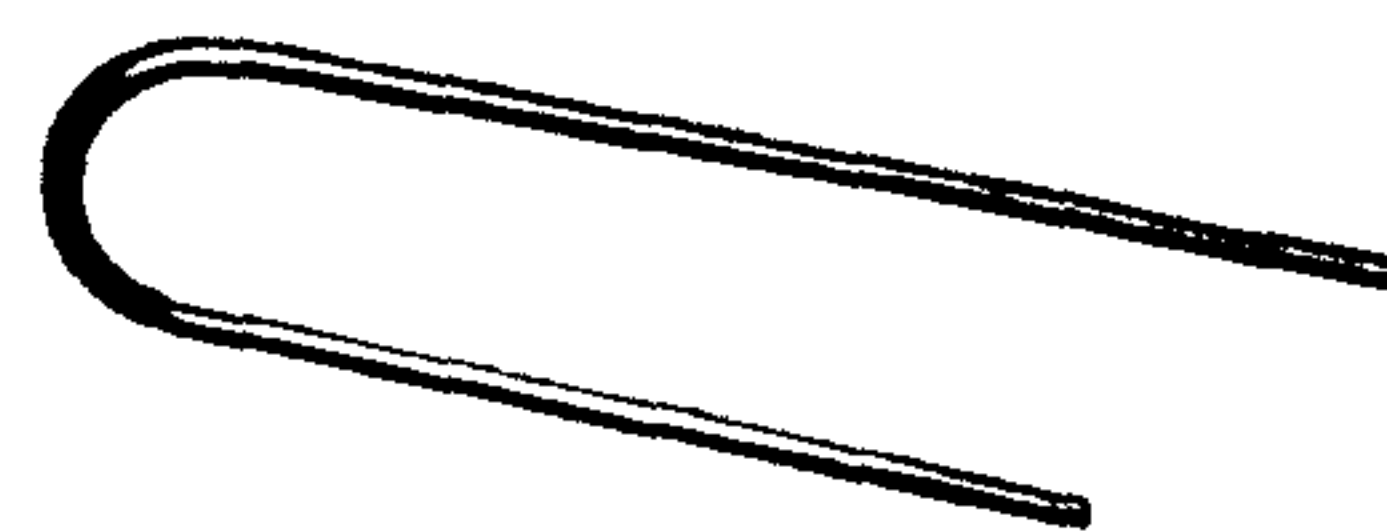
Chapter 5: Accepted for publication by the Journal of Animal Ecology.

Chapter 6: Submitted to Journal of Experimental Marine Biology and Ecology.

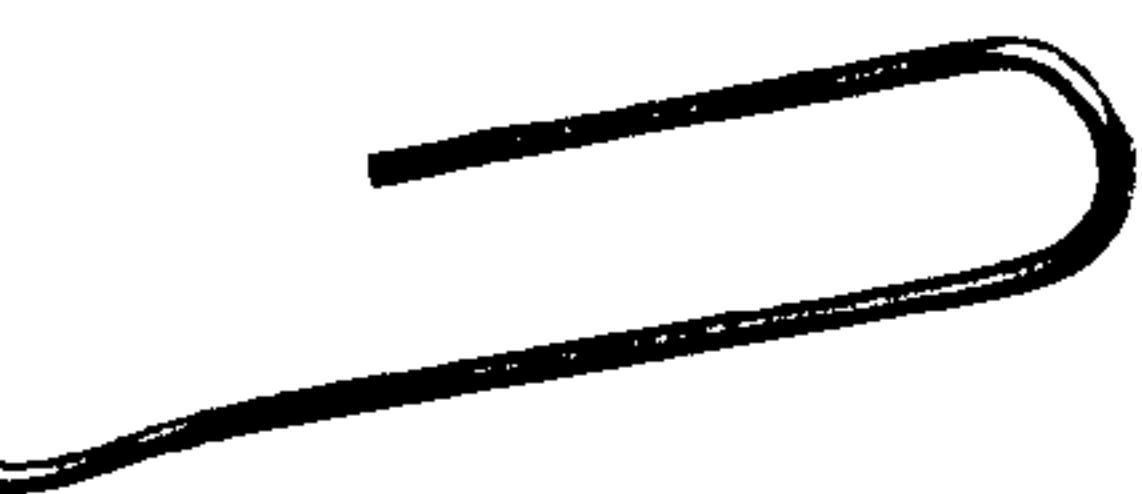
Chapter 2

Recovery of a sandflat habitat and community following different intensities of physical disturbance

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Chapter 3

➤ comparison of the macrofaunal and meiofaunal response to physical disturbance

3.0 Abstract

Physical disturbance is an important component in the regulation of benthic community structure. Although the benthic environment is subject to a range of natural physical disturbances (e.g. tidal scouring and foraging activities) there is growing concern about the effects of anthropogenic physical disturbances on the dynamics of soft sediment infaunal communities. Many studies of the effects of man-made impacts on benthic communities have been restricted to the macrofaunal components of the benthos. However, although the standing stock biomass of meiofauna is lower than that of macrofauna, the high turnover of meiofaunal organisms results in a higher productivity. Assessing the impacts of physical disturbance on meiofaunal communities is therefore key to our understanding of the effect of anthropogenic disturbances on the functioning of benthic assemblages. This chapter describes an experiment that investigated the effects of physical disturbance on the macrofaunal and meiofaunal (nematode) components of an intertidal sand flat assemblage. Both macrofaunal and meiofaunal communities exhibited significantly lower abundances, species richness, evenness and Shannon Wiener diversity following the disturbance treatment. Although the macrofaunal community showed a more negative response to the disturbance than the meiofaunal community, there were significant differences in assemblage structure for both components of the biota for at least 32 days after the disturbance. This study highlights the need to further investigate the effects of physical disturbances on all components of the benthos in order to fully understand the effects of anthropogenic physical disturbances on important benthic processes.

3.1 Introduction

Physical disturbance is a key factor in structuring marine benthic communities (e.g. Hall, 1994). Soft sediment habitats are subject to numerous natural disturbances including tidal scouring and currents, storms and the foraging activities of a variety of organisms (e.g. Oliver and Slattery, 1985; Austen et al, 1998). Physical disturbance to the seabed also occurs as a result of various anthropogenic activities including bottom fishing (Jennings and Kaiser, 1998; Hall and Harding, 1997) and aggregate extraction (Kenny and Rees, 1996). Such disturbance events result in the displacement, damage or emigration of those organisms living within the sediment matrix, and usually result in reduced abundances of organisms and changes to community structure (Hall, 1994). The benthic assemblage may subsequently undergo a period of recovery through a variety of processes including larval and post larval settlement, the temporal extent of which will be dependent on, for instance, habitat type and the intensity and spatial scale of the initial disturbance (Smith and Brumsickle, 1989; Thrush et al., 1995).

The benthic fauna of soft-sediment communities is usually considered under two major size classes: macrofauna and meiofauna. Macrofauna are defined as those organisms that are retained on a 500 μm mesh sieve. Intertidal soft sediments commonly support a fairly low diversity of macrofauna, though certain species may be found in very high abundances. Meiofauna are defined as those organisms that will pass through a 500 μm mesh sieve but are retained on meshes of 40 – 63 μm (Higgins and Thiel, 1988). The meiofaunal component of the soft sediment benthos is usually dominated by nematodes, which may make up between 60-90% of the number of taxa within an assemblage (Coull, 1999). In addition, meiofauna tend to have significantly higher species diversity than the macrofauna. A typical intertidal sand flat may support around 100 species of nematodes alone (Warwick and Platt, 1983), whilst the concomitant macrofaunal community is likely to consist of between 10-20 species of all taxa.

Studies that have investigated processes within benthic assemblages have tended to be restricted to the consideration of either the meiofaunal or the macrofaunal component of the benthos, rarely both (but see Warwick et al., 1990; Somerfield et al., 1995). The temporal or spatial scale of the process under investigation may determine the focus on different components of the benthos. For example meiofauna are the ideal subjects for manipulative laboratory experiments due to their high

diversity, small size and hence short generation times (Warwick, 1993). Conversely, macrofauna are more difficult to maintain for use in laboratory studies, but are commonly the subject of manipulative field experiments. The utility of meiofauna in the study of community responses to pollution is well recognised (see Coull and Chandler, 1992). However, taxonomic expertise in the identification of soft sediment macrofauna is more widespread than for the identification of meiofaunal organisms, which may be a significant factor in the choice of subject in many studies. Nevertheless, studies that purport to examine community responses to some form of experimental or natural gradient omit major components of that community if only one subset of the fauna is examined (e.g. Dernie et al., 2002).

There is growing concern regarding the effects of anthropogenic disturbances such as bottom fishing activities on soft sediment benthic communities. This has led to numerous studies that have investigated the impacts of such disturbances on benthic assemblage structure and recovery processes (Hall and Harding, 1997; Jennings and Kaiser, 1998; Collie et al., 2000; Kaiser et al., 2002). Nevertheless, many of these studies have been restricted to the response of the macrofaunal assemblage (but see Schratzberger and Jennings, 2002), largely as a result of their importance as prey for species at higher trophic levels and concerns relating to declines in their abundance and diversity as a conservation issue. However, due to their high turnover rates, meiofaunal communities make a significantly higher contribution towards carbon production than macrofauna (Warwick and Price, 1979), thus it is of key importance to assess the impacts of anthropogenic physical disturbances on this component of the benthos.

Meiofauna have been well studied in terms of their response to bioturbation as an agent of natural physical disturbance and hence determinant of community diversity (e.g. Thistle, 1980; Austen et al., 1998; Warwick et al., 1986; Warwick et al., 1990). Microcosm experiments have shown that muddy sediment nematode assemblages are less resilient to physical disturbances than those from sandy habitats (Schratzberger and Warwick, 1998). Recent research that examined the effects of trawling disturbance on meiofaunal communities produced conflicting results (Schratzberger et al., 2002; Schratzberger and Jennings, 2002). Whilst one experimental study was unable to detect changes to nematode diversity or biomass following beam trawling disturbance (Schratzberger et al., 2002), a study on real fishing grounds found significantly lower diversity in nematode communities in highly trawled areas in the North Sea (Schratzberger and Jennings, 2002). Thus, there is a

pressing need to obtain robust experimental field data that addresses the impacts of physical disturbances on meiofaunal assemblages.

The response of meiofauna and macrofauna to anthropogenic disturbances may be expected to differ, yet there are very few studies that directly compare the effects of perturbative activities on both components of the biota simultaneously (but see Warwick et al., 1990; Somerfield et al., 1995). It is pertinent to assess both the magnitude of the initial response of macrofauna and meiofauna to a given disturbance and the rates at which the different components of the community may recover from such disturbances. Thus, in the present study, a disturbance experiment was undertaken that investigated the initial impact of physical disturbance upon the meiofaunal and macrofaunal components of the benthic assemblage and the subsequent recovery trajectories of the different components of the biota.

3.2 Methods

The study was undertaken at Traeth Melynog, an extensive, sheltered sandflat located to the north of Aber Menai point on the south east of Anglesey (Fig. 3.1).

3.2.1 Field and laboratory work

Five replicate 2 m x 2 m square plots were created for both control and disturbance treatments. Plots were arranged in a Latin square design marked out with bamboo canes with 5 m separating each plot within the experimental area (Fig. 3.1). On day 0 (9th May, 2000) the disturbed treatment plots were dug out to a depth of 10 cm. The sediment removed was deposited approximately 100 m away from the experimental plot. This method of disturbance resulted in the partial defaunation of the plot, the exposure of the underlying sediment and a change to the topography of the bed with the formation of disturbed 'pits'. The following samples were taken from each plot on day 1, 4, 8 and 32 following the disturbance treatment:

- a) **Macrofauna:** Five PVC cores (90mm diameter x 120mm deep) of sediment were taken haphazardly within each replicate treatment and control plot, sieved through a 0.5 mm mesh and macrofaunal invertebrate material retained in the sieve preserved in 4% buffered formalin. Macrofauna were subsequently identified to the lowest possible taxonomic level in the laboratory.
- b) **Meiofauna:** Three 10 mm diameter syringe core samples of sediment were taken to a depth of 3 cm haphazardly within each replicate treatment and control. Samples were preserved in 4% buffered formalin. In the laboratory, samples

were decanted five times onto a 63µm sieve and organisms extracted with Ludox using the procedures of Somerfield and Warwick, (1996). Nematodes (which comprised the dominant meiofaunal taxon) were identified to genus (Warwick and Platt, 1983, 1988).

3.2.2 Statistical Treatment

The data from the samples taken within each plot for each of the macrofaunal and meiofaunal component were amalgamated. This resulted in data for five replicate plots for each treatment/ biotic component, which were used for all subsequent statistical analyses.

3.2.2.1 Univariate analysis

The data for the total number of species, total number of individuals, Margalef's index of species richness, Pielou's index of evenness and the Shannon-Wiener diversity index of meiofaunal and macrofaunal communities in treatment and control plots were plotted to allow a comparison of meiofaunal and macrofaunal community attributes. The effect of the disturbance treatment on the total number of species, total number of individuals, Margalef's index of species richness, Pielou's index of evenness and the Shannon-Wiener diversity index of meiofaunal and macrofaunal communities was analysed using the following repeated measures ANOVA model (Hall and Harding, 1997):

$$y_i(k)_j = \beta_{jk} + \gamma_i(k) + \varepsilon_i(k)_j$$

where

$y_i(k)_j$ = The response of plot i to treatment k at time j

β_{jk} = The effect of treatment k at time j

$\gamma_i(k)$ = The random effect attributable to plot i to treatment k

$\varepsilon_i(k)_j$ = The residual error variation

Since any changes in the composition of the disturbed assemblages occurred against a background of natural fluctuations within control communities, the relative response of disturbed communities in comparison to control communities was also calculated and plotted in order to facilitate the interpretation of our results. This allowed a direct comparison of the magnitude of the response of a variety of diversity measures (number of species, number of individuals, Margalef's index of species richness, Pielou's evenness and Shannon-Wiener diversity) for the macrofaunal and nematode assemblages following the disturbance treatment. By plotting these data

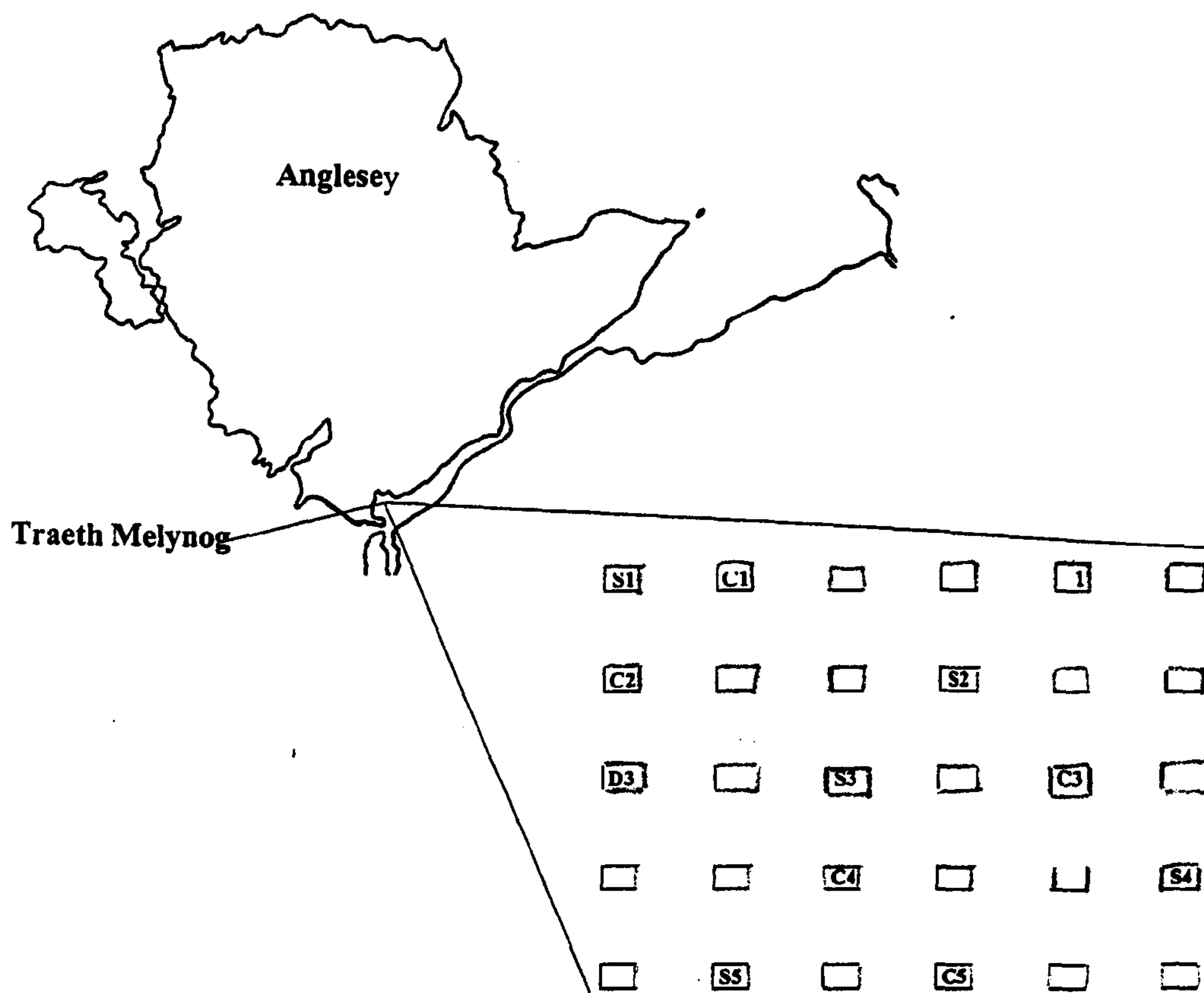


Figure 3.1: Position of experimental site on Anglesey with the inset of the layout of experimental replicate plots at Traeth Melynog. C-control plots; S-disturbed plots.

with 2 SE of the mean, it is possible to determine on which dates there were significant differences between disturbed and control communities, since error bars will cross the x-axis (i.e. the line of zero response) when no significant difference occurs. This approach also has the advantage that it is possible to compare the magnitude of response of different community parameters sampled at different levels of sampling effort (e.g. macrofaunal sample volume of 3,817 cm³ vs. meiofaunal sample volume of 45 cm³) for different components of the community. In order to assess the effects of the disturbance treatment on relative species abundances, k-dominance curves were plotted for control and disturbed assemblages on each sampling occasion for both macrofauna and meiofauna.

The six most common nematode taxa were selected for further analysis of abundance data. An initial power analysis indicated that the experimental design had sufficient power to allow a 90 % chance of detecting a 10% change for the following groups: *Microlaimus*, *Bathylaimus*, *Viscosia*, *Odontophora*, *Eleutherolaimus* and *Daptonema*. Although some of these taxa do not represent the numerically most dominant nematodes, they were represented in the meiofaunal assemblage on every sampling date. Repeat measures ANOVA were performed on the $\ln(n+1)$ transformed abundance data and relative abundances were calculated and plotted for each taxonomic group.

3.2.2.2 Multivariate analysis

Multivariate analyses of the data were performed using the PRIMER software (Warwick and Clarke, 1994). Non-metric multidimensional scaling plots were constructed for both the macrofaunal and nematode assemblages using similarity matrices calculated using the Bray-Curtis index of similarity and four-root transformed data. Tests for significant differences between the community composition of control and disturbed plots were performed using *a priori*, one-way analysis of similarities (ANOSIM) tests for each sampling date. ANOSIM tests were also performed on the separate treatments for both meiofauna and macrofauna, to test for the effect of time on benthic community structure.

The extent to which the responses of the meiofaunal and macrofaunal components of the community were concurrent was examined using the RELATE procedure. This test calculates a test statistic, ρ , that indicates the level of correlation between two sets of multivariate community data (in this case the macrofauna and meiofauna) where a value that approaches zero denotes no relationship between the data sets,

and values of ρ that approach 1 indicate that the two patterns are highly similar (Clarke and Warwick, 1994).

3.3 Results

At least 49 different taxa were identified within the nematode assemblages, in comparison to only 32 different species found within the macrofaunal assemblages (Table 3.1). The nematode assemblage had a higher index of Margalef's species richness and Shannon Wiener diversity and additionally showed higher equitability in terms of Pielou's evenness than the macrofaunal community (Table 3.1). Figure 3.2 summarises the effects of the disturbance treatment on species richness, abundance, Margalef's index of species richness, Pielou's index of evenness and the Shannon-Wiener diversity index for both the meiofaunal and macrofaunal component of the community.

Table 3.1: Comparison of macrofaunal and meiofaunal community attributes at Traeth Melynog Values relate to the control community data averaged over the four sampling occasions with \pm standard errors. d = Margalef's index of species richness; J' = Pielou's evenness index, H' = Shannon-Wiener diversity index.

	<i>Meiofauna (nematodes)</i>	<i>Macrofauna</i>
Total taxa identified	49	32
d	2.90 \pm 0.03	2.34 \pm 0.13
J'	0.72 \pm 0.02	0.46 \pm 0.01
H'	2.11 \pm 0.06	1.28 \pm 0.05

Repeat measures ANOVA tests that compared univariate community parameters for differences between control and disturbance treatments revealed a significant reduction in the $\ln(n+1)$ -transformed total numbers of individuals and Pielou's evenness for both the meiofaunal and macrofaunal assemblages in response to the disturbance treatment (Tables 3.2 and 3.3, Fig. 3.2). There was a significant decrease in Shannon-Wiener diversity for the disturbed nematode community, and for the macrofauna in terms of total numbers of species. Interestingly, Margalef's index of species richness was significantly higher in the disturbed nematode communities, but significantly lower in the disturbed macrofaunal communities. For the meiofaunal component, all community attributes showed a significant change over time with the exception of Pielou's evenness. For the macrofaunal component of the community, the $\ln(n+1)$ -transformed total number of individuals, Pielou's

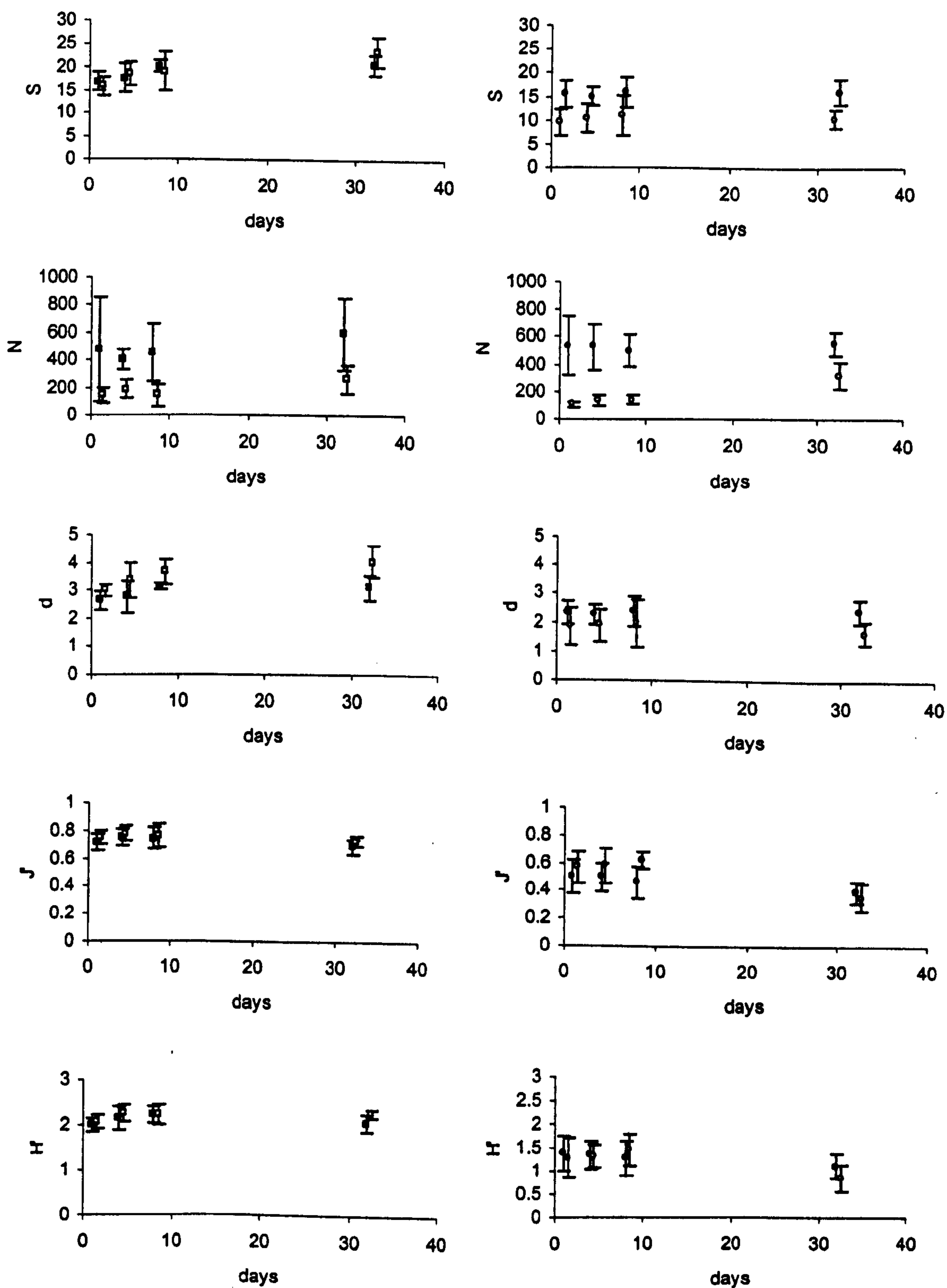


Figure 3.2: The number of species (S), numbers of individuals (N), Margalef's index of species richness (d), Pielou's index of evenness (J') and the Shannon Weiner diversity index (H') for meiofauna (squares) and macrofauna (circles) in control (filled symbols) and disturbed (open symbols) plots over time.

evenness and Shannon-Wiener diversity index changed significantly with time. There were no significant interactions between treatment and time for any of the meiofaunal community attributes. In contrast, there were interactions between treatment and time for the \ln number of individuals, Pielou's evenness and Shannon Wiener diversity within the macrofaunal assemblage. This implies that temporal changes observed in disturbed and control treatments were similar within the meiofaunal component of the community, whereas the response of the macrofaunal community in control and disturbed plots did not follow the same pattern with time.

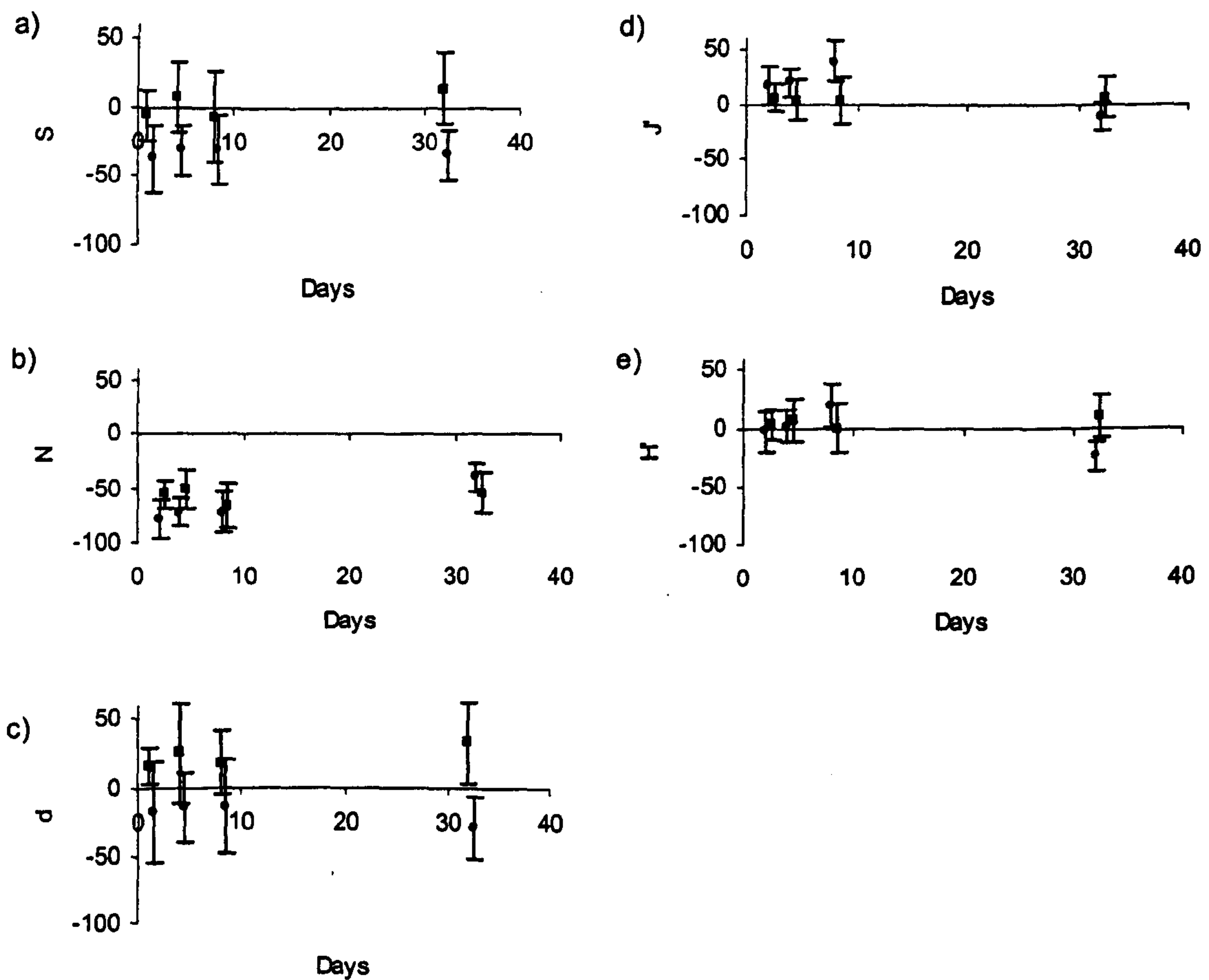


Figure 3.3: Relative abundances of number of species (S), number of individuals (N), Margalef's index of species richness (d), Pielou's evenness (J') and Shannon-Wiener diversity index (H') in disturbed plots compared to control plots for macrofauna (squares) and meiofauna (circles) communities.

The relative responses of the meiofaunal and macrofaunal components of the benthic community to the disturbance treatment were generally more pronounced for

the macrofauna (Fig. 3.3). For example, the initial impact of the disturbance on total numbers of individuals was a reduction of approximately 55% in the nematode community, and 80% in the macrofaunal community (Fig. 3.3b). Figure 3.3c highlights the difference in response of Margalef's index of species richness of the macrofaunal and meiofaunal communities. Figure 3.3 also highlights the lack of any clear 'recovery' (i.e. approach towards a zero response) trend for any of the community attributes within the time-span of the current study.

Table 3.2: Repeated measures ANOVA tables for meiofaunal community attributes.

		<i>df</i>	<i>SS</i>	<i>MS</i>	<i>F</i>	<i>P</i>
No. of species Between plots	Treatment	1	2.1	2.4	0.5	0.485
	Residual	8	41.6	4.7		
Within plots	Day	3	173.8	58.1	12.17	<0.001
	Treatment*day	3	23.1	7.7	1.61	0.21
	Residual	24	110	4.8		
Ln no. individuals Between plots	Treatment	1	9	9	55.6	<0.001
	Residual	8	3.7	0.3		
Within plots	Day	3	1.5	0.5	2.6	0.04
	Treatment*day	3	0.4	0.1	0.8	0.5
	Residual	24	3.3	0.1		
Margalef's index Between plots	Treatment	1	3.86	3.86	27.02	0.001
	Residual	8	1	0.11		
Within plots	Day	3	3.4	1.14	7.95	0.001
	Treatment*day	3	0.41	0.14	0.95	0.44
	Residual	24	3.29	0.14		
Pielou's evenness Between plots	Treatment	1	0.01	0.01	4.56	0.04
	Residual	8	0.015	0.002		
Within plots	Day	3	0.019	0.006	2.82	0.06
	Treatment*day	3	0.003	0.0001	0.05	0.98
	Residual	24	0.052	0.0022		
Shannon-Wiener index Between plots	Treatment	1	0.1	0.11	5.04	0.035
	Residual	8	0.22	0.18		
Within plots	Day	3	0.19	0.065	3.1	0.047
	Treatment*day	3	0.044	0.015	0.7	0.562
	Residual	24	0.48	0.021		

Table 3.3: Repeated measures ANOVA tables for macrofaunal community attributes.

		<i>df</i>	<i>SS</i>	<i>MS</i>	<i>F</i>	<i>P</i>
Number of species Between plots	Treatment	1	280	280	91.23	<0.001
	Residual	8	98.5	12.3		
Within plots	Day	3	3.7	1.2	0.4	0.75
	Treatment*day	3	2.9	0.967	0.31	0.82
	Residual	23	73.9	3.1		
Ln no. individuals Between plots	Treatment	1	14.1	14.1	414.4	<0.001
	Residual	8	0.8	0.1		
Within plots	Day	3	2	0.7	19.4	<0.001
	Treatment*day	3	1.5	0.5	14.67	<0.001
	Residual	24	0.8	0.03		
Margalef's index Between plots	Treatment	1	2.46	2.46	24	<0.001
	Residual	8	3.32	0.42		
Within plots	Day	3	0.15	0.05	0.5	0.69
	Treatment*day	3	0.22	0.07	0.72	0.55
	Residual	24	2.46	0.1		
Pielou's evenness Between plots	Treatment	1	0.045	0.045	17.22	<0.001
	Residual	8	0.15	0.019		
Within plots	Day	3	0.18	0.06	23.11	<0.001
	Treatment day	3	0.062	0.017	6.72	0.002
	Residual	24	0.062	0.003		
Shannon-Wiener Between plots	Treatment	1	0.024	0.024	1.31	0.26
	Residual	8	1.87	0.23		
Within plots	Day	3	0.97	0.32	17.83	<0.001
	Treatment*day	3	0.27	0.089	4.91	0.008
	Residual	24	0.44	0.018		

Table 3.4: Repeat measures ANOVA for the six most abundant nematode taxa at Traeth Melynog. Where different transformations have been used these have been indicated by Sqrt = square root, ln = natural log.

		<i>df</i>	<i>SS</i>	<i>MS</i>	<i>F</i>	<i>P</i>
Sqrt <i>Microlaimus</i>	Between plots					
	Treatment	1	449	449	63.5	<0.001
	Residual	8	158	16	2.2	
Within plots	Day	3	46	15	2.1	0.14
	Treatment	3	5	2	7.1	0.87
	day					
	Residual	23	163	7		
Ln <i>Bathylaimus</i>	Between plots					
	Treatment	1	2.3	2.1	5.2	0.03
	Residual	8	5.8	0.7	1.8	
Within plots	Day	3	1.2	0.4	1	0.4
	Treatment	3	0.5	0.2	0.4	0.74
	day					
	Residual	24	9.3	0.4		
Ln <i>Viscosia</i>	Between plots					
	Treatment	1	7.9	7.9	38.3	<0.001
	Residual	8	5.5	0.7	3.3	
Within plots	Day	3	0.9	0.3	1.4	0.27
	Treatment	3	1.2	0.4	1.9	0.16
	day					
	Residual	24	4.8	0.2		
Ln <i>Odontophora</i>	Between plots					
	Treatment	1	1.7	1.7	2.4	0.14
	Residual	8	4	0.5	0.7	
Within plots	Day	3	3.7	1.2	1.7	0.2
	Treatment	3	2.1	0.7	1	0.43
	day					
	Residual	24	16.9	0.7		
Ln <i>Eleutherolaimus</i>	Between plots					
	Treatment	1	5.8	5.8	18	<0.001
	Residual	8	3.8	0.5	1.5	
Within plots	Day	3	1.9	0.6	1.9	0.15
	Treatment	3	1.6	0.5	1.6	0.2
	day					
	Residual	24	7.5	0.3		
Ln <i>Daptonema</i>	Between plots					
	Treatment	1	4.2	4.2	16.2	0.001
	Residual	8	2.9	0.4	1.4	
Within plots	Day	3	1	10.3	1.3	0.3
	Treatment	3	0.3	0.1	0.4	0.77
	day					
	Residual	24	5.9	0.3		

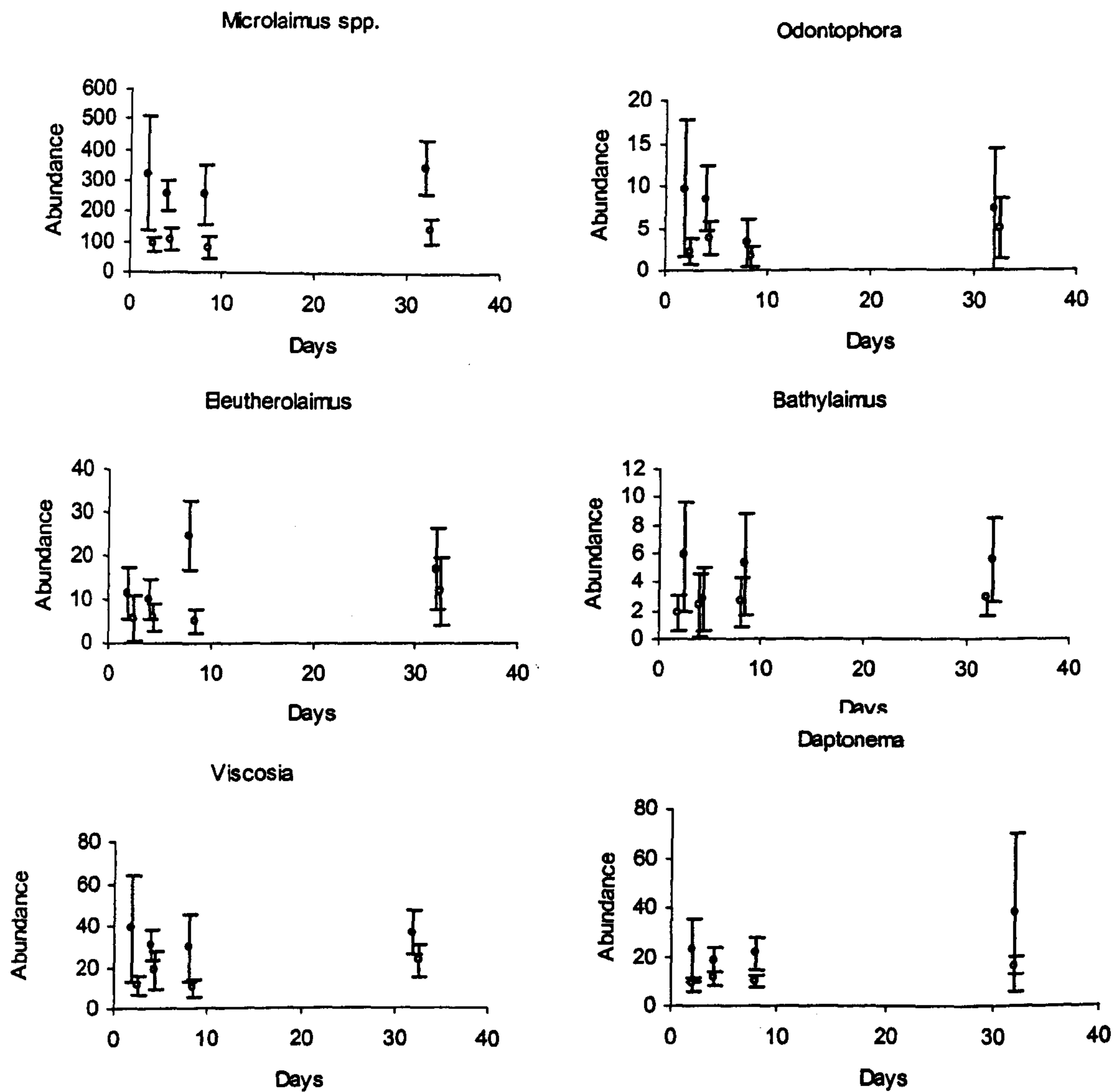


Figure 3.4: Abundances of key meiofauna taxa on Traeth Melynog in control (filled circles) and disturbed (open circles) plots over time. Note different scales.

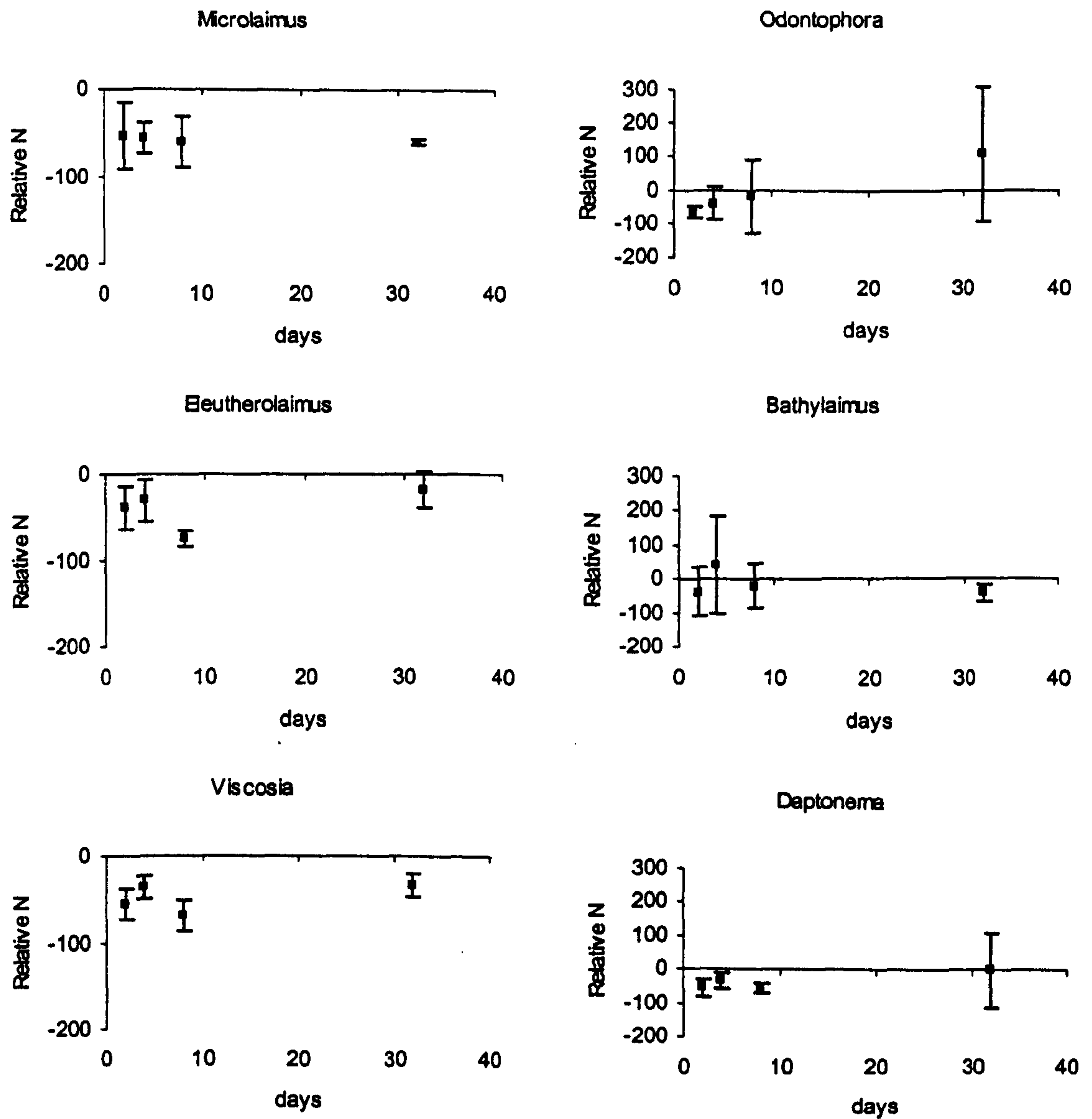


Figure 3.5: Relative total number of individuals (N) of key nematode taxa over time. Note difference in scales.

Repeat measures ANOVA indicated that five of the six most common nematode taxa at the experimental site showed a significantly negative response to the disturbance treatment (Table 3.4 and Fig. 3.4). The only taxon that did not show a significant response to the disturbance treatment was *Odontophora*. Nevertheless, Figure 3.5d indicates that *Odontophora* did have a significantly lower abundance within the disturbed treatment on the first sampling occasion. The inability to detect a significant difference attributable to the disturbance treatment for *Odontophora* is likely to have been affected by the large increase in variability exhibited by this group during the course of the experiment. *Microloaimus* and *Viscosia* were found in significantly lower abundances relative to undisturbed plots throughout the experiment (Fig. 3.5). Repeat measures ANOVA detected no significant effect of time for any of these taxa.

The disturbance treatment did not have a noticeable effect on the shape of the k-dominance curves plotted for the nematode communities in the control and disturbance treatments, which are almost superimposed on one another other (Fig. 3.6). In contrast, the k-dominance curves plotted for the macrofaunal community, indicated much stronger differences between treatments (Fig. 3.7). In particular, there is an increase in the percentage dominance of low ranking species within the disturbed treatment on sampling occasion 1 and 4 (days 2 and 32). This is related to very high numbers of the mud snail, *Hydrobia ulvae*, within treatment plots on these dates. A comparison of figures 3.6 and 3.7 indicates a much higher dominance exhibited by the macrofauna (55-80% of the abundance due to a single species) in comparison the nematode assemblage (40% of the abundance due to one genus).

ANOSIM tests indicated that significant differences occurred between disturbed and control treatments for both the meiofaunal and macrofaunal communities throughout the experiment (Table 3.5). Thus, recovery from the disturbance treatment had not occurred in either the nematode or the macrofaunal communities after 32 days. The MDS ordination plots indicated a clear split between the communities found in both the control and disturbed plots for both the macrofaunal and meiofaunal assemblages (Fig. 3.8). In addition, there is a clear temporal shift in meiofaunal community composition in both the control and disturbed assemblages (from the bottom to the top of the MDS plot) (Fig. 3.8a). Both the control ($R=0.421$, $P=0.001$) and disturbed ($R=0.607$, $P=0.008$) nematode communities changed significantly with time. This pattern is not apparent in the MDS plot for the disturbed macrofaunal

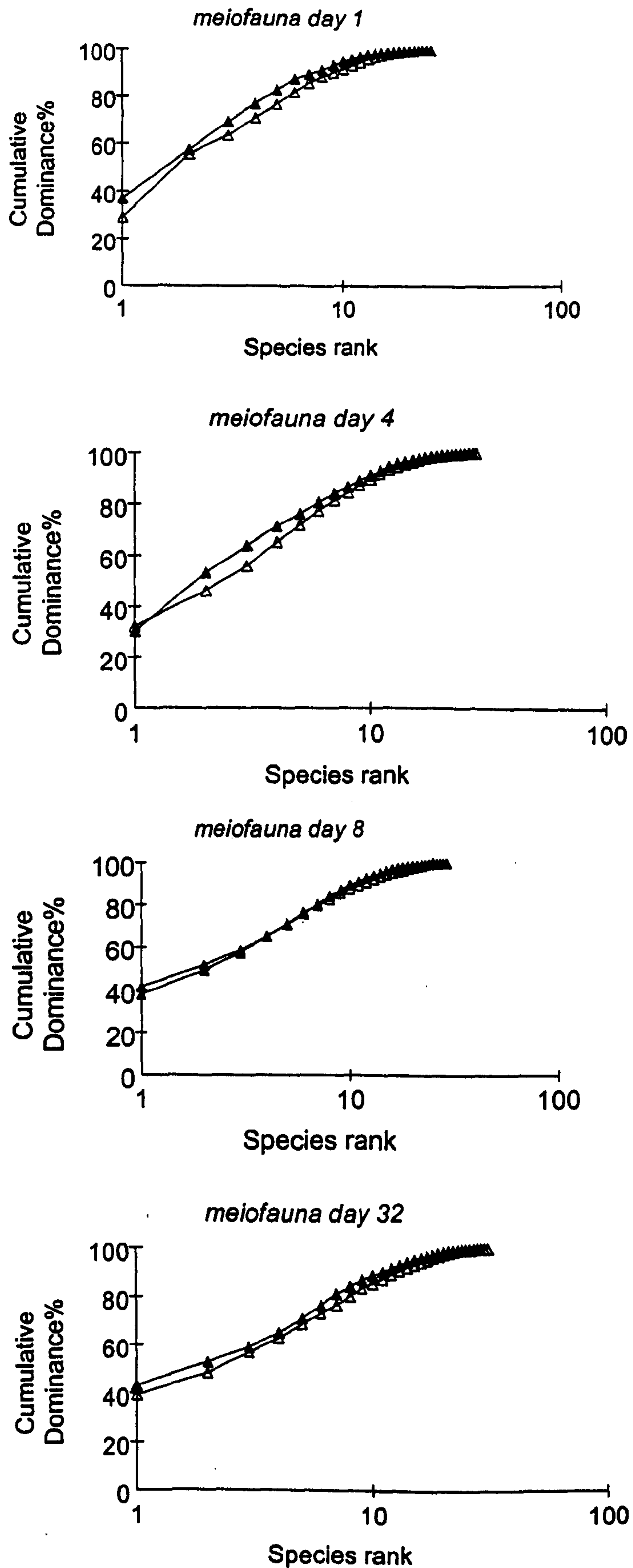


Figure 3.6: Cumulative dominance plots for control (filled triangle) and disturbed (open triangle) meiofaunal communities on the four sampling occasions

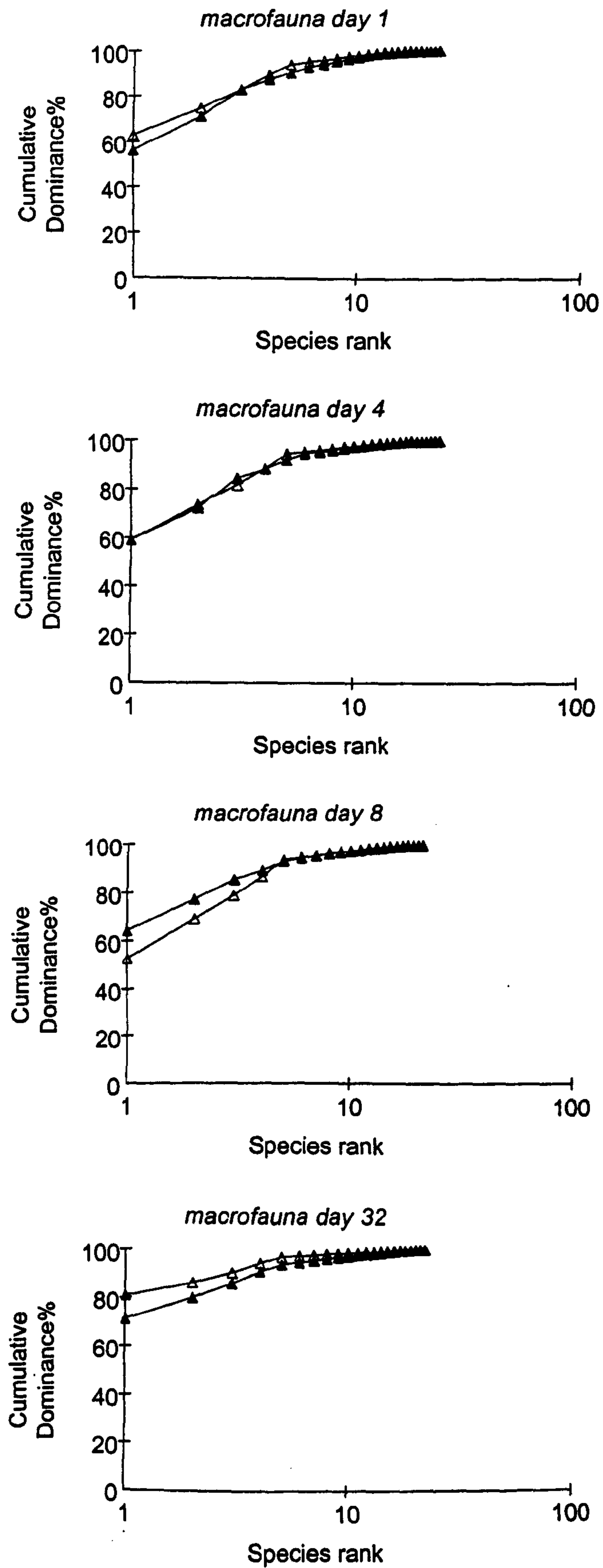


Figure 3.7: Cumulative dominance plots for control (filled triangle) and disturbed (open triangle) macrofaunal communities on the four sampling occasions.

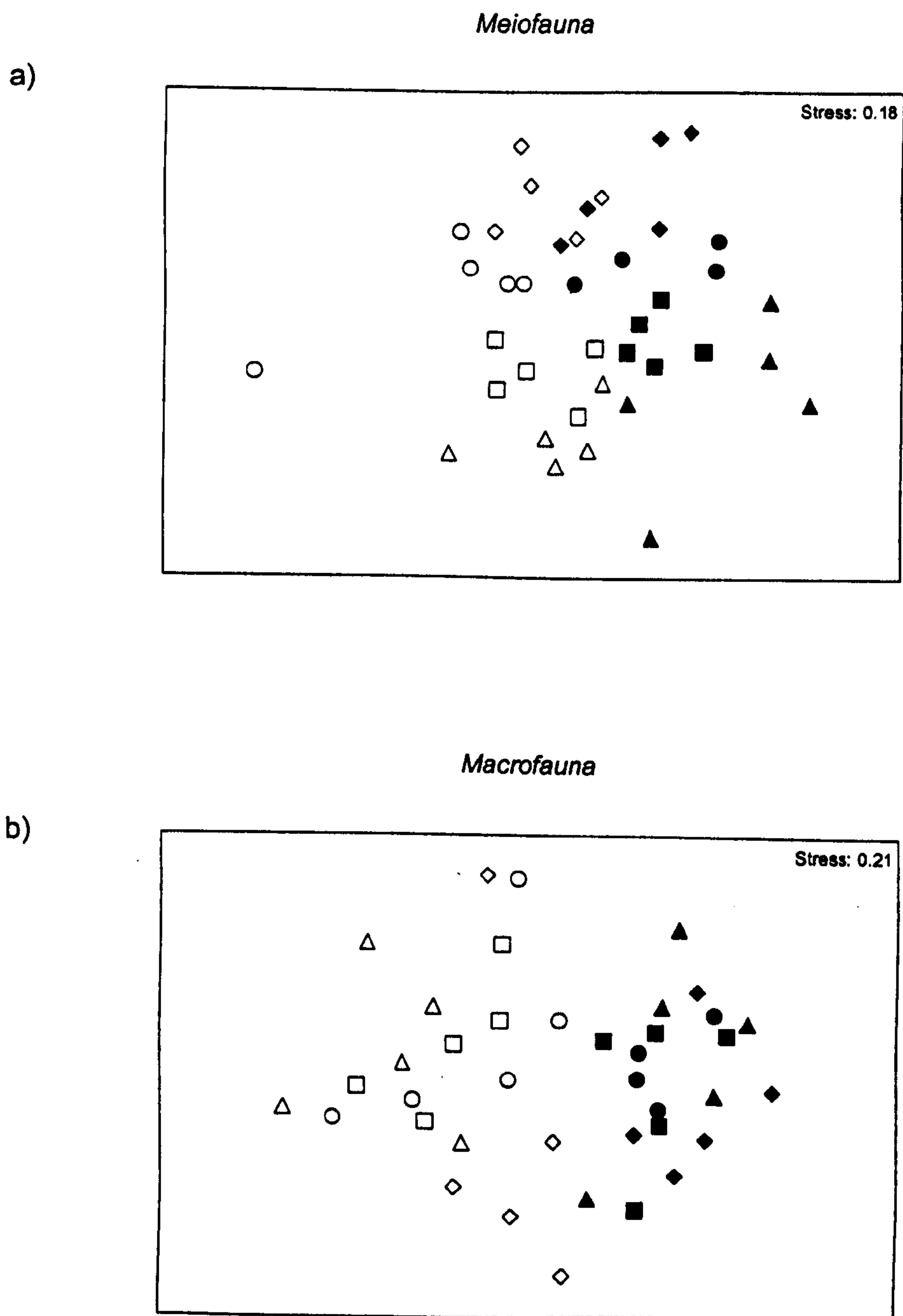


Figure 3.8: Non-metric multi-dimensional scaling plots showing a) meiofaunal community and b) macrofaunal community structure change over the course of the experiment. Filled symbols = controls, open symbols = disturbed plots. Triangles (day 1), squares (day 4), circles (day 8), diamonds (day 32).

assemblage. This is confirmed by an ANOSIM test that indicated that there was no significant effect of time on the disturbed macrofaunal community data ($R=0.07$, $P=0.21$). However, the ANOSIM test detected a significant effect of time on the macrofaunal control communities ($R=0.172$, $P=0.028$). The RELATE analysis indicated that there was a significant, though relatively weak, correlation between the multivariate data sets for macrofauna and meiofauna ($Rho=0.282$, $P=0.001$). The weakness of this association may be attributable to the differences in the magnitude and rate of response of the macro and meiofaunal communities in response to disturbance.

Table 3.5: Pairwise comparisons (ANOSIM) of meiofaunal and macrofaunal community data from disturbed and undisturbed plots on each sampling occasion.

<i>Day</i>	<i>Meiofauna</i>		<i>Macrofauna</i>	
	R statistic	P-value	R statistic	P-value
2	0.46	0.016	0.92	0.008
4	0.40	0.008	0.80	0.008
8	0.39	0.024	0.54	0.008
32	0.42	0.008	0.53	0.008

3.4 Discussion

Physical disturbance had a detectable negative impact on both the macrofaunal and meiofaunal assemblages. Differences in the assemblage structure for both components of the benthos as a result of the disturbance persisted throughout the duration of the experiment. A detailed analysis of the recovery trajectory of the macrofaunal community at this site has been described elsewhere (See Chapter 2; Dornie et al., 2003). The long-term influence of the disturbance treatment on nematode community structure was unexpected. Previous experiments with soft sediment meiofauna have tended to show that recolonisation occurs quickly (within hours/days) (Coull and Palmer, 1984). For example, in Sherman et al.'s (1983) study of the recolonisation of mimicked stingray feeding pits, nematode abundance had returned to control levels within 25 hrs. However, Schratzberger and Warwick (1998) detected significant differences in the total abundance of nematodes in disturbed communities for two days following a disturbance treatment in a microcosm experiment. More sensitive multivariate tests detected significant differences in community structure between control and disturbed treatments for 16 days following disturbance in the same experiment. Thus, other studies do provide evidence of long term (> 1 week) disturbance effects on nematode communities (e.g. Chandler and Fleeger, 1980). However, it is difficult to directly compare the results from the present relatively large-scale field study with those from small-scale microcosm experiments where conditions are tightly controlled and nematode community dynamics may be affected by other factors (for example, lack of food or outside supply of recruitment).

The greatest effect of the disturbance treatment was on the total abundances of macrofauna and meiofauna. The initial impact of physical disturbance was a decrease of c. 80% in macrofaunal abundance whilst the decrease in nematode abundance was c. 55%. Ingole et al. (2000) reported a 50% decrease in meiofaunal density following a disturbance treatment in a deep-sea soft sediment habitat. However, Sherman et al., (1983) reported reductions in nematode abundances of c. 80% as a result of sediment disturbance by rays. Since the upper layers of the sediment were removed as part of the disturbance manipulation in the present study, a decrease in abundance is expected. It seems likely that the removal of sediment was more successful in extracting a greater proportion of the macrofaunal organisms than the nematode component. Inevitably, small volumes of the original sediment would have remained within the disturbed plots, aiding the recovery of the smaller, meiofaunal individuals.

The recovery mechanisms for macrofauna and meiofauna may differ following a disturbance event. Whilst the macrofaunal species gradually colonised the disturbed plots via active and post larval migration (see Dernie et al. 2003), the rapid turnover of nematode communities suggests that *in situ* reproduction could be an important mechanism for recovery for this group. Nematodes show continuous asynchronous breeding, and typically have generation times of around one month (Warwick and Price, 1979). Presumably, for those experiments studying the effects of disturbances on nematode communities within the constraints of microcosm chambers, this is the only possible recovery mechanism available to the community. However, there is evidence to suggest that nematodes can disperse both through suspension in the water column and through holobenthic infaunal immigration (Chandler and Fleeger, 1983). Nematodes are sub-surface dwellers, many of which display morphological and behavioural adaptations that reduce their vulnerability to resuspension. However, they have been reported as present in the water column (Bell and Sherman, 1980), although less frequently than crustacean meiofauna (i.e. copepods) (Bell and Sherman, 1980; Coull and Palmer, 1984). Chandler and Fleeger (1980) investigated the mechanisms through which meiofauna colonised azoic sediments. Copepods and nauplii colonised azoic sediment chambers by movement in suspension to ambient densities within two tidal cycles, whilst nematodes colonised the sediment chambers both through transport in suspension and migration through the sediment, but had not reached ambient densities after 29 days. The present study cannot distinguish between the different possible modes of recolonisation (*in situ* reproduction; active migration; passive settlement) that occurred following the disturbance treatment, nevertheless, it is likely that all three mechanisms influenced the recovery process.

Assuming that recovery occurred largely through *in situ* reproduction, it might be expected that the recovery of the meiofaunal community would have occurred within the time frame of this experiment. Thus, other factors within the disturbed plots may have influenced community structure in the longer-term. The physical environment within disturbed plots was altered as a result of the treatment. Surface water was present within the disturbed pits throughout the course of the experiment. In addition, the process of disturbance may have affected sediment stability through the removal of surficial sediments where biological cohesion between sediment grains as a result of extra-polymeric substances (EPS) produced by bacteria, diatoms and nematodes stabilises the bed (e.g. Daborn et al., 1993; Dade et al., 1990). It is possible that the sediment matrix and infaunal inhabitants within disturbed plots were more vulnerable to wave-induced disturbance for some time following the disturbance event, and this

prevented communities from attaining a composition similar to the adjacent control community levels (see also Thrush et al., 1996). Palanques et al., (2001) reported that sediments disturbed by bottom trawling were less cohesive for several days after initial disturbance and were more prone to subsequent resuspension.

Nematode community structure is highly influenced by the bioturbatory activities of the concomitant macroinfauna (e.g. Austen et al. 1998; Warwick et al. 1995). Whilst the macroinfaunal community structure changed in response to disturbance this may also have influenced the structure of the associated meiofaunal community. The interaction between different components of the benthos underlines the importance of studying all aspects (biotic and abiotic) of the sediment matrix in understanding benthic processes. It should be acknowledged that until recently the microbial component of soft sediment marine communities has largely been ignored due to limitations in our ability to differentiate diversity at this level (e.g. Biles, 2002). Incorporating the response of microbial communities to disturbance events would further enhance our understanding of the effects of perturbative activities on benthic systems.

This experiment has shown a long-term (at least 32 days) effect of a physical disturbance event on meiofaunal community structure. The disturbance was comparable to various anthropogenic disturbances that occur worldwide in the intertidal zone, including bait digging and hydraulic dredging. Recent work has produced conflicting results when considering the impacts of bottom fishing disturbances on nematode communities. Schratzberger et al. (2002) used a BACI experimental design to assess the effects of beam trawling on nematode community attributes. The authors detected no effect of trawling on nematode diversity or biomass, and only a mild effect on community structure. However, this study was hampered by a low power to detect changes due to the high variance in the data. When nematode communities on actual fishing grounds were investigated, Schratzberger and Jennings (2002) found fewer nematode species, lower diversity and lower species richness in heavily trawled areas. The experimental data from the current study indicates that nematode communities may be more resilient than macrofaunal communities to physical disturbance. Nevertheless, the long term effect on nematode abundance reported in this study, coupled with the higher productivity characteristics of nematode assemblages, indicates that the impacts of anthropogenic disturbances on meiofaunal communities may be highly significant in terms of benthic ecosystem functioning, and thus warrants further study.

Chapter 4

An *in situ* device for the measurement of sediment properties relevant to ecological studies

4.0 Abstract

Characterisation of soft sediment habitats by granulometry is an ubiquitous but time consuming process. However, granulometry may not yield data that represent the physical characteristics of the environment to which organisms respond. This chapter describes an *in situ* device for the measurement of sediment properties based on the penetration of a weighted cone into the sediment. Given the construction of the equipment and its mode of operation, the data should reflect differences in the shear strength of different substrata. It is hypothesised that inter site variations in cone penetration should reflect changes in strength, grain size distribution and sediment fabric (sorting, shape and packing of sediment grains). The equipment was tested at 15 sites of varying silt and clay content in control sediments and areas that had been subject to a physical disturbance treatment. Penetration data were significantly related to measures of the percentage silt and clay content, organic content and water content of the sediment when tested in the field. Penetration data also correlated with biological measures of community characteristics such as the Shannon-Weiner diversity index and Margalef's index of species richness. However, the penetrometer device could not detect any changes to sediment properties as a result of the physical disturbance treatment. Nevertheless, this equipment provides a useful tool for the rapid assessment of sediment characteristics and may provide a usefool technique for benthic ecologists.

4.1 Introduction

Benthic communities that inhabit soft sediments have been shown to be closely associated with physical characteristics of their environment (Warwick and Uncles, 1980; Warwick et al., 1991; Yates et al., 1993). Physical disturbances including natural events (e.g. tidal scouring; foraging activities; glacial scour) and anthropogenic disturbances (e.g. bottom fishing; bait digging; aggregate extraction) impact upon both the infaunal biota (e.g. Hall and Harding, 1997; Kaiser et al., 2001) and the sediment matrix that they inhabit (e.g. Thrush et al., 1996; Palanques et al., 2001). As a result, it is necessary to consider the impact of physical disturbance on both the habitat and on the associated fauna.

Investigations of the relationship between infaunal communities and sediment structure have frequently used granulometry techniques to characterise the physical composition of soft sediment habitats. This process involves the disaggregation and drying of sediments that are subsequently passed through a set of sieves of decreasing mesh size. Each sediment fraction is then weighed, resulting in detailed information concerning the proportions of different grain sizes within the sample (Buchanan and Kain, 1984). However, such techniques may not meaningfully represent the habitat encountered by the organism (Snelgrove and Butman, 1994), leading to difficulty in relating community patterns to measured sediment parameters that may have lost their relevance to benthic fauna once disaggregated. For example, the homogenisation of sediment samples required for granulometric analysis breaks down natural aggregates (such as faecal pellets) and the *in situ* fabric of the sediment, and does not reflect the vertical variations often encountered in natural sediment deposits (Pearson, 2001). Granulometric analysis is also time consuming, and the number of replicate samples taken may be limited by temporal, logistical and financial constraints. Therefore it would be highly desirable if there existed a simple portable device that measured a single parameter of the sediment that also related to the composition of the associated animal assemblage. Any device that could be used easily and instantaneously in the field would overcome the analytical problems associated with the disruption of samples when using intrusive and destructive techniques (e.g. Black and Paterson, 1997; Tolhurst et al., 2000).

The present study examined the potential application of a device in which the penetration distance of a weighted cone-tipped rod into the test sediment is measured. This equipment is effectively a simplified and hybrid version of other standard geotechnical test instruments – namely the laboratory fall-cone test, and the

field cone penetration test instrument (CPT). The device consisted of a weighted cone that was allowed to free fall into the sediment and the depth of penetration then measured. The more sophisticated CPT ensures a controlled, constant rate of penetration (usually 2 cm s^{-1}) and enables the quantification of the resistance stress imposed on the cone tip and the frictional resistance stress experienced by the sidewalls of the rod. Geotechnical engineers have devised empirical inter-relationships between the measurements of these tests and many of the properties that they need for foundation design purposes – the most crucial of which is shear strength. Readers are referred to British Standards (1991) for a description of one type of laboratory fall-cone penetration test instrument, and to Meigh (1987) for the equivalent information relating to CPT. In addition Hakanson (1986) discusses the use of a slightly more complex 3 cone penetrometer in the context of ecological planning and aquatic pollution control.

The instrument proposed in this study, whilst less technical in design than those used by geotechnical engineers, should also provide a means of parameterising the strength of the test sediment. Nevertheless there are limitations of the equipment on a geotechnical level. One can define the shear strength of a test sediment in two ways; drained and undrained strength. This is related to the way in which water either drains from (in the case of a coarse sand for example) or remains within (in the case of low permeability material such as clay) the test area on application of the test instrument. As the extent of drainage is not controlled during the test it is not possible to define the type of strength that has been measured. In addition, the rate of application of the load (free falling in this case) has some effect on the measured strength (Koumoto and Houlsby, 2001). Despite these possible extraneous effects on the reliability of penetration devices, empirical relationships between penetration values and the physical properties of the sediment are likely to occur. For the purposes of this study it was unlikely that any of the above limitations would mask any relationship with biological parameters.

The main reason that empirical inter-relationships between cone penetration, shear strength and other physical parameters may be expected stems from the fact that the shear strength of the sediment depends upon three fundamental controls:

- (i) the number of and area of intergranular contacts per unit volume of sediment
- (ii) the stress across the intergranular contacts

- (iii) the amount of intergranular chemical cohesion present

In the field of geotechnics, the first of these is often parameterised in the form of either porosity or water content (assuming the test sample is saturated). Furthermore, empirical studies (Hamilton and Bachman, 1982) have shown that there is a correlation between porosity and mean grain diameter. The second control is directly related to the depth of overburden, so that shear strength would normally be expected to increase with depth in a sediment provided that the first and third of these controls do not change. The third control on shear strength is directly related to the amount of clay minerals present in the sediment since these produce intergranular chemical attraction. Presumably this would also be affected by biological cohesion as produced by the extra-polymeric substances associated with the presence of interstitial bacteria, diatom and other biota in surface sediments (Grant, 1987; Paterson and Black, 1999). It is thus clear that the shear strength of sediments is directly related to physical aspects of the habitat that are of biological interest, i.e. porosity and mean grain diameter, and chemical (or biological) cohesion which will affect the overall stability of a sediment deposit.

Physical disturbance resuspends and homogenises the upper layers of sediment, leading to a reduction in stability (Thrush et al., 1996; Palanques et al., 2001) and alteration of seabed topography (e.g. Newell et al., 1998). Hauton and Paterson (2003) detected a reduction in the shear strength of sediments within the furrows created by subtidal hydraulic suction dredging using a shear vane device. Hydraulic dredging is a particularly severe form of disturbance that involves the fluidisation of the upper 30 cm of the sediment (Tuck et al., 2000) and thus might be expected to produce more dramatic changes in the physical characteristics of the sea bed in comparison to other, less intense disturbances such as bait digging or the collection of shellfish species using manual techniques. Nevertheless, it might be expected that there would be a change to sediment penetrability following a disturbance, which might be detected by the device described here.

The device tested is a simplified version of previously devised standard geotechnical tests and it is intended that, like the standard tests, the interpretation of the results should be empirical in nature given the difficulty in controlling the drainage conditions in close proximity to the apparatus. The aims of the present study were to:

- i) Establish the relationship between penetrometer readings and granulometrically derived sediment parameters (in this case, the proportion of silt and clay particles at specified sites), proportion of organic content and water content.
- ii) Investigate any potential relationship between penetrometer measurements and community attributes such as univariate measures and diversity indices derived from community data obtained from a range of study sites with different sediment characteristics.
- iii) Investigate the ability of the penetrometer device to detect changes to sediment properties that may have arisen as a result of a uniform physical disturbance treatment applied at a range of experimental sites with different sediment characteristics.

4.2 Methods

A simple cone penetration device was constructed as in Figure 4.1. To measure penetration, the equipment was allowed to rest on the sediment surface, the inner pole was raised a set distance above the sediment surface (5 cm) and was then dropped and allowed to penetrate the sediment until it stopped. The distance of penetration (in mm) was measured using the scale bar at the top of the equipment. Some care was taken with the field measurements from the device. The penetrometers' progress through the sediment may be halted by stones, shell debris etc., or made easier if taken just over a lugworm hole for instance. Algae on the sediment surface would also affect the measurements taken, and was moved before application of the test. However, usually it was clear when a measurement had been affected by some other factor such as the presence of a shell below the sediment surface. During this study, such measurements were ignored and another reading taken.

4.2.1 Testing the equipment in the field

The cone penetration equipment was tested at fifteen sites along the Menai Strait, North Wales (Figure 4.2). Sites were chosen to include a variety of sediment types that ranged from very clean sand that contained less than 2% silt and clay to muddy sediments with over 70% silts and clay content. Each site consisted of a control and disturbed plot of 1 m x 4 m dimensions. The physical disturbance treatment consisted of the removal of the upper 10 cm of sediment with a spade that resulted in a large reduction in macrofaunal and meiofaunal abundance within disturbed plots, in

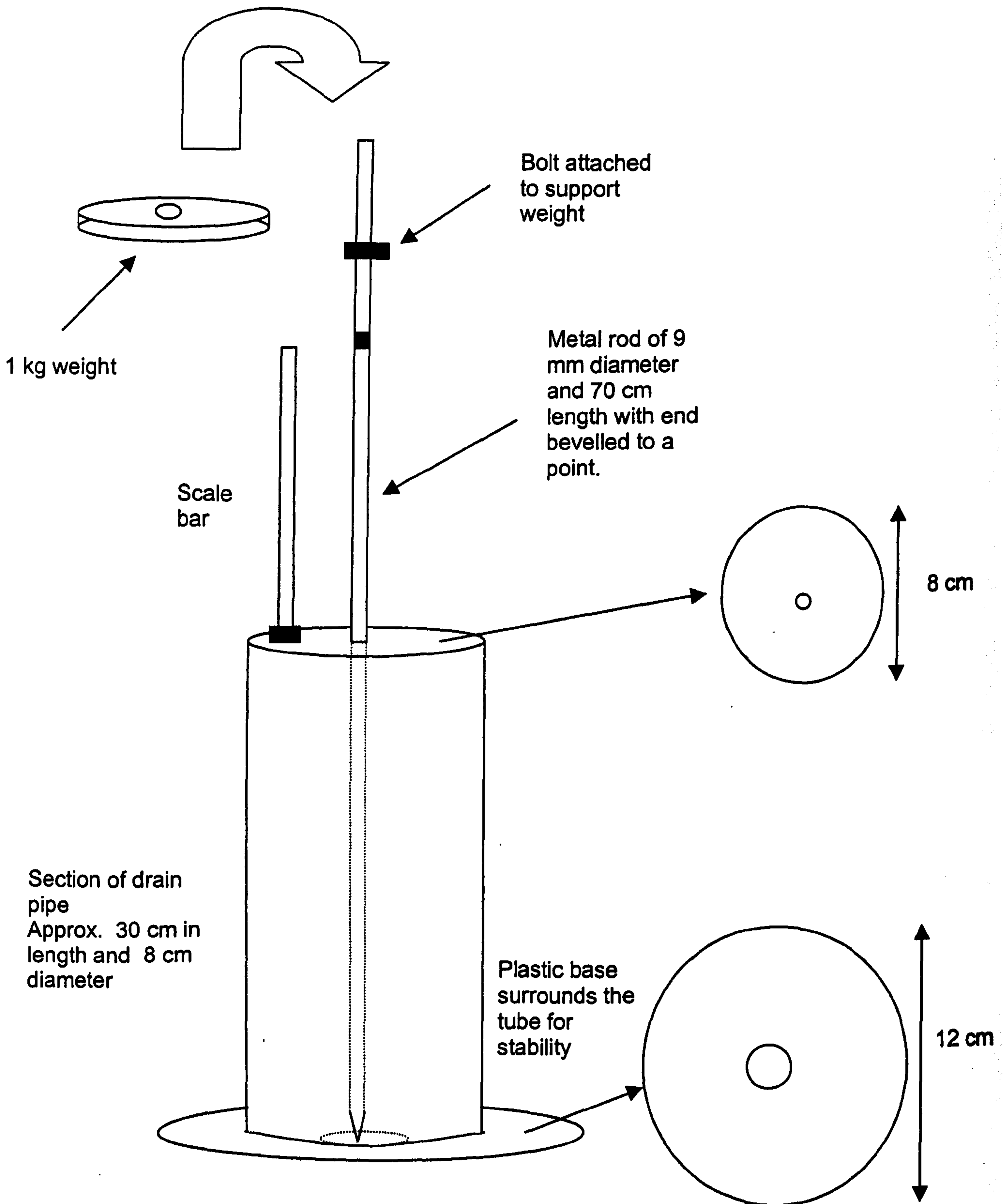


Fig. 4.1: The cone penetrometer device. Cone consist of a 70mm length, 9 mm diameter steel rod, bevelled at the tip to give a 63.61 mm^2 frontal cone area, weight 482 g.

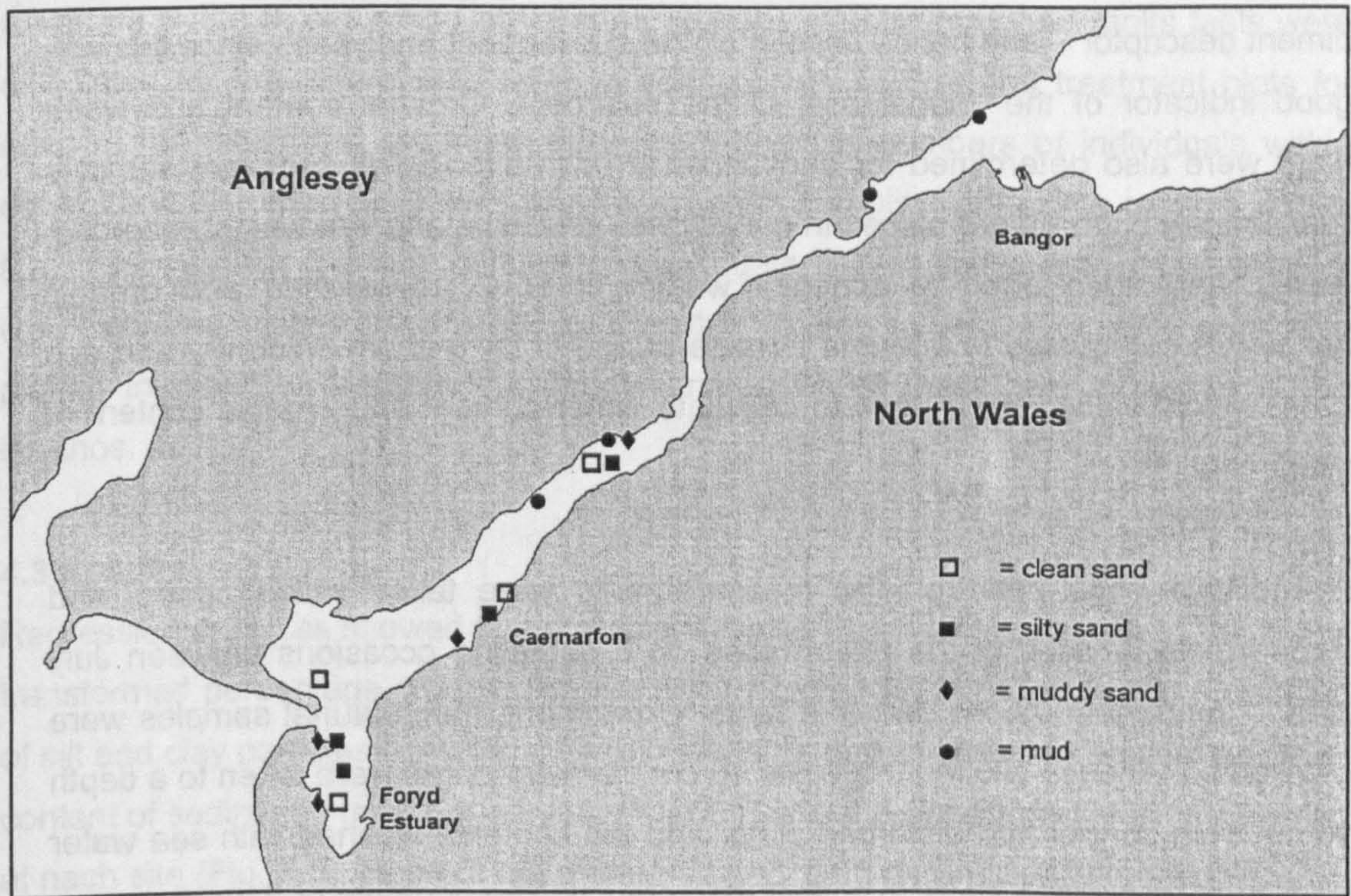


Figure 4.2: Position of experimental sites along the Menai Strait, North Wales including approximate description of different sediment types.

addition to the formation of a depression in the sediment surface (see Chapter 5 for detailed information). The sediment was removed to a location approximately 50 m from the treatment plot so that it would not influence the infilling of the manipulated plots.

Grain size distributions of sediments at each site were determined by standard granulometric analysis of samples collected at the beginning and end of the experiment (approximately six months later) using a method developed from Buchanan and Kain, (1984). Sediment samples consisted of small cores of approximately 100 cm³ volume taken to a depth of 5 cm. Sediment was wet sieved through a 63 µm sieve to separate the silt and clay fraction, which was subsequently dried under hot lights, weighed and used for the calculation of percentage of silts and clays. The remaining sediment was also dried and then sieved through a series of Wentworth sieves (2mm, 1mm, 0.5mm, 0.25mm, 0.125mm and 63µm) on a mechanical sieve shaker for 15 minutes. Each sediment fraction was then weighed (± 0.001 g). This resulted in detailed information concerning the grain size distributions at each site. The percentage silt and clay were chosen as the granulometric

sediment descriptor – and hence used in all the subsequent analyses - since this was a good indicator of the 'muddiness' of the sediment. Organic content and water content were also determined for sediments at each site. Small sediment samples (approximately 6 cm³) were placed in preweighed crucibles and wet weight recorded. Samples were then dried to constant weight at 80°C, re-weighed and organic material was combusted in a muffle furnace at 550°C for 6 hours. Wet, dry and ash free dry weight values were used to calculate water content and organic content of the sediment.

Four replicate cone penetrometer measurements were taken within control and disturbed plots at each of the fifteen sites on 5 sampling occasions between July 2001 and January 2002. As part of a larger experiment, macrofaunal samples were also collected. At each site four replicate 10 cm diameter cores were taken to a depth of 10 cm from control and disturbed plots, and the contents washed with sea water through a 0.5 mm mesh sieve to collect macrofauna. The contents of the sieve were preserved in 4% buffered formalin solution and stored for subsequent identification in the laboratory. Organisms were identified to species level whenever possible. Diversity indices were calculated using the PRIMER software package (Warwick and Clarke, 1994).

4.2.2 Statistical treatment

Each of the measured sediment parameters were regressed on the mean penetrometer reading obtained for control plots at each site to investigate the degree to which sediment parameters could be predicted from the penetration readings. In addition, the relationships between the environmental parameters and the macrofaunal communities at different sites were investigated using correlation analyses. The biological indices used for this analysis were the total number of species per sample, the total number of individuals per sample, Margalef's index of species richness, Pielou's index of equitability and the Shannon-Wiener diversity index. Since the percentage silt and clay data were not normal even after transformation, the non-parametric Spearman's rank correlation was used for all correlative analyses for comparability.

For the purposes of this study, examination of the effects of the disturbance treatment on the infaunal community were restricted to the response of total numbers of individuals within control and disturbed plots over time (further analysis of the biological response to disturbance in this experiment is described in detail in

Chapters 5 and 6, see also Dernie et al., 2003b). Wilcoxon signed ranks tests were calculated for the differences between each pair of control and treatment plots for each of the measured sediment parameters and the numbers of individuals within control and disturbed plots over all sites on each sampling date. The relative values (i.e. response) for the total number of individuals and penetrometer measurements (i.e. disturbed values as a proportion of the control values) over time were also plotted in order to facilitate the direct comparison of these two attributes of the benthos.

4.3 Results

Regression analyses showed that significant relationships existed between the arcsin transformed percentage organic content ($r^2=0.72$, d.f.=12, $P<0.001$), the proportion of silt and clay particles ($r^2=0.69$, d.f.=13, $P<0.001$), and the arcsin transformed water content of sediments ($r^2=0.56$, d.f.=13, $P<0.001$) with the penetrometer data recorded at each site (Fig. 4.3). None of the measured sediment parameters were significantly correlated with either the total number of species or Pielou's index of evenness (Table 4.1). The total number of individuals was significantly correlated with all measured physical parameters. All parameters except water content were significantly correlated with Margalef's index of species richness, while penetration and silt and clay content were also significantly correlated with the Shannon Wiener diversity index. The best correlation occurred between penetration values and Margalef's index of species richness ($r_s=-0.665$, $P=0.007$).

Table 4.1: Spearman's rank order coefficient (r_s) for diversity indices against penetration, organic content, water content and % silt and clay values. Significant correlations (at the 0.05 level) in bold.

	<i>Penetration</i>		<i>Organic content</i>		<i>Water content</i>		<i>Silts/clays</i>	
	r_s	P	r_s	P	r_s	P	r_s	P
No. species	0.477	0.073	-0.454	0.089	-0.141	0.617	-0.396	0.144
No. individuals	0.538	0.038	0.525	0.044	0.636	0.011	0.596	0.019
Margalef's	-0.665	0.007	-0.639	0.010	-0.468	0.079	-0.643	0.010
Pielou's	-0.352	0.198	-0.239	0.390	-0.221	0.428	-0.414	0.125
Shannon	-0.531	0.042	-0.450	0.092	-0.371	0.173	-0.561	0.030

Wilcoxon signed rank tests indicated that there were no significant differences in any of the physical characteristics measured within disturbed plots in comparison to control plots with the exception of the penetrometer data on day 63 (Table 4.2).

However, figure 4.4b indicates an outlier within the penetration data on this sampling occasion. By removing this data point and re-running the Wilcoxon signed ranks test a significant difference between the control and disturbed penetrometer values was no longer apparent ($W=64$, $P=0.842$).

Table 4.2: Wilcoxon's signed rank test for differences between sediment characteristics within control and disturbed plots on each sampling date. W = test statistic, P = probability value, M = estimated median.

Day	Penetration			Organic content			Water content		
	W	P	M	W	P	M	W	P	M
15	53	0.71	-2.06	48	0.31	-0.15	39	0.14	-1.1
35	35	0.16	-4.5	53	0.45	-0.03	46	0.27	-0.8
63	24	0.04	-12.3	46	0.27	-1.88	58	0.62	-0.59
105	45	0.64	-1.9	87	0.13	0.14	72	0.51	0.31
213	46	0.71	-4.63	46	0.55	0.13	64	0.84	0.17

Significant differences in the total numbers of individuals within control and disturbed plots occurred throughout the duration of the experiment (Table 4.3). A comparison of Figs 4.4a and b highlights the difference in response of total numbers of individuals and penetrometer values to the physical disturbance treatment. Whilst the total number of individuals clearly indicated a negative response to the disturbance followed by a gradual increase in numbers of individuals over time, penetrometer values show little response to the disturbance at any point during the experiment. Margalef's index of species richness was also plotted since this diversity index gave the best correlation with penetration values. This data showed a limited negative response following the disturbance, with a high variability in relative response over the duration of the experiment.

Table 4.3: Wilcoxon's signed rank test for differences between the numbers of individuals within control and disturbed plots on each sampling date. W = test statistic, P = probability value, M = estimated median.

Day	W	P	M
15	136	<0.001	226
35	131	0.001	225
63	117	0.012	97
105	117	0.001	258
213	87	0.033	124

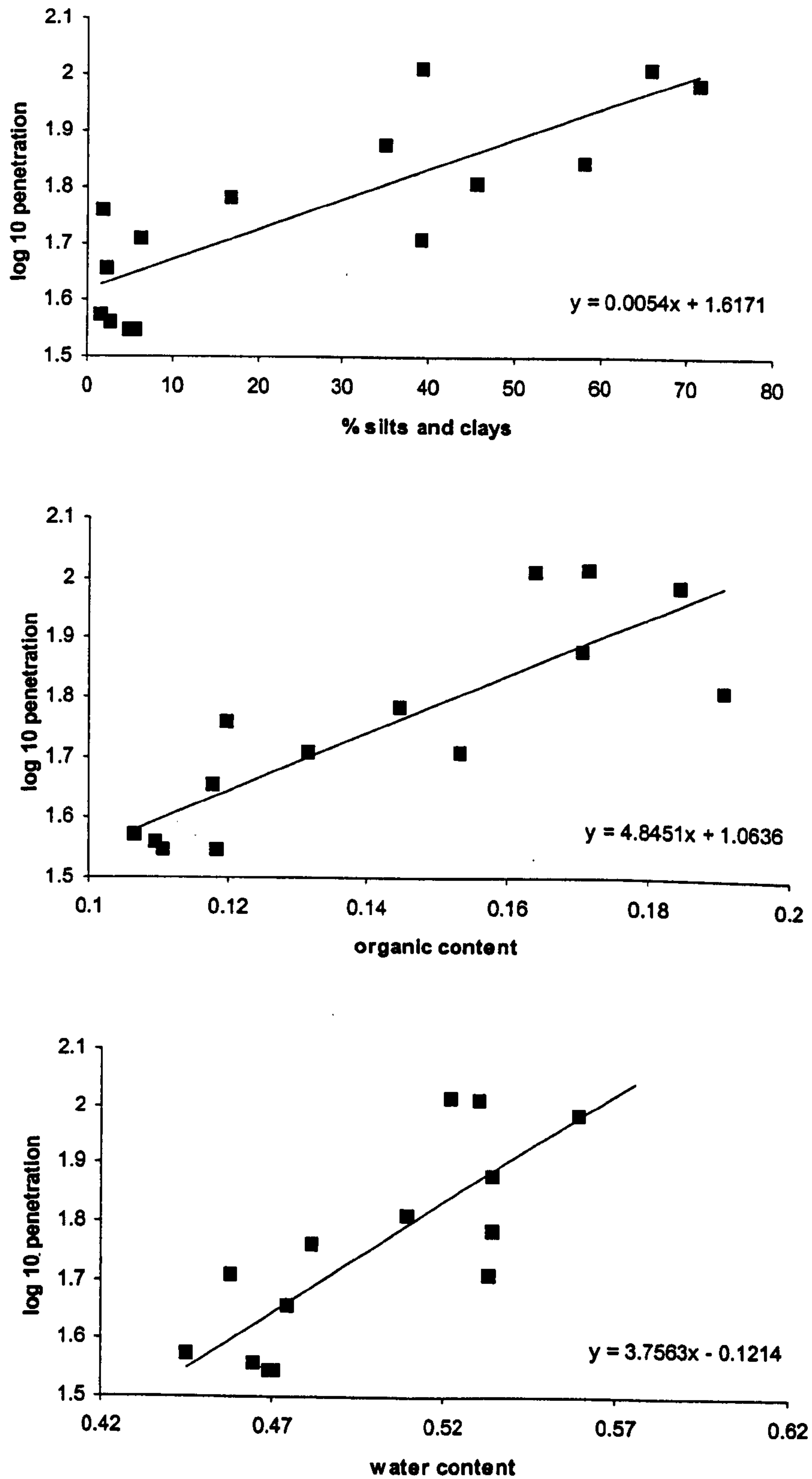


Figure 4.3: Log₁₀ transformed depth of penetration data against a) percentage silts and clays, b) organic content and c) water content.

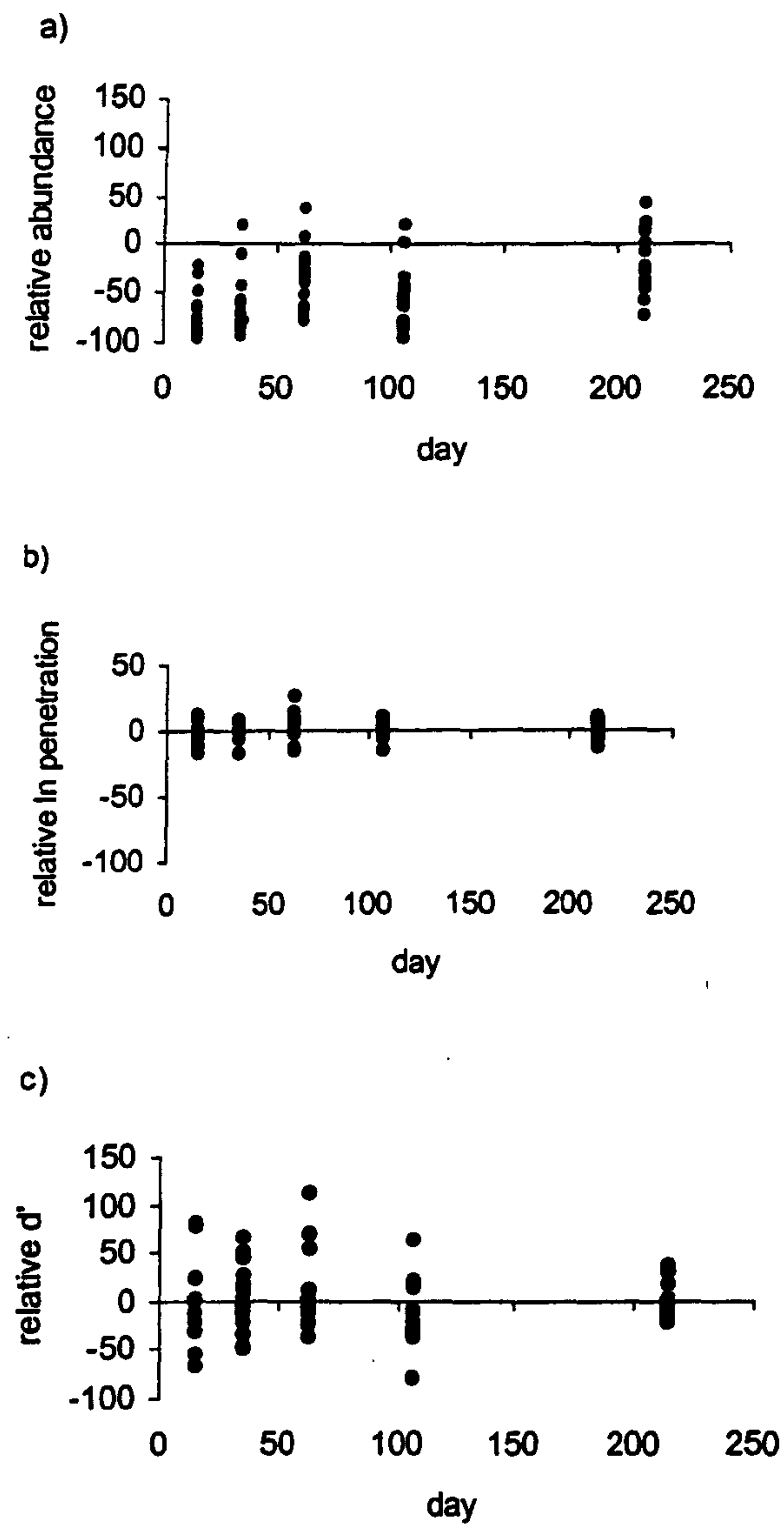


Fig. 4.4: Relative values of a) penetration depth (mm) and b) infaunal abundance (numbers per replicate) and c) Margalef's index of species richness between control and disturbed plots over time. NB –scales not equal.

4.4 Discussion

4.4.1 Prediction of sediment parameters

The penetrometer device is easy to construct with inexpensive materials, and can be used to take *in situ* measurements in the field very rapidly. Despite the fact that the equipment was relatively unsophisticated, regression analyses indicated that there was a good relationship between the percentage of silts and clays, organic content, water content and the penetrometer data. R-squared values for these relationships ranged from 0.56 to 0.72, indicating that the prediction of other sediment parameters based on penetrometer data would be reliable within the context of an ecological study where the broad characterisation of sediment characteristics was required. Granulometric analysis of sediment samples usually requires several days to complete although analysing samples for organic content and water content is less time consuming (approximately 6 hours). However, in comparison a number of replicate penetrometer readings can be obtained *in situ* in just a few seconds. Furthermore, as the measurements are taken *in situ* and are an empirical measurement of the physical properties of the sediment in its natural state, they may have more direct relevance to biological community data. Hence, this equipment would appear to be a useful tool to rapidly assess sediment characteristics that are of interest to benthic ecologists.

4.4.2 Correlation with diversity indices

As might be expected, correlations between environmental data and community composition were not as high as between the different environmental parameters. Nevertheless, penetration values did correlate well with total numbers of individuals, Margalef's index of species richness and the Shannon diversity index. The same pattern was found between both the proportion of silts and clays and these indices. This is not surprising considering the close relationship between these two environmental variables and indicated that species richness and diversity decreased in a predictable manner with increasing penetration values, i.e. from clean sands to muddier sediments. This pattern is supported by numerous studies of the distribution of benthic assemblages (e.g. Pearson and Rosenberg, 1978; Bonsdorff and Pearson, 1999). The lack of correlation between the physical parameters and the other diversity indices highlights the difficulty in determining those physical factors that have the greatest influence on community structure and composition in soft sediment communities. Nevertheless, it is clear that the penetrometer provides data that are well related both to other physical parameters and to the communities inhabiting the

different sediment types, and thus is a meaningful technique in studies that attempt to relate benthic community patterns to sedimentary parameters.

Animal-sediment relationships are a complex and debated area of benthic ecology (for a review see Snelgrove and Butman, (1994)). Since all the physical parameters measured in the present study are inter-related autocorrelation is inevitable. It is not argued that by using this penetration device a more appropriate aspect of the sediment fabric from a biological perspective is being measured. Indeed, very few studies have provided very strong evidence for causality in animal-sediment relationships (Snelgrove and Butman, 1994) and further work is still required to elucidate the causal mechanisms behind benthic community distributions. Nevertheless this equipment has advantages over the more commonly used granulometric techniques as it can be used in situ, thus overcoming difficulties with destructive sampling techniques that affect sediment properties, (e.g. Tolhurst et al., 2000) and it is a particularly rapid method for collecting data related to physical parameters. Furthermore little training is required to use this device, it requires no electrical supply and is easy to transport.

4.4.3 Detection of the effects of physical disturbance

In the present study, no effect of the physical disturbance treatment on sediment characteristics was apparent as measured from the penetration values, organic content or water content of the sediment. Since the experimental disturbance involved the removal of the upper 10 cm of sediment within disturbed plots it is likely that there were changes to physical attributes of the sediment, however the sampling techniques described here may not have been adequately sensitive to detect these changes. In addition, the first samples were collected two weeks after the application of the disturbance due to constraints of the tide such that the initial effects of the disturbance may have been ameliorated by successive tides even though the physical impressions made by the disturbance were evident for the majority of, or throughout, the experiment. Other studies have detected changes to sediment characteristics following disturbance events. In particular, the formation of pits as a result of physical disturbances may result in the deposition of fine materials within depressions. This has been detected as an increase in the organic content of sediments (e.g. Oliver and Slattery, 1985) and an increase in the proportion of smaller grain sizes in disturbed areas (e.g. Kenny and Rees, 1996) where changes in sediment topography alter the depositional environment (Probert, 1984). High shear stress values are characteristic of well-consolidated sediments that would be

disrupted by physical disturbance. Hence as cone penetration is related to the bulk shear properties of the sediment, it is perhaps surprising that the penetrometer device was unable to detect any changes to sediment characteristics. Although Hauton and Paterson (2003) detected a significant decrease in shear strength following fluidisation of the bed by hydraulic dredging, this form of disturbance is a more intense disturbance than that used within this study, such that effects on shear strength may have been larger and therefore more easily detected. In particular, fluidisation of the bed as a result of dredging may be more pronounced sublittorally as the sediment is actively mixed with water. In contrast, physical disturbance occurring during low tide in the intertidal zone does not bring the sediment in contact with water and in addition daily tidal exposure could expedite the restoration of shear properties of these sediments.

Although a significant difference was found between penetration values within control and disturbed plots on day 63, this result was influenced by particularly high penetration readings in the disturbed plot in comparison to the control plot at one particular site. On removal of this data-point the significant effect was no longer apparent. Closer inspection of field notes indicates that the site where these particular data were collected was a muddy sand area noted to have collected a substantial amount of algae within the disturbed plot on that particular sampling occasion. Macroalgae had become caught around the bamboo canes marking out the disturbed plot and may have caused significant erosion or disturbance to the sediment structure within the plot as a result of tidal water movement.

4.4.4 Limitations of the equipment

Penetrometer measurements could be affected when there is a marked change in sediment grain size with depth into the sediment. Particle size selection by certain deposit feeders can alter the vertical structure of the sediment and result in a biogenically graded bed where organism densities are sufficiently high (e.g. Rhoads and Stanley, 1965). This would also result in marked changes in shear strength with depth, and thus affect the cone penetrometer readings. This is a problem common to granulometric techniques, where any vertical variation in grain size distribution is lost during the analysis of the sample. It is also important to note that whilst the penetrometer has proved useful over the range of typical intertidal sediments as measured in the present study, this may not easily be extrapolated to sediment habitats beyond this range. For instance, the shear strength of a gravel bed could not be measured with the device described herein as a cone of these dimensions would

not penetrate the bed. In addition, although penetration increased with 'muddiness' it is likely that the cohesive forces in a sediment dominated by clay particles would reduce penetration values despite the substratum containing a greater proportion of very fine particles.

4.4.5 Conclusions

This cone penetrometer equipment provides a useful method for the rapid assessment of sediment parameters. It should ideally be used for large scale survey work where a significant variety of soft sediment habitats would be encountered since it is not sensitive enough to detect smaller changes to sediment structure such as those resulting from physical disturbance events in intertidal areas. Care should be taken in interpreting data from heterogeneous habitats where factors other than shear strength might affect the penetration of the cone device (such as surface algae, pebbles or shells etc.). However, the strong relationship between penetration (and thus sediment shear strength) and other commonly measured sediment parameters could make this device very useful for the rapid *in situ* characterisation of benthic habitats.

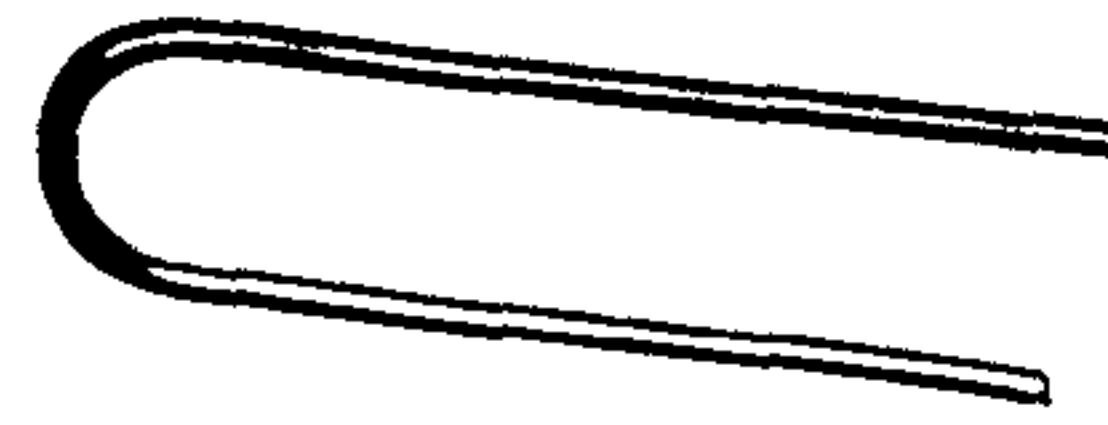
Chapter 5

Recovery of benthic communities following physical disturbance: an empirical test of predictions

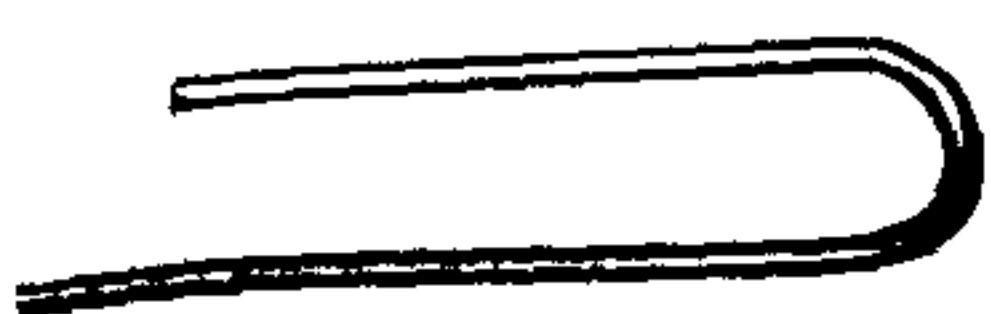
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Also available as:

Dernie, K. M., Kaiser, M. J. and Warwick, R. M. (2003). Recovery rates of benthic communities following physical disturbance. *Journal of Animal Ecology* 72.6: 1043-1056.



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Chapter 6

The response of individual taxa and functional groups to physical disturbance over a range of habitats

6.0 Abstract

Benthic assemblages are subject to a variety of different natural and anthropogenic physical disturbance regimes. It is anticipated that communities from areas of high natural levels of disturbance (e.g. shallow, wave exposed sandy habitats) will recover more rapidly from physical disturbance than communities from areas with subjected to low levels of natural disturbance (e.g. sheltered muddy habitats). However, since most studies have been restricted to investigating recovery of the benthos from one habitat type, it is difficult to draw all but general conclusions about responses of the fauna over a range of habitats. The present study examined the biological responses of intertidal soft sediment assemblages to a uniform physical disturbance treatment with particular reference to the relative importance of abiotic (i.e. sediment type) and biotic (taxa and functional components of the community) factors in determining the recovery rates of the disturbed assemblage. The results indicated that although the initial impact on the total numbers of individuals was more severe for the assemblages from muddy habitats, this was not apparent for individual taxa and functional groups, which responded similarly over all habitats. An investigation of the response of the total numbers of individuals to disturbance masked the different recolonisation patterns of certain key groups. For example the abundance of epibenthic mobile species exceeded ambient levels at the beginning of the experiment, whereas all other groups were found in reduced numbers within disturbed plots. Although the response of different taxa and functional groups differed from one another, the recovery rates of individual taxa were similar over all sediment types. This suggests that environmental factors did not directly influence the recovery rate of individual taxa and that biotic (behavioural and morphological adaptations) are more important in determining recovery rates. These findings are discussed in relation to the power of the experiment to elucidate the key factors in determining recovery rates.

6. 1 Introduction

Physical processes in the marine environment will determine to a varying extent both the physical characteristics of the seabed and its associated biota (Hall, 1994; Hall et al., 1994; Pearson, 2001). The impacts of anthropogenic physical disturbances such as bottom fishing (e.g. Kaiser and Jennings, 1998), bait digging (e.g. Brown and Wilson, 1997) and aggregate extraction (e.g. Kenny and Rees, 1996) occur globally over intertidal and shallow coastal shelf benthic habitats and occur against a background of a range of natural disturbance regimes. The ability of different benthic communities to recover from anthropogenic disturbances is a fundamental consideration with respect to the sustainability of such activities and is currently the focus of much research into the influence of human activities on benthic community structure and dynamics (e.g. Hall and Harding, 1997; Collie et al., 2000; Kaiser et al., 2002).

A dominant paradigm regarding the response of the infaunal community to a physical disturbance event is that communities that occur in areas subjected to high levels of natural disturbance will, in general, tend to recover more rapidly than those environments that typically experience low levels of natural physical disturbance (Collie et al, 2000; Auster and Langton, 1999; Kaiser, 1998). Examples of habitats that experience high levels of natural disturbance would include near-coast coarse sediments subjected to frequent tidal scour and severe wave action, whereas examples of low energy habitats would include sheltered embayments and estuarine mud sediments. This difference in the rate of response for different habitats may be attributable to the physical characteristics of the sediment, the environmental characteristics of the specific location and the life history traits of organisms that occur in the different habitats. In habitats that experience strong tidal currents, recovery of disturbed communities may be facilitated by bed load transport processes that transport adult fauna into defaunated areas (Hall et al., 1994). Additionally, many species typical of such habitats have behavioural and morphological adaptations that reduce their vulnerability to disturbances, including burrowing behaviours or high mobility, and short generation times that facilitate rapid recolonisation following disruption of the habitat (Gorzelay and Nelson, 1987). In contrast, communities that inhabit muddy, depositional environments experience less frequent physical disturbance events and hence tend to be longer-lived, slow growing species that will consequently have slower recolonisation rates (e.g. Sainsbury et al., 1998).

At present, it is difficult to construct quantitative, and generally applicable predictions of the response of benthic populations and communities to physical disturbance due to the specificity of individual published studies with respect to, for example, the scale and intensity of the initial disturbance, the time of year of the disturbance, and the geographic location (*sensu lato* Collie et al., 2000). It is necessary to test the association between the rate of recovery of the physical attributes of the sediment environment and its biological components if useable predictive tools are to be developed to facilitate sustainable management of marine sediment habitats (Dernie et al., 2003a). In a previous study, the recovery rate of the total abundance of infaunal invertebrates could be predicted based on the rate of habitat restoration (the rate of infilling of disturbed pits) (Dernie et al., 2003b). The aim of the current study was to investigate the effects of a uniform physical disturbance treatment applied to benthic communities across a range of soft sediment habitats and examine in detail the subsequent response of components (individual taxa and functional groups) of the community.

The analysis of community response can focus on a number of different taxonomic, behavioural and structural aspects of the assemblage. Most commonly, individuals are initially divided taxonomically into different species and genera. It is then possible to investigate the responses of different species within the community, which may differ greatly from the response of the assemblage taken as a whole. Presumably, an actively mobile species such as the errant, carnivorous polychaete *Nephtys hombergii*, would recolonise a disturbed area more quickly than a sedentary species such as the tubeworm *Lanice conchilega*, for example. Different species can be grouped together where they have common functional attributes that relate to fundamental processes such as feeding and relative motility (Pearson, 2001). This approach is useful as it crosses taxonomic boundaries and can be helpful for solving ecosystem level problems (Padilla and Allen, 2000). In the context of the present study, single species may be restricted to a limited range of sediment types and present in abundances too low to allow meaningful analysis. Studying groups of organisms with specific functional attributes may allow a better understanding of the responses of different key components of the benthic assemblage to physical disturbances. A number of functional group attributes have been used in benthic ecology studies, including relative mobility (Thayer, 1983), feeding behaviour (Fauchald and Jumars, 1979) and bioturbatory activity (Swift, 1993). Clearly, the focus of the individual study will determine the functional groupings considered. For the purposes of investigating the response to physical disturbance, the present study

included an analysis of groups of organisms with different relative mobility and from different feeding guilds. The importance of the relative motility of different groups of organisms has clear implications for the rate of recolonisation of disturbed and defaunated areas by different species (e.g. Beukema et al., 1999; Peck et al., 1999). The responses of different feeding groups are of interest in order to investigate the potential for specific feeding groups to utilise possible food resources that occur as a result of disturbance. Other studies have detected an influx of particular feeding groups into recently disturbed habitats (e.g. scavengers (Ramsay et al., (1998); Oliver and Slattery, (1985)).

The present study reports a detailed investigation of the response of a number of key taxa, taxonomic and functional groups following the application of a uniform physical disturbance treatment across a range of soft sediment habitats. In particular, the analysis focused on the relative importance of biotic (i.e. species/functional group) and abiotic (percentage silt and clay values of the sediment which will give an indication of the hydrodynamic regime) factors in determining this response.

6.2 Methods

6.2.1. Experimental design and sampling

Sixteen sites of varying sediment types were chosen along the Menai Strait, North Wales at approximately mid-shore level (Figure 6.1). Percentage silt and clay values of sediments from these sites were derived through granulometric analysis (see Buchanan and Kain, 1984) and ranged from clean sands (<2% silt and clay) to muds (>60% silt and clay). In a previous study (Dernie et al., (2003b); Ch 5), the rate of restoration of these habitats was found to be a useful predictor of the rate of recovery of total numbers of individuals in the community following a physical disturbance. However, habitat restoration data was only available for 12 of the 16 sites used during this experiment, thus percentage silt and clay data were used as the key habitat descriptor for the purposes of the present analyses. At each site two 1 x 4 m plots, positioned at least 5 m apart and parallel to the incoming tide, were marked out using bamboo canes. On the 12th of July, 2001, one plot at each site was subject to a physical disturbance treatment, which marked the beginning of the experiment. The treatment consisted of removing the upper 10 cm of sediment and depositing this material at least 50 m away from the disturbed plot. Control and disturbed plots were sampled at each site on day 15, 35, 63, 107 and 213 following the disturbance treatment. On each sampling occasion, four 90 mm diameter x 120 mm depth cores were taken haphazardly within each plot. These macrofaunal samples were sieved

over a 0.5 mm mesh sieve with seawater and the residue retained on the sieve fixed in 4% buffered formalin solution. Samples were subsequently washed in the laboratory and organisms identified to the lowest possible taxonomic level.

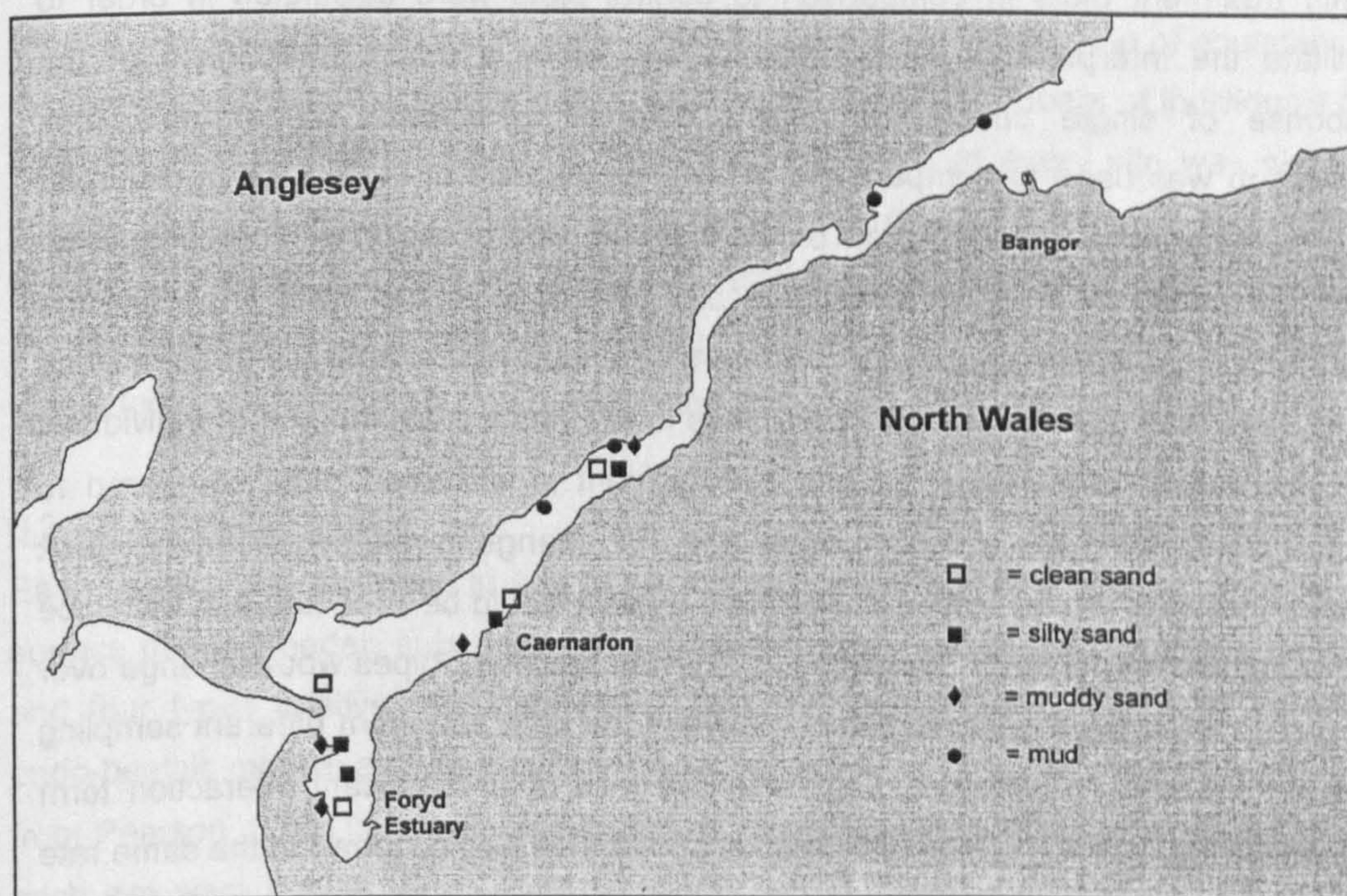


Figure 6.1: Position of experimental sites along the Menai Strait, North Wales. Sites are grouped according to the percentage silt and clay content of sediment: Clean sand sites (<3% silt and clay), silty sand (5-20% silt and clay), muddy sand (35-45% silt and clay) and muds (>55% silt and clay).

6.2.2 Statistical analysis

Community data from the four cores taken at each experimental plot at every site on each sampling occasion were amalgamated prior to any statistical analyses.

6.2.2.1 The total number of individuals

In order to compare the responses of individual components of the community to that of the entire assemblage, an initial analysis of the response of the total numbers of individuals at experimental sites was undertaken. The mean $\ln(n + 1)$ transformed number of individuals in control plots at each site over every sampling occasion was plotted against percentage silt and clay content. Analysis of variance (ANOVA) was

used to investigate trends in the overall abundance of individuals over different habitat types and to test for differences in the total abundances of individuals within control plots on the different sampling dates. Since the total number of individuals tended to vary substantially with habitat type, the relative abundance of individuals within treatment plots in comparison to control plots were calculated in order to facilitate the interpretation of the results and allow a direct comparison of the response of single species inhabiting different sediments. Spearman's rank correlation was used to compare the relative abundance of individuals in disturbed plots in comparison to control plots on the first sampling occasion with percentage silt and clay values in order to investigate any difference in the initial impact of the disturbance on assemblages within different sediment types. Analysis of covariance (ANCOVA) was used to test for differences in the relative abundance of individuals over increasing percentage silt and clay content in disturbed plots compared to control plots on the five sampling occasions. If a change in relative abundance took place at different rates in different sediment types it would be expected that the slope of the relative response of organisms in different sediment types would change over time and thus a significant interaction between the data sets from different sampling occasions would be detected. Conversely, a lack of a significant interaction term would indicate that any changes in relative abundance had occurred at the same rate over all sediment types. The relative data for the numbers of individuals in disturbed plots compared to control plots over all sites was plotted against time. Regression analysis was performed on the relative data to investigate whether there was a significant change relative abundance of individuals over time regardless of sediment type.

6.2.2.2 Individual taxa

Three species (the spionid polychaete, *Pygospio elegans*, the tellin bivalve, *Macoma balthica*, and the tubificid oligochaete, *Tubificoides benedii*), one genus (*Corophium* spp.) and two polychaete families (Cirratulidae and Capitellidae) were present at a majority (over 10) of the sites over the time-span of the experiment and were therefore selected for further analysis. The data were then analysed in a similar manner to the data for the total number of individuals. The mean abundance of individual taxa within control plots over all sampling dates was calculated and correlation analyses performed to determine their patterns over increasing percentage silt and clay content of the sediment. Correlation analysis was performed on relative responses of the key taxa on the first sampling occasion to investigate any difference in the initial disturbance impact on the same taxon over different

sediment types. ANCOVA was used to test for differences between the initial response of different taxa over different sediment types. Relative values of abundance were plotted for each sampling occasion. ANCOVA was used to investigate the effect of time and percentage silt and clay values on the relative response of different species/taxa, and any interaction between time and percentage silt and clay values that would indicate a disparity in the rate of change of abundance in different sediment types. In addition, the relative data for numbers of individuals of each taxon in disturbed plots compared to control plots at every site was plotted against time. Regression analyses were performed on these data to investigate whether there was a significant change in relative abundance over time. Where a significant response over time was detected, a further ANCOVA test was performed to test for significant differences between the responses of the different taxa.

6.2.2.3 Functional groups

Each species was assigned to one of six feeding guilds (active carnivore, omnivore, surface deposit feeder, subsurface deposit feeder, filter feeder and interface feeder and four types relative mobilities (tubicolous (i.e. sedentary), epi-benthic mobile, endo-benthic mobile, and semi-mobile) (see Table 6.1). These groups were adapted from Pearson, (2001) and references therein. The abundance data for each taxon at each site were pooled within each functional group. The mean abundances of the different functional groups in control plots at each site over the duration of the experiment were calculated. These abundances were converted to a proportion of the total number of individuals at each site to facilitate a comparison of community structure between different sites. The proportion of assemblages made up by each functional group within control sediments was plotted against percentage silt and clay content to investigate the existence of trends in the relative abundances of different functional groups within different sediment types. Correlation analyses were performed on these data to investigate any trends in proportional abundance of different functional groups with increasing percentage silt and clay content of the sediment. All subsequent analyses were performed on the relative abundances as for the individual taxa (Section 6.2.2.2).

6.3 Results

6.3.1 Total numbers of individuals

There was a significant increase in the numbers of individuals in control plots with increasing percentage silt and clay content of the sediment ($F_{1,79}=22.07$ $P<0.001$; Fig. 6.2a) but there was no significant difference in the numbers of individuals in

Table 6.1: Functional groupings assigned to species found at experimental sites along the Menai Strait.

Feeding groups (F): sdf = surface deposit feeder; ssdf- sub surface deposit feeder; ac=active carnivore, ff= filter feeder; if = interface feeder; om = omnivore.

Mobility (M): endo-b = endobenthic mobile; epi-b = epibenthic mobile; semi = semi-mobile

Species	M	F	Species	M	F
<i>Myriochele</i> spp	tub	sdf	<i>Capitomastus</i> spp	endo-b	ssdf
<i>Sphaerodopsis baltica</i>	endo-b	ssdf	Capitellidae	endo-b	ssdf
<i>Malmgrenia arenicolae</i>	epi-b	ac	Terribellidae	tub	ff
<i>Pholoe baltica</i>	epi-b	ac	<i>Eupolymnia</i> spp	tub	ff
<i>Mysta picta</i>	endo-b	ac	Ampharetidae	tub	ff
<i>Eumida sanguina</i>	endo-b	ac	<i>Amphicteis</i>	tub	ff
<i>Eteone</i> spp	endo-b	ac	Pectinaria	tub	ff
Phyllodoceidae spp	endo-b	ac	<i>Lanice conchilega</i>	tub	ff
<i>Glycera</i> spp.	endo-b	ac	<i>Owenia fusiformis</i>	tub	ff
<i>Micronephtys</i> spp	endo-b	ac	Sabellidae	tub	ff
Hesionidae	endo-b	ac	Oligochaeta	endo-b	ssdf
<i>Gyptis</i> spp.	endo-b	ac	<i>Tubificoides benedii</i>	endo-b	ssdf
<i>Exogone hebes</i>	endo-b	om	Enchytraeidae	endo-b	ssdf
<i>Hediste diversicolor</i>	endo-b	om	<i>Bathyporeia sarsi</i>	epi-b	sdf
<i>Nephtys</i> spp.	endo-b	om	<i>Gammarus salinus</i>	epi-b	o
<i>Scoloplos armiger</i>	endo-b	ssdf	<i>Corophium arenarium</i>	epi-b	sdf
<i>Aonides</i> spp.	semi	sdf	<i>Corophium volutator</i>	epi-b	sdf
<i>Polydora horseshoe</i>	semi	sdf	<i>Crangon crangon</i>	epi-b	ac
<i>Polydora straight</i>	semi	sdf	<i>Eurydice pulchra</i>	epi-b	ssdf
<i>Pygospio elegans</i>	semi	sdf	<i>Carcinus maenas</i>	epi-b	o
<i>Laonice</i> spp.	semi	sdf	<i>Hydrobia ulvae</i>	semi	ssdf
<i>Streblospio benedictii</i>	semi	sdf	<i>Retusa obtusa</i>	semi	ssdf
<i>Spiophanes bombyx</i>	semi	sdf	<i>Mysella bidentata</i>	semi	sdf
<i>Spio filicornis</i>	semi	sdf	<i>Cerastoderma edule</i>	semi	if
<i>Scololepis</i> spp.	semi	sdf	<i>Spisula subtruncata</i>	semi	sdf
<i>Spio martinensis</i>	semi	sdf	<i>Macoma balthica</i>	semi	if
Paraonidae	semi	sdf	<i>Scrobicularia plana</i>	semi	sdf
<i>Malacoceros</i> spp	semi	sdf	Juvenile bivalve indet.	semi	sdf
<i>Magelona filiformis</i>	semi	sdf	<i>Abra alba</i>	semi	sdf
<i>Tharyx</i> spp	endo-b	sdf	<i>Fabulina fabula</i>	semi	sdf

control plots on the different sampling occasions ($F_{4,79}=0.57$, $P=0.683$), suggesting that there were no large fluctuations in overall abundance during the course of this experiment. The relative abundance of individuals was significantly correlated with the percentage silt and clay content of the sediment on the first sampling occasion ($r_s=-0.632$, $P=0.009$). Communities from sandier sediments exhibited a less negative response to the disturbance than the communities from muddier habitats (Fig. 6.2b). Relative abundances increased (i.e. became less negative) over time (Fig. 6.2c). Analysis of covariance revealed a significant effect of time ($F_{4,77}=12.70$, $P<0.001$) and percentage silt and clay content ($F_{1,77}=21.31$, $P<0.001$) on the relative

abundance of individuals in disturbed plots compared to control plots. There was no significant interaction term for this test ($F_{4,66}=1.06$, $P=0.383$), indicating that the rate of change in relative abundances was similar over all habitat types (see also Fig 6.2c). Analysis of variance of the relative response of individuals over all habitat types indicated a significant increase in relative abundance over time ($F_{1,75}=29.64$, $P<0.001$) (Fig. 6.3).

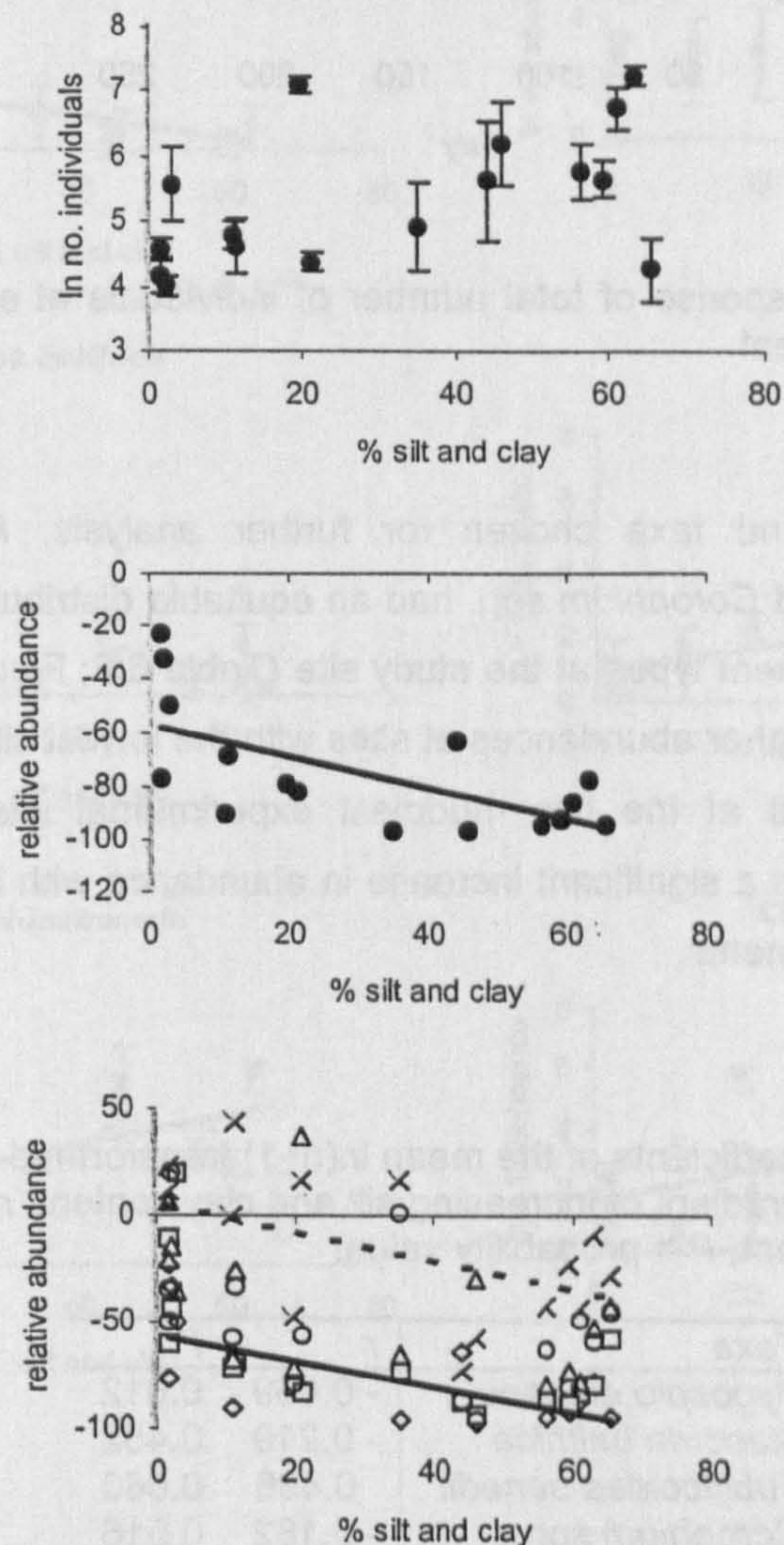


Figure 6.2: a) Mean total $\ln(n + 1)$ abundance of individuals within control plots over the experimental period. Error bars represent 95 % confidence intervals, b) Relative response of individuals on day 15 c) Relative response of individuals on day 15 (open diamonds), 35 (open squares), 63 (open triangles), 107 (open circles) and 213 (crosses). Solid trend line = community response over sediment type on day 15, dotted trend line = community response over sediment type day 213. Trend lines for the response on other dates omitted to improve clarity.

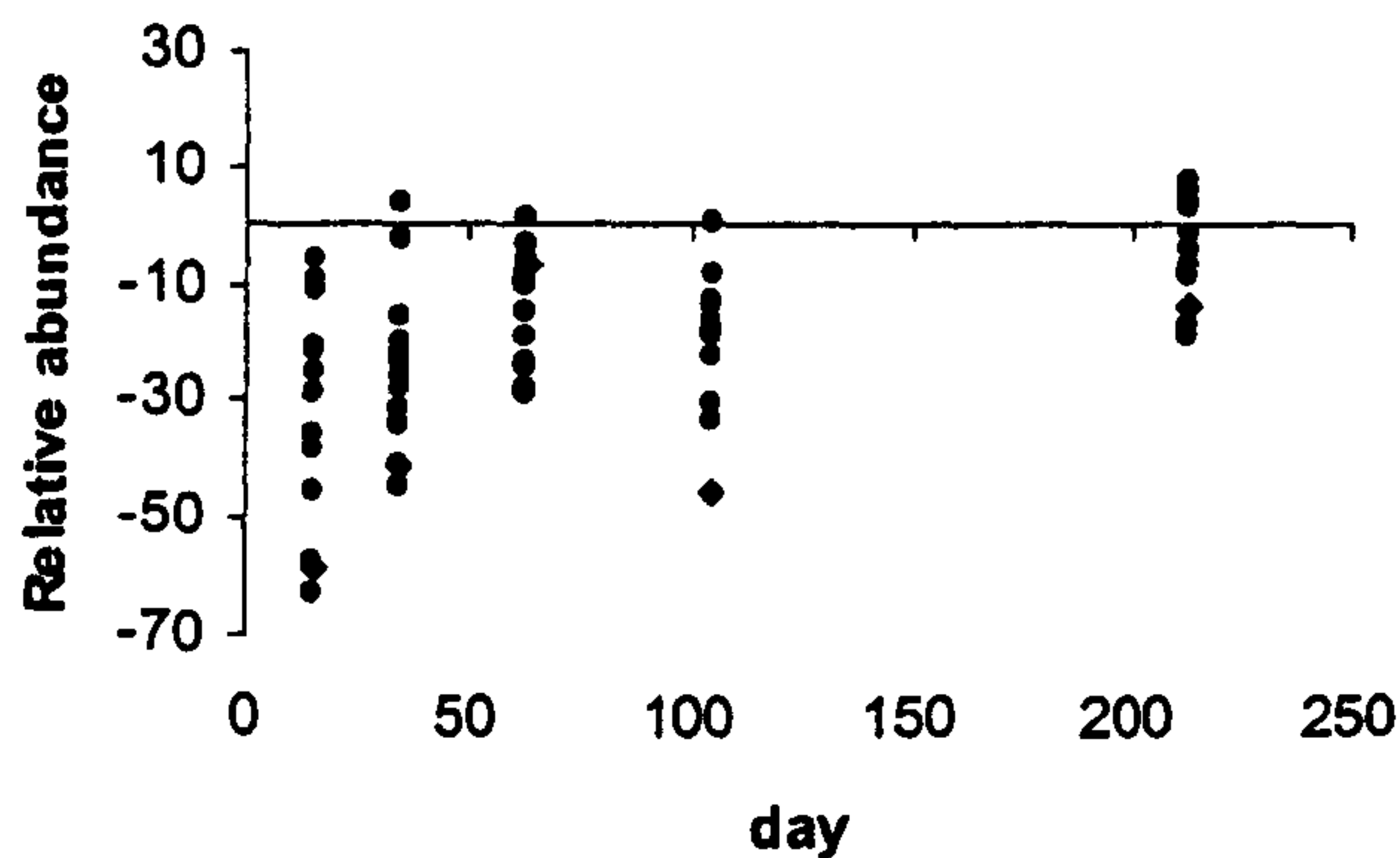


Figure 6.3: Relative response of total number of individuals at every site over the duration of the experiment.

6.3.2 Individual taxa

Of the six species and taxa chosen for further analysis, *Macoma balthica*, *Tubificoides benedii* and *Corophium* spp. had an equitable distribution of abundance over the range of sediment types at the study site (Table 6.2; Figure 6.4). *Pygospio elegans* was found in higher abundances at sites with the lowest silt and clay content while none were found at the two muddiest experimental sites. Cirratulid and capitellid worms showed a significant increase in abundance with increasing silt and clay content of the sediments.

Table 6.2 Correlation coefficients of the mean $\ln(n+1)$ transformed abundance of individual taxa along a gradient of increasing silt and clay content. r_s = Spearman's rank correlation coefficient, P = probability value.

Taxa	r	P
<i>Pygospio elegans</i>	- 0.669	0.012
<i>Macoma balthica</i>	- 0.219	0.452
<i>Tubificoides benedii</i>	0.496	0.060
<i>Corophium</i> spp.	- 0.182	0.516
Cirratulidae	0.574	0.032
Capitellidae	0.648	0.009

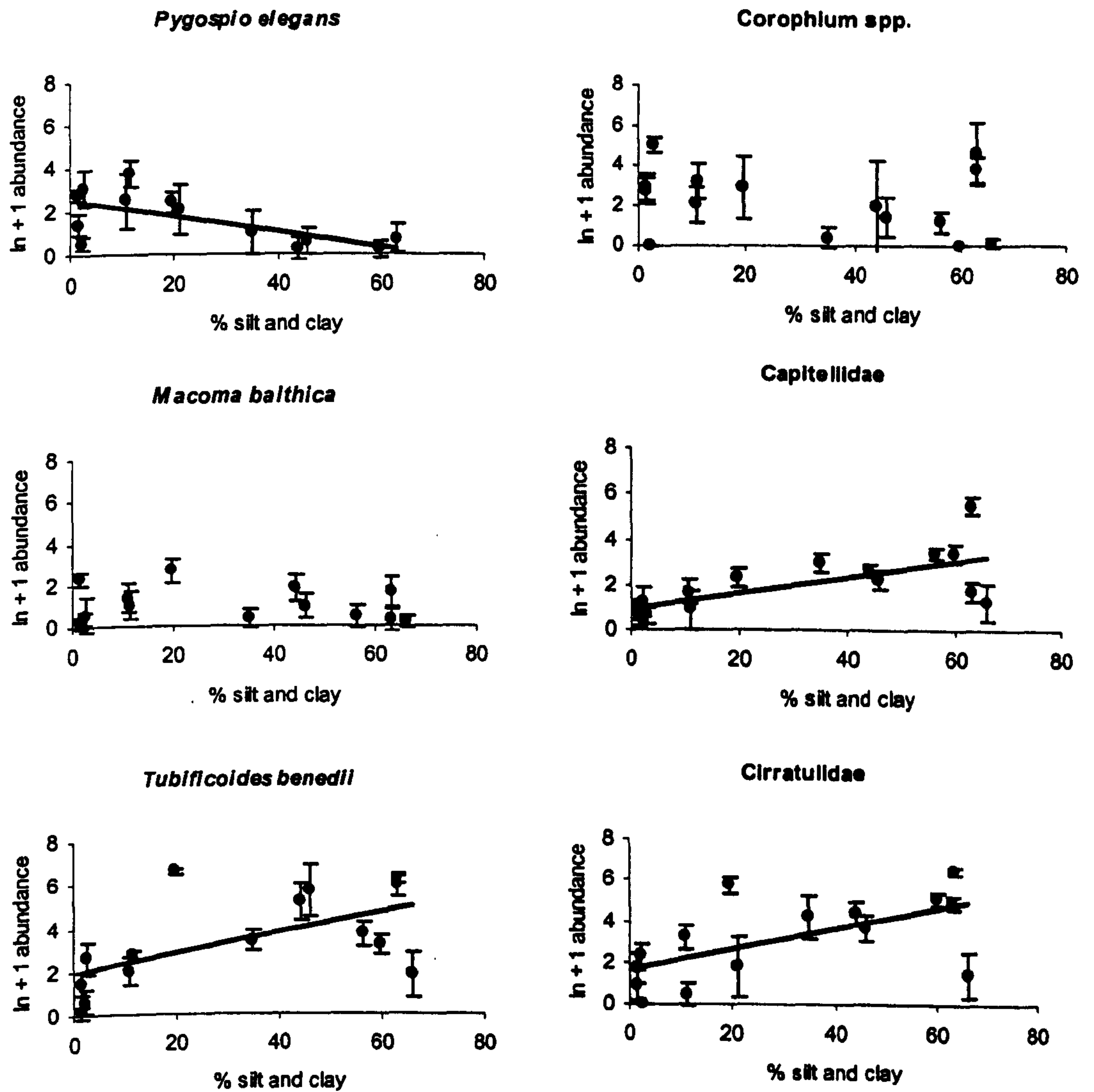


Figure 6.4 Mean abundance of key species/taxa present within control plots at experimental sites over the duration of the experiment. Error bars represent 95% confidence intervals.

For each individual taxon studied, the abundance within the disturbed plots was generally lower than that in the control plots on the first sampling occasion (15 days following the initial disturbance). However, for *M. balthica* and *P. elegans* this response appeared more negative in the sandier sediments (Fig. 6.5). Although some trends were apparent between the magnitude of the initial response to physical disturbance and increasing silt and clay content of the sediments, none of these correlations were significant (Fig. 6.5, Table 6.3.). This suggests that the initial impact of the disturbance treatment was similar for all of the taxa analysed regardless of the habitat type from which they were sampled. Analysis of covariance of these data detected no significant effect of sediment type ($F_{1,75}=0.2$, $P=0.656$) and no significant difference in the initial response of the different species ($F_{5,75}=1.73$, $P=0.14$)

Table 6.3: Correlation analyses of the response of key taxa to physical disturbance along a gradient of increasing silt and clay content on the first sampling occasion (day 15). r_s = Spearman's rank correlation coefficient, P = probability value.

<i>Taxa</i>	r_s	P
<i>Pygospio elegans</i>	0.502	0.096
<i>Macoma balthica</i>	0.189	0.655
<i>Tubificoides benedii</i>	- 0.385	0.141
Corophium spp.	- 0.213	0.465
Cirratulidae	0.103	0.764
Capitellidae	- 0.114	0.687

All of the taxa examined showed a trend of increasing relative abundance (i.e. a less negative response) within disturbed plots compared to control plots over the course of the experiment with the exception of *Macoma balthica*. This species exceeded control abundances in the disturbed plots with the highest silt and clay content on the first sampling occasion and had declined to approximately ambient levels on the last sampling date (Fig. 6.6). ANCOVA detected a significant difference with time for the response of *Tubificoides benedii* (Table 6.4), which occurred in higher relative abundances in disturbed plots in comparison to control plots in the sandier sites over the duration of the experiment. Nevertheless, there were no significant interaction terms from any of the above tests indicating that the recovery of individual taxa occurred at a similar rate (decline in relative abundance per day) in all habitat types.

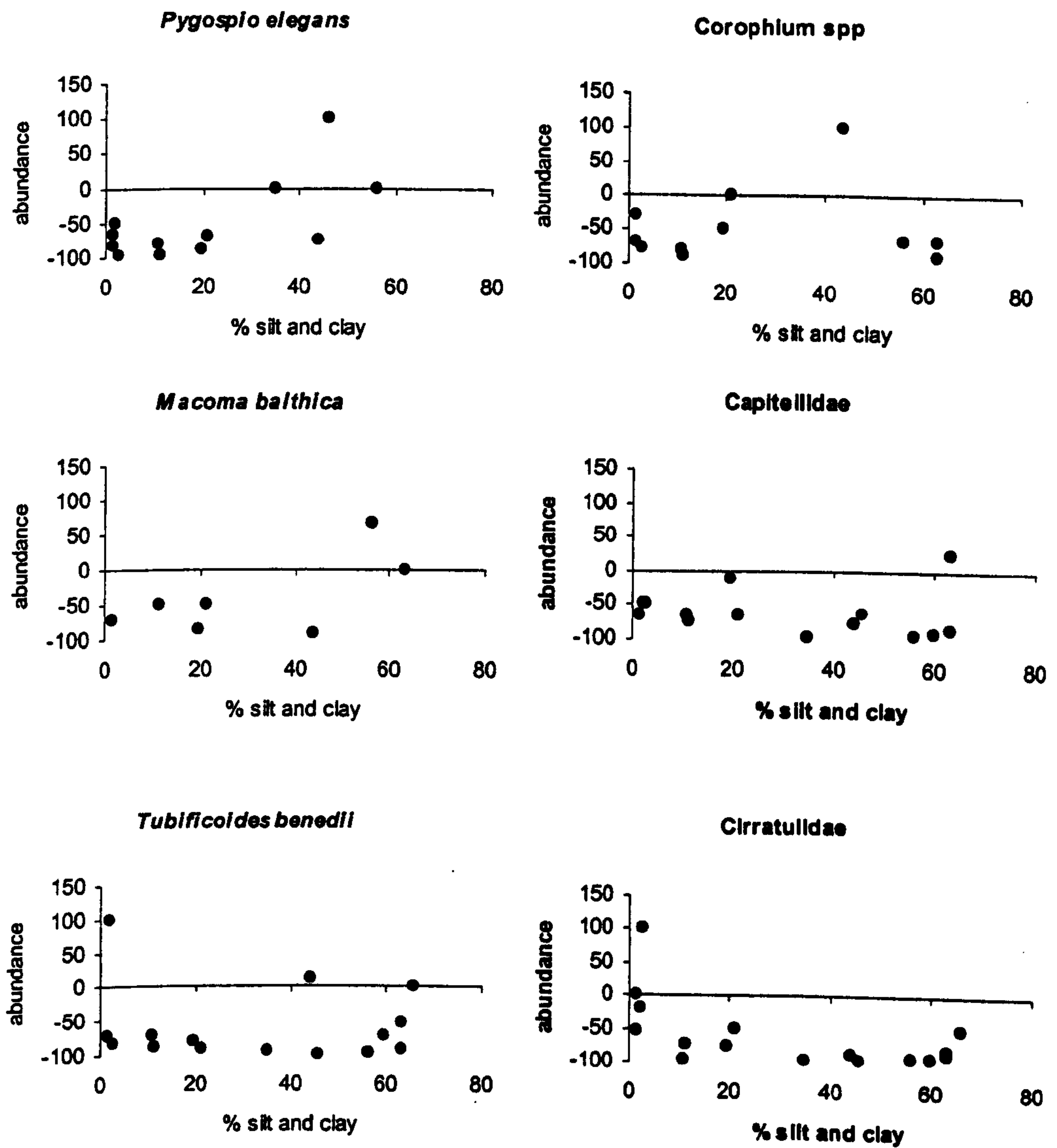


Figure 6.5: Relative $\ln + 1$ abundance of key species/taxa within disturbed plots compared to control plots over a range of sediment types on the first sampling occasion (15 days following the disturbance treatment).

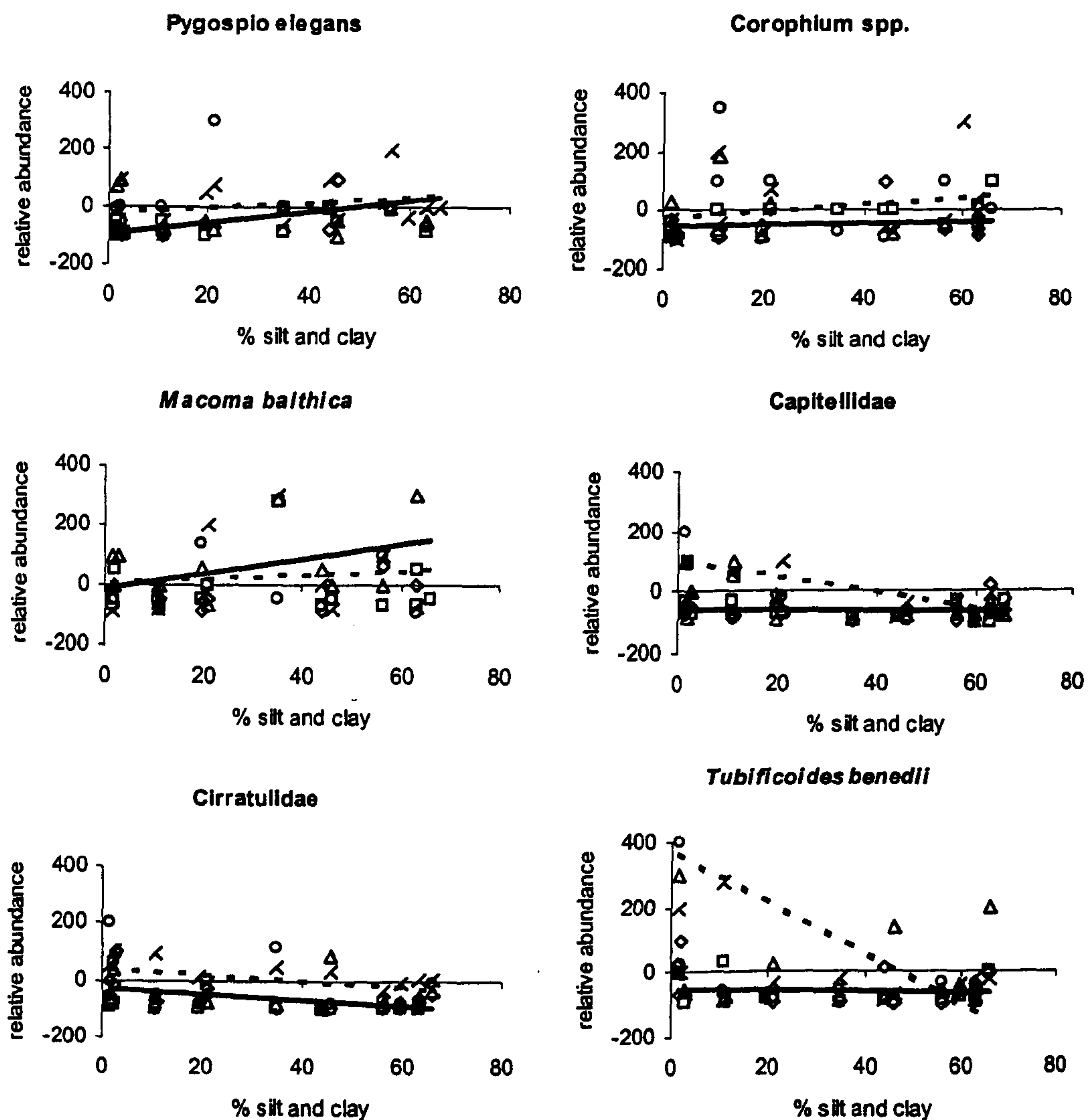


Figure 6.6: Relative response of key taxa within disturbed plots compared to control plots on day 15 (open diamonds), 35 (open squares), 63 (open triangles), 107 (open circles) and 213 (crosses). Solid trendline = community response over sediment type on day 15, dotted trendline = community response over sediment type day 213. Trendlines for the response on other dates omitted to improve clarity.

Table 6.4: ANCOVA table for the relative abundance of the key species/taxa on every sampling date.

	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>F</i>	<i>P</i>
<i>Pygospio elegans</i>					
Sediment type	1	8.22	8.22	6.84	0.01
Day	4	11.95	2.99	2.48	0.05
Interaction	4	5.77	1.44	1.2	0.32
Residual	56	67.32	1.2		
<i>Macoma balthica</i>					
Sediment type	1	0.61	0.1	0.52	0.47
Day	4	3.22	0.81	0.69	0.60
Interaction	4	1.75	0.4	0.37	0.83
Residual	46	53.85	1.17		
<i>Tubificoides benedii</i>					
Sediment type	1	5.59	5.59	3.4	0.07
Day	4	17.91	4.48	2.73	0.04
Interaction	4	3.99	0.99	0.61	0.66
Residual	65	16.79	1.64		
<i>Corophium</i> spp.					
Sediment type	1	9.89	9.89	8.29	0.006
Day	4	1.8	0.45	0.38	0.82
Interaction	4	3.67	0.92	0.77	0.55
Residual	52	62.04	1.19		
Cirratulidae					
Sediment type	1	11.07	11.07	7.76	0.007
Day	4	21.25	5.31	3.72	0.009
Interaction	4	10.93	0.23	0.16	0.96
Residual	61	87.08	1.43		
Capitellidae					
Sediment type	1	9.36	9.36	8.7	0.004
Day	4	3.47	0.87	0.52	0.52
Interaction	4	2.19	0.55	0.52	0.723
Residual	64	67.56	1.06		

There was a significant increase in the relative abundances of *P. elegans*, *T. benedii* and Cirratulidae in disturbed plots compared to control plots over the duration of the experiment (Table 6.5, Fig. 6.7). Although positive correlation coefficients also indicated a trend for increasing relative abundances for the other groups (*Corophium* spp., *M. balthica* and Capitellidae), these were not significant. ANCOVA tests were used to compare the regressions for the response of *P. elegans*, *T. benedii* and Cirratulidae over time, these confirmed that the response relative to control plots varied significantly with time ($F_{1,179}=39.21$, $P<0.001$) and that there was a significant difference in the response between different species ($F_{2,179}=3.33$, $P=0.038$). However, there was no significant interaction term for this test ($F_{1,179}=1.11$, $P=0.33$) indicating that the rate of change in relative abundance of these species was similar over time.

Table 6.5: Spearman's rank correlation coefficients for the relative abundance of key species/taxa with time (days).

<i>Taxa</i>	r_s	P
<i>Pygospio elegans</i>	0.363	0.003
<i>Macoma balthica</i>	0.038	0.781
<i>Tubificoides benedii</i>	0.362	0.001
Corophium spp.	0.239	0.061
Cirratulidae	0.476	<0.001
Capitellidae	0.218	0.062

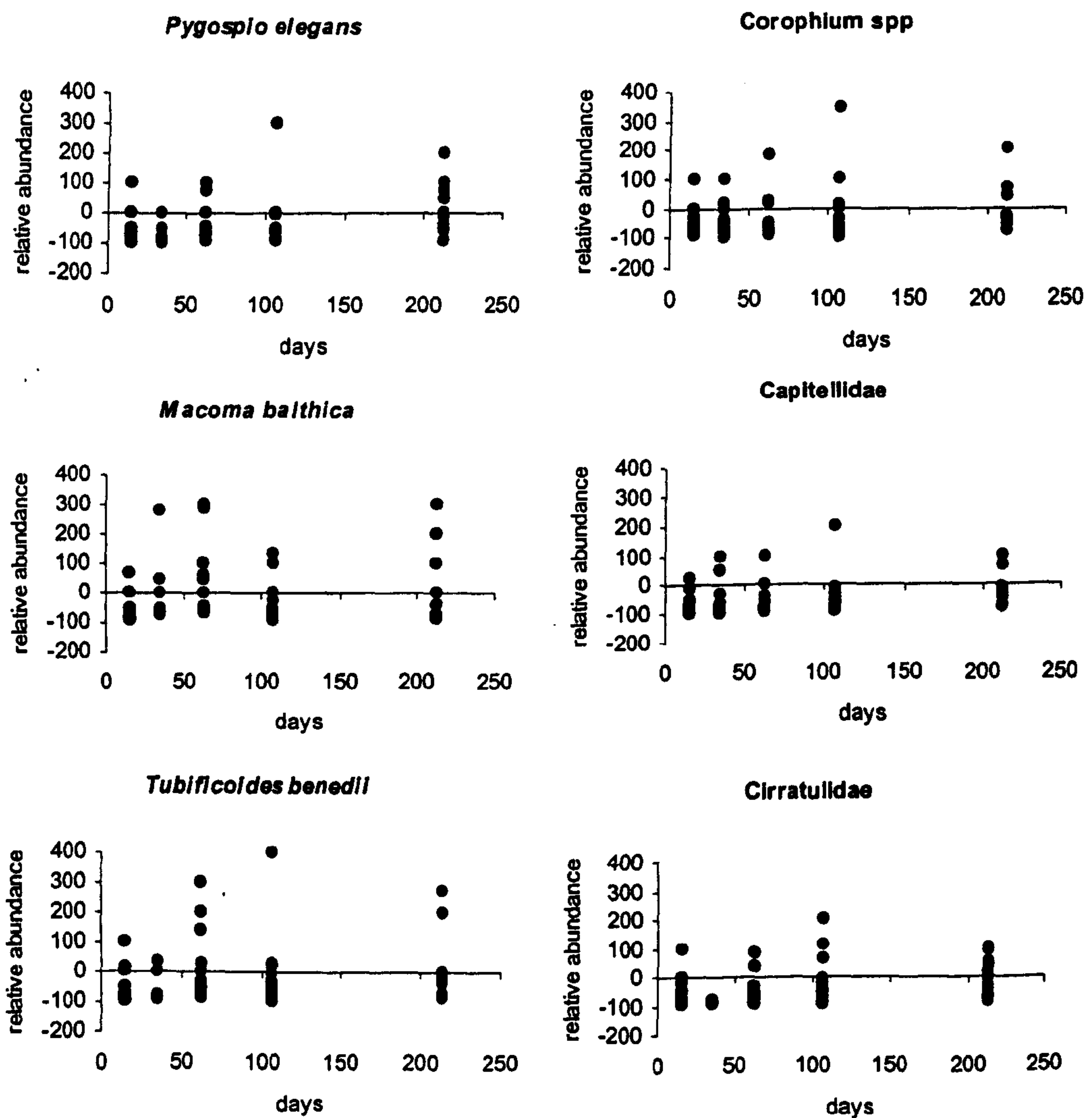


Figure 6.7: Relative response of key taxa at every site over time.

6.3.3 Functional Groups

Feeding types

A significantly larger proportion of active carnivores and interface feeders occurred within the sandier sediments than in the muddier sediments, whilst surface deposit feeders represented a larger proportion of the communities in muddier sediments (Table 6.6, Fig. 6.8). Filter feeders and sub-surface deposit feeders were present in similar proportional abundances within communities from different sediment types

Table 6.6: Spearman's rank correlation coefficients for the proportional abundance of feeding groups in control plots with percentage silt and clay content.

<i>Feeding group</i>	r_s	P	n
Active carnivore	-0.524	0.04	11
Filter feeder	-0.1	0.71	9
Interface feeder	-0.759	0.001	2
Omnivore	-0.426	0.01	5
Surface deposit feeder	0.012	0.97	22
Subsurface deposit feeder	-0.029	0.91	10

None of the feeding groups displayed any significant difference in response over the range of sediment types on the first sampling occasion, indicating that the initial impact of the disturbance was similar in all habitats (Table 6.6). Accordingly, ANCOVA detected no significant effect of sediment type ($F_{1,75}=3.63$, $P=0.06$). However, there was a significant difference in the response of the different feeding groups to the disturbance ($F_{5,75}=3.9$, $P=0.003$).

Table 6.6: Correlation analyses of the relative abundance of feeding groups within disturbed plots compared to control plots along a gradient of increasing silt and clay content on the first sampling occasion (day 15). r_s = Spearman's rank correlation coefficient, P = probability value.

<i>Feeding group</i>	r_s	P
Active carnivore	-0.16	0.56
Filter feeder	-0.25	0.43
Interface feeder	-0.13	0.63
Omnivore	0.2	0.45
Surface deposit feeder	-0.39	0.13
Subsurface deposit feeder	-0.3	0.26

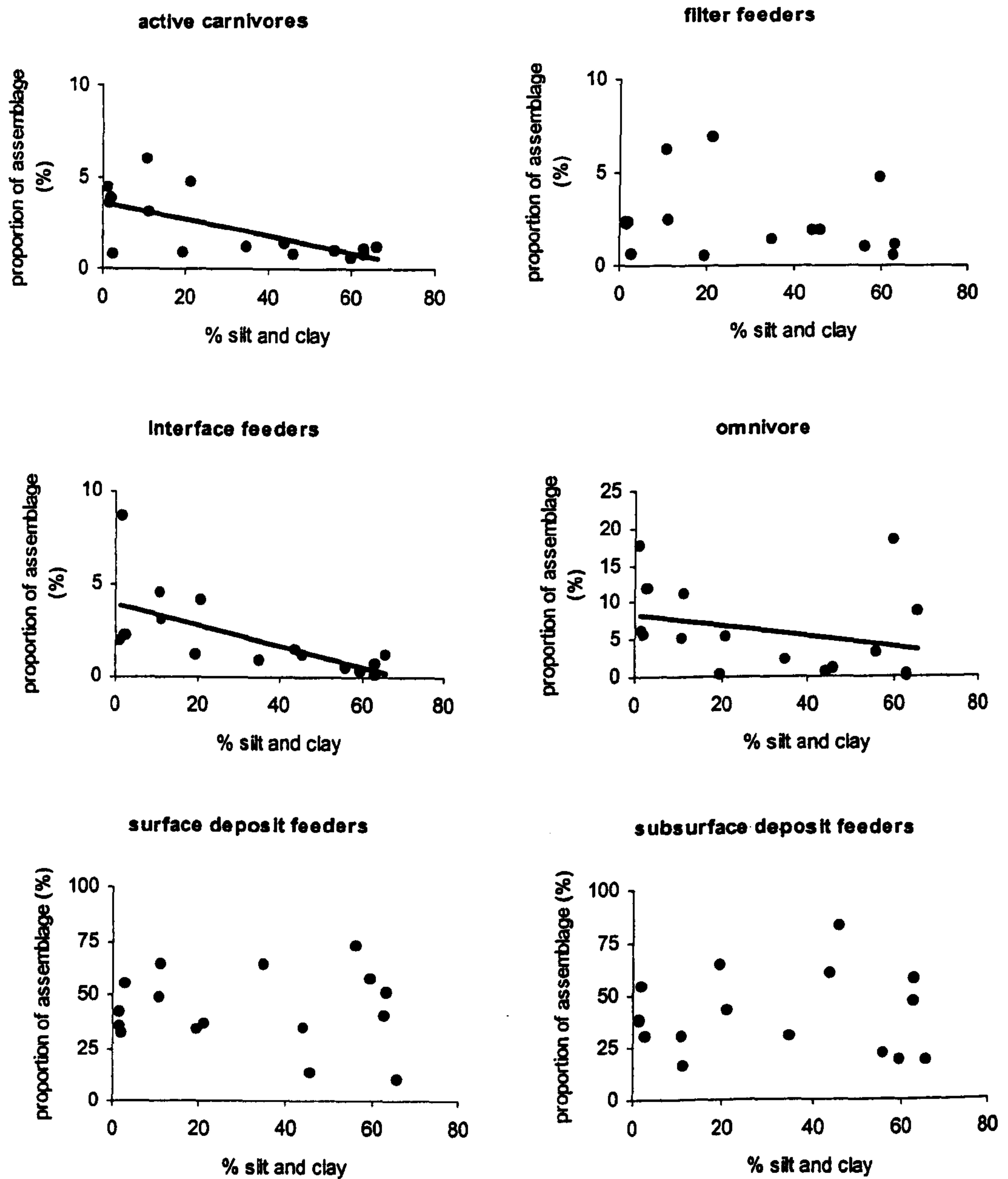


Figure 6.8: The percentage proportion of different feeding groups within assemblages over different sediment types. Note that different scales have been used to improve clarity.

ANCOVA analyses revealed no significant difference or interaction between the relative abundances of the feeding groups in different sediment types with time (Table 6.8; Fig. 6.10). However, a test of the response data for every sampling occasion did indicate a significant effect of sediment type on the response of the filter-feeding group.

Table 6.8: ANCOVA table for the relative abundance of different feeding groups on the every sampling date.

	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>F</i>	<i>P</i>
Active carnivore					
Sediment type	1	1.77	1.77	2.36	0.13
Day	4	5.13	1.28	1.71	0.16
Interaction	4	0.3	0.07	0.1	0.98
Residual	61	45.6	0.75		
Filter feeder					
Sediment type	1	4.6	4.6	5.9	0.02
Day	4	1.9	0.5	0.64	0.64
Interaction	4	1.94	0.48	0.62	0.65
Residual	58	45.22	0.78		
Interface feeder					
Sediment type	1	0.48	0.48	0.34	0.56
Day	4	0.81	0.20	0.14	0.96
Interaction	4	0.62	0.16	0.11	0.96
Residual	41	57.2	1.39		
Omnivore					
Sediment type	1	0.01	0.01	0.01	0.93
Day	4	3.92	0.98	1.28	0.29
Interaction	4	3.16	0.79	1.03	0.4
Residual	58	44.55	0.79		
Surface deposit feeder					
Sediment type	1	0.54	0.54	0.64	0.43
Day	4	8.29	2.07	2.45	0.06
Interaction	4	0.76	0.19	0.22	0.92
Residual	68	44.85	0.77		
Subsurface deposit feeder					
Sediment type	1	2.51	2.51	2.61	0.11
Day	4	4.47	1.12	1.16	0.34
Interaction	4	1.87	0.47	0.49	0.75
Residual	67	64.46	0.96		

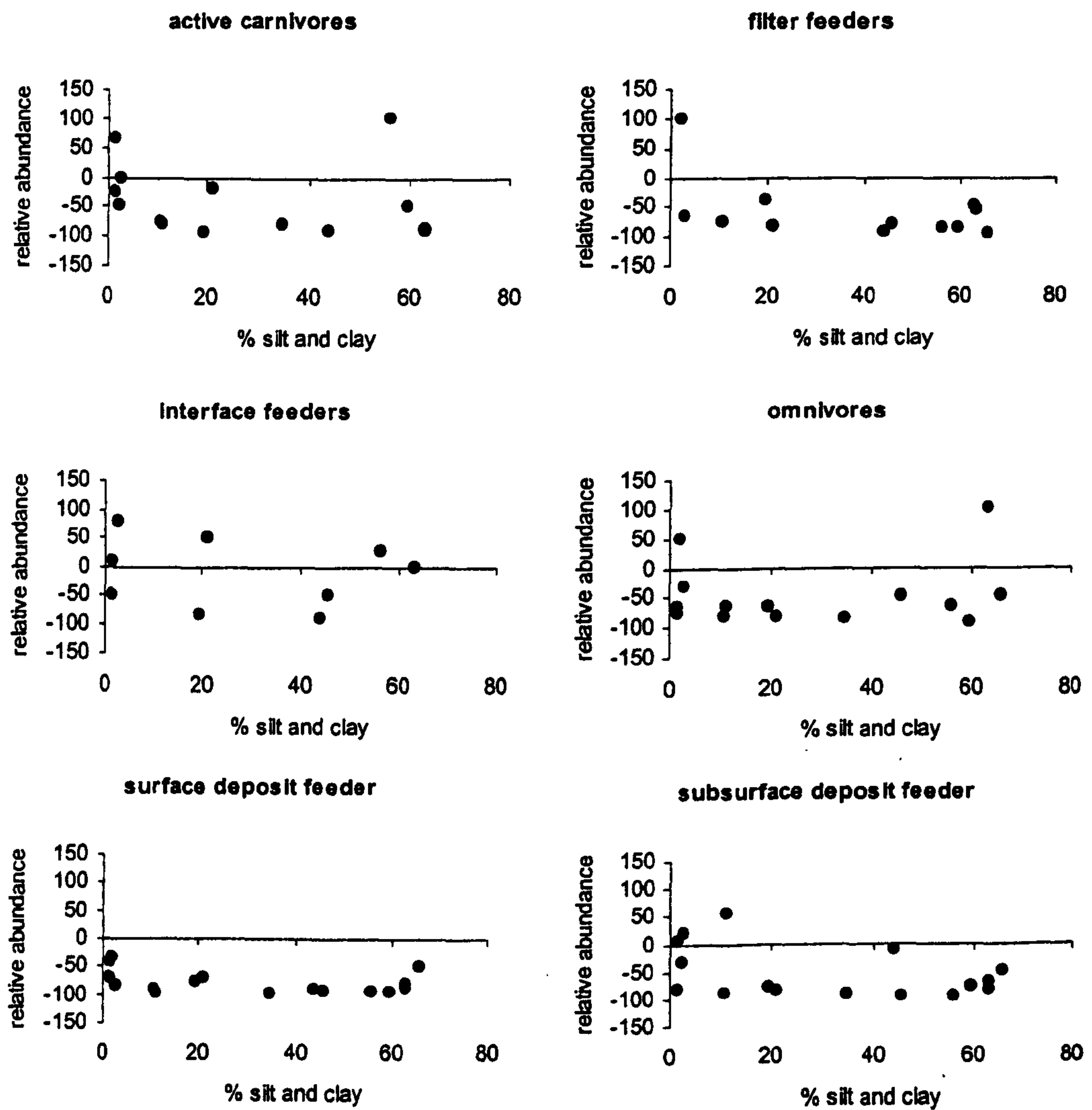


Figure 6.9: The relative abundances of feeding groups within disturbed plots compared to control plots along a gradient of increasing silt and clay content on the first sampling occasion (day 15).

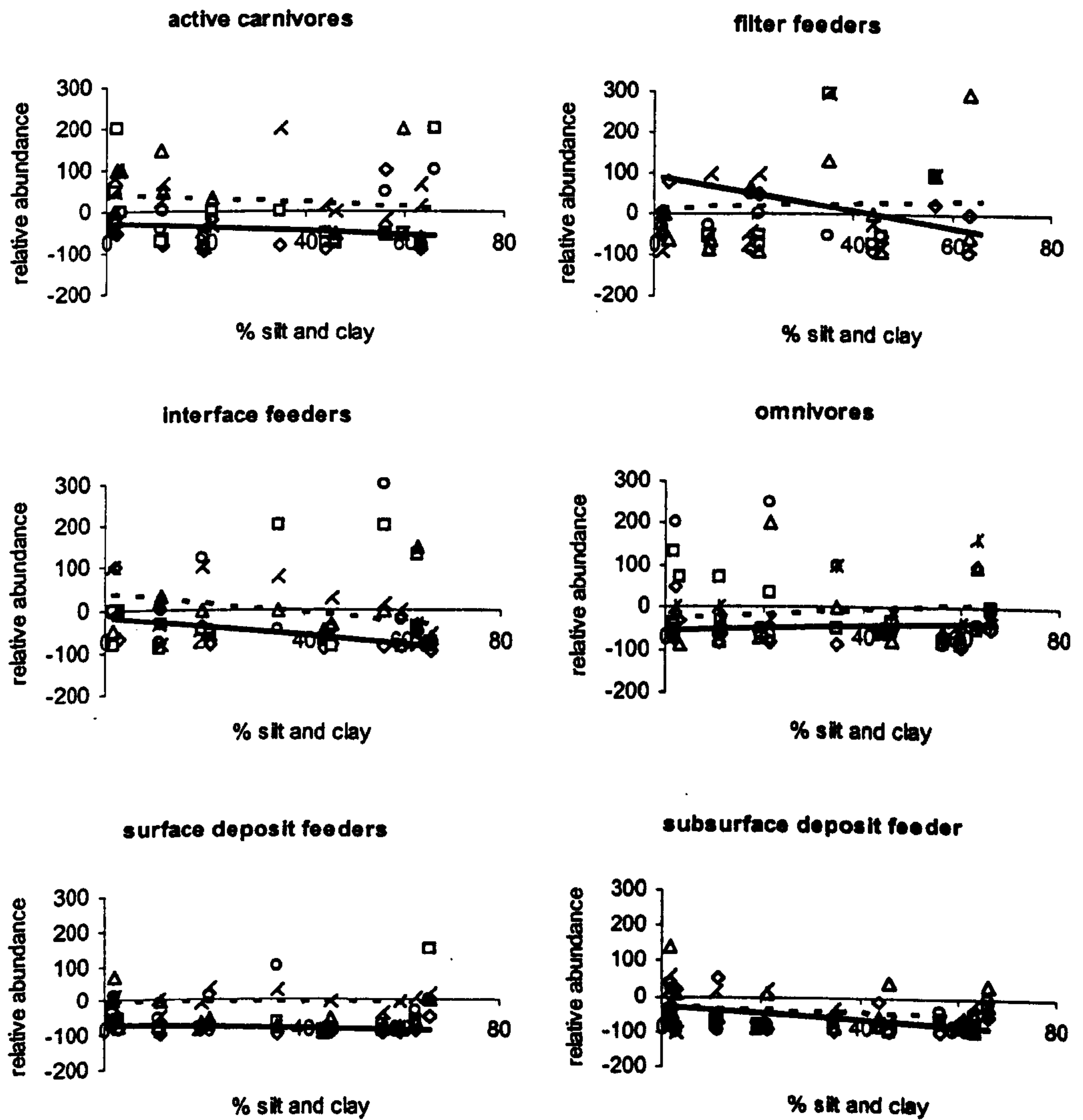


Figure 6.10: Relative response of different feeding groups within disturbed plots compared to control plots on day 15 (open diamonds), 35 (open squares), 63 (open triangles), 107 (open circles) and 213 (crosses). Solid trendline = community response over sediment type on day 15, dotted trendline = community response over sediment type day 213. Trendlines for the response on other dates omitted to improve clarity.

There was a significant increase in the relative abundance of active carnivores, filter feeders, surface deposit feeders and sub-surface deposit feeders in disturbed plots compared to control plots over the duration of the experiment (Table 6.8, Fig. 6.11). ANCOVA of the relative abundance data for these groups indicated a significant difference in the responses of the four groups ($F_{3,286}=7.29$, $P<0.001$) and confirmed a significant effect of time ($F_{1,286}=42.73$, $P<0.001$). There was no significant interaction between these data, indicating that the rate of change of relative abundance over time was similar for all groups.

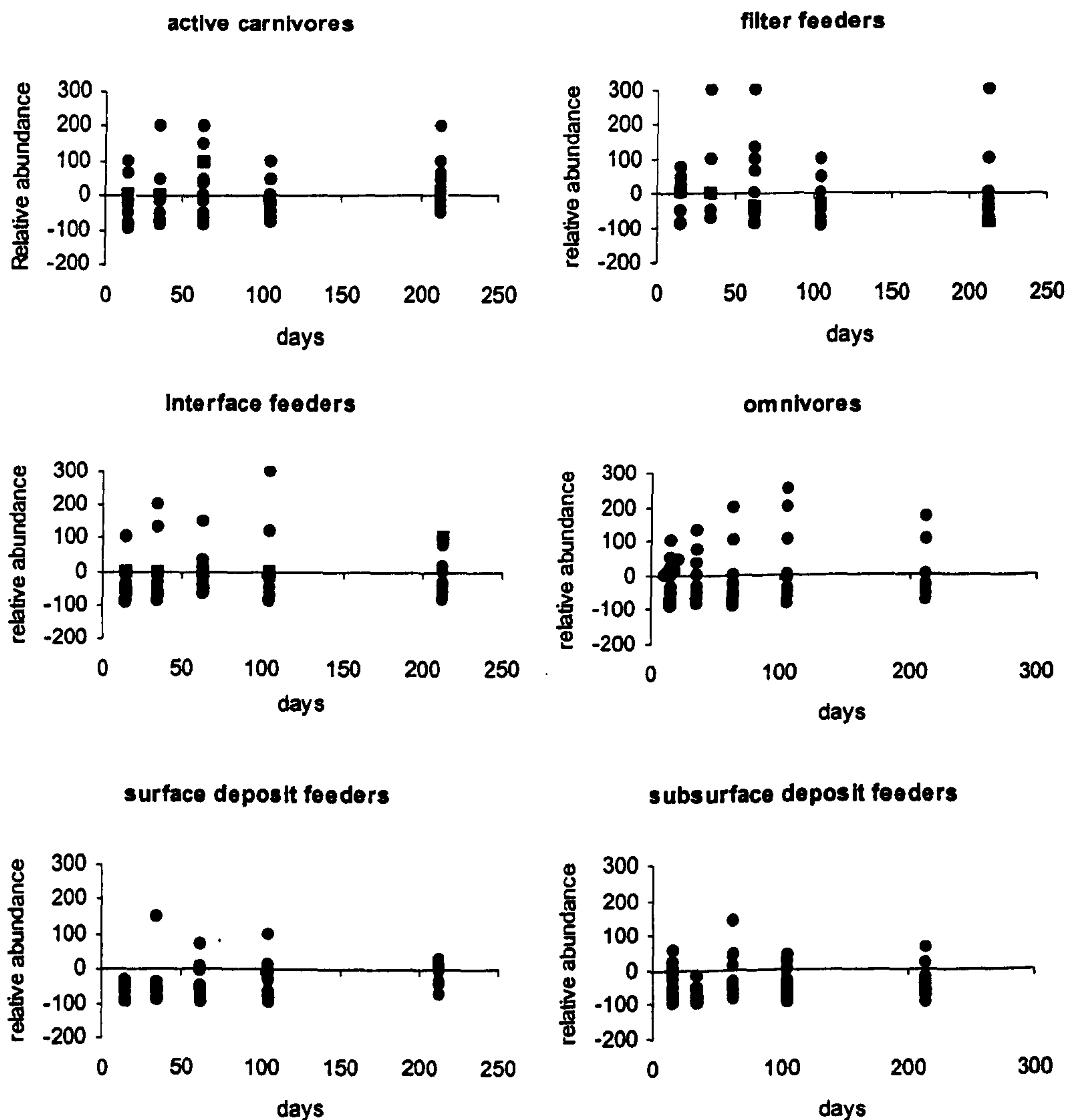


Figure 6. 11 Relative response of feeding groups at all sites over time.

Table 6.9: Spearman's rank correlation coefficients for the relative abundance of feeding groups with time (days).

<i>Feeding group</i>	r_s	P
Active carnivore	0.334	0.004
Filter feeder	0.319	0.008
Interface feeder	-0.053	0.714
Omnivore	0.23	0.059
Surface deposit feeder	0.582	<0.001
Subsurface deposit feeder	0.234	0.038

Mobility

Epi-benthic mobile and semi-mobile groups within assemblages were present in higher proportions in the sediments that had the lowest percentage silt and clay content (Table 6.10, Fig. 6.12). Endo-benthic and tubicolous organisms were evenly distributed over the range of sediment types present in this study (Fig. 6.12). Correlation analyses detected no relationship between the initial responses of endo-benthic mobile, epi-benthic mobile or semi-mobile groups across the different sediment types. Disturbed muddy sediments supported a lower relative abundance of tubicolous organisms than the sandier sediments (Table 6.11, Figure 6.13). However, ANCOVA revealed detected no significant effect of sediment type on the initial impact of the disturbance treatment for any group ($F_{1,57} P=0.86$). There was a highly significant difference in the relative response of the different mobility groupings ($F_{3,57}=25.49, P=0.001$). This was attributable to the increased relative abundance of epi-benthic mobile individuals in disturbed plots while all other mobility types decreased in abundance within disturbed areas (Fig. 6.13).

Table 6.10: Spearman's rank correlation of proportions of different mobility types in sites with percentage silt and clay content of sediment.

<i>Mobility</i>	r_s	P	n
Endo-benthic mobile	0.374	0.154	22
Epi-benthic mobile	-0.682	0.004	8
Semi-mobile	-0.847	<0.001	21
Tubicolous	0.3	0.259	9

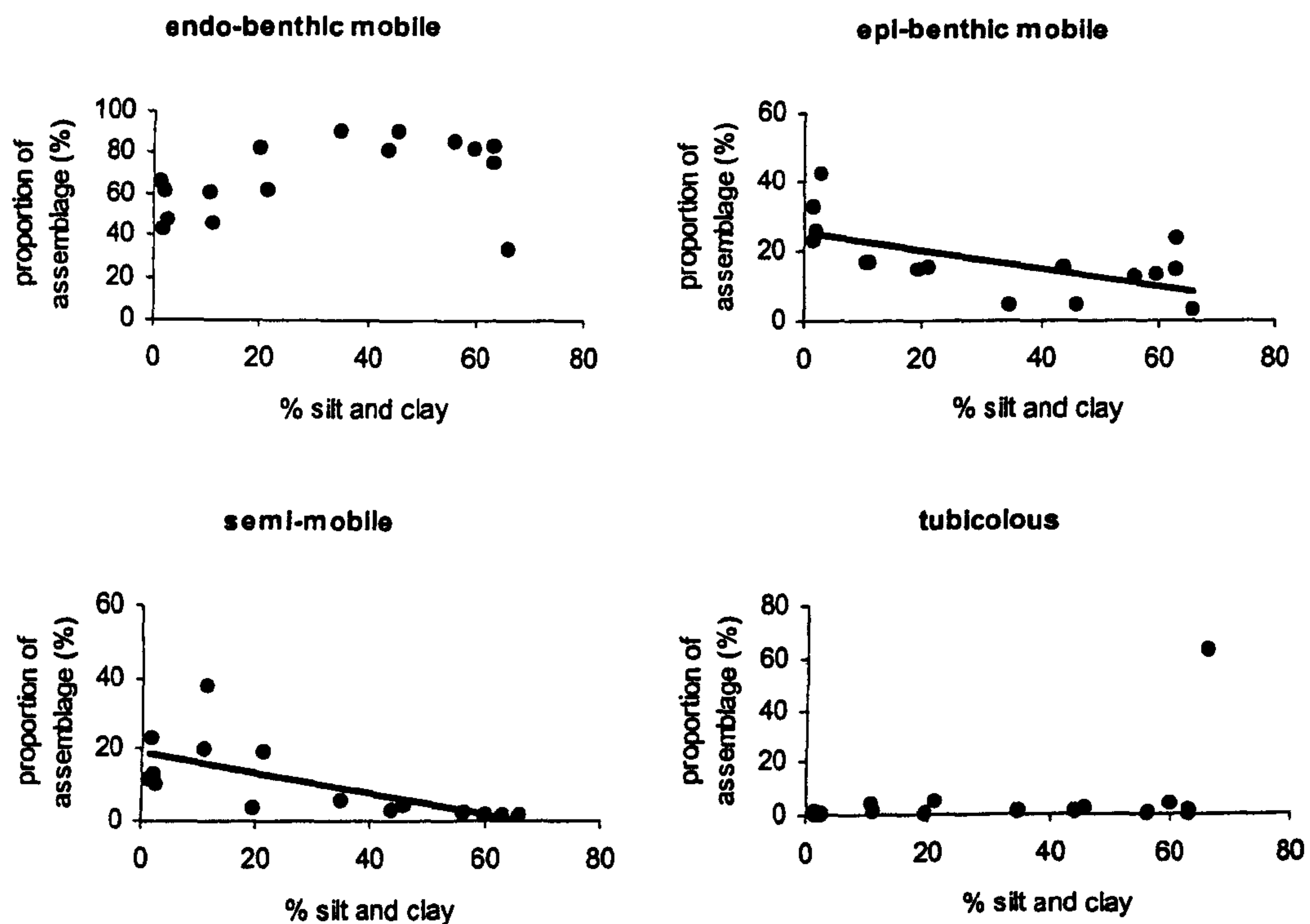


Figure 6.12: The percentage proportion of different mobility groups within assemblages over different sediment types.

Table 6.11: Correlation analyses of the relative abundance of different groups of mobility along a gradient of increasing silt and clay content on the first sampling occasion (day 15). r_s = Spearman's rank correlation coefficient, P = probability value.

<i>Mobility</i>	r_s	P
Endo-benthic mobile	-0.24	0.37
Epi-benthic mobile	-0.28	0.29
Semi-mobile	0.31	0.24
Tubicolous	-0.64	0.008

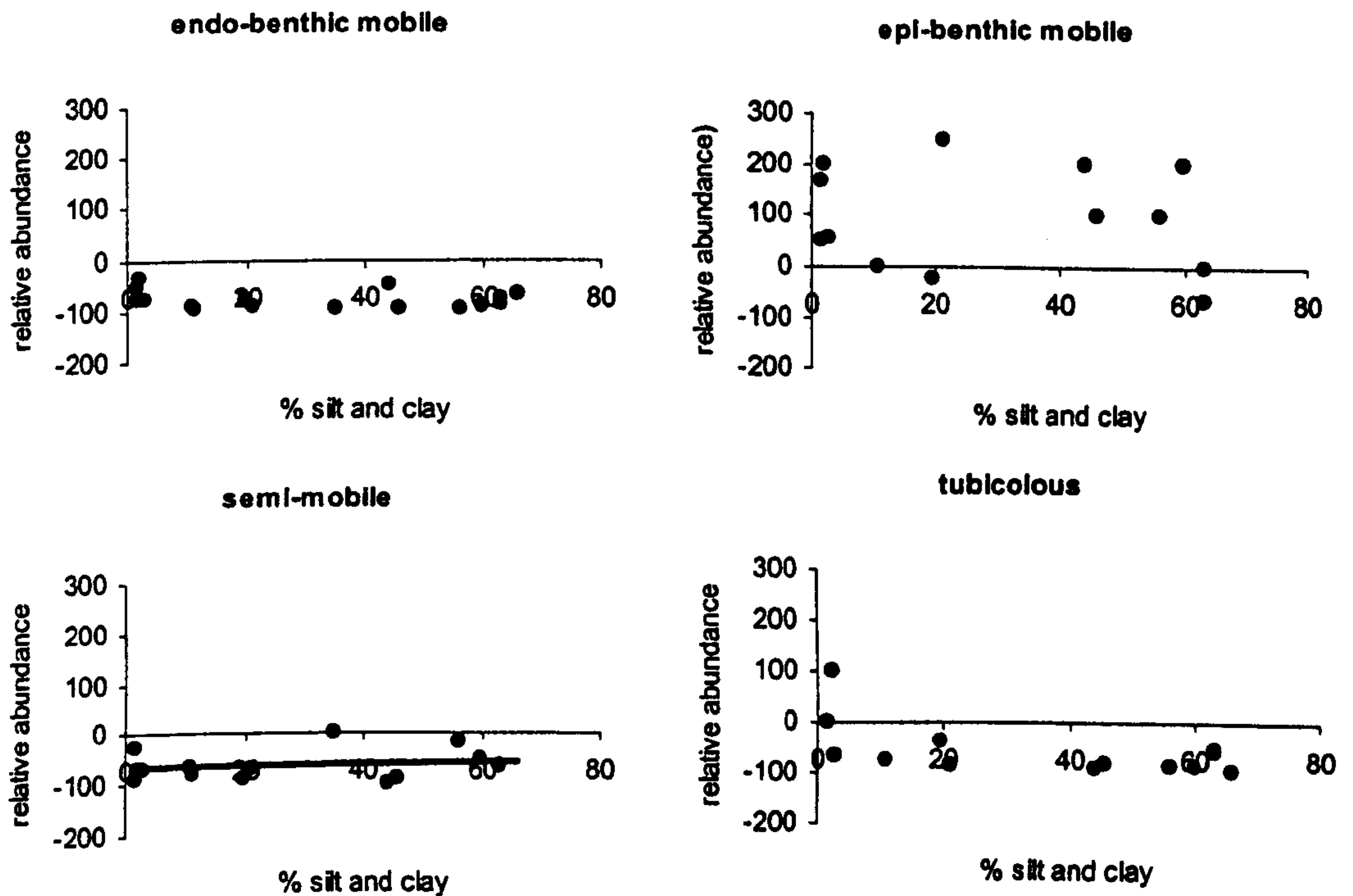


Figure 6.13: The relative abundances of mobility groups within disturbed plots compared to control plots along a gradient of increasing silt and clay content on the first sampling occasion (day 15).

There was a trend for increasing relative abundances within disturbed plots compared to control plots in the endo-benthic mobile, tubicolous and semi-mobile groups over time in all sediment types, while the relative abundances of the epibenthic mobile group decreased over the same period (Fig. 6.14). However, ANCOVA tests only detected a significant over time in the relative abundances of epibenthic mobile species. There were no significant interactions for any of the ANCOVA tests, indicating that changes in relative abundances occurred at a similar rate over all sediment types (Table 6.11).

Table 6.12: ANCOVA table for the ln+100 relative abundance of different mobility types on the first (day 15) and last (day 213) sampling date.

	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>F</i>	<i>P</i>
Endo-benthic mobile					
Sediment type	1	0.13	0.13	0.1	0.750
Day	4	2.59	0.27	0.23	0.59
Interaction	4	2.59	0.92	0.76	0.55
Residual	70	84.67	1.2		
Epibenthic mobile					
Sediment type	1	0.01	0.01	0.02	0.89
Day	4	11.05	2.75	3.49	0.01
Interaction	4	0.79	0.19	0.25	0.91
Residual	60	47.44	0.79		
Semi-mobile					
Sediment type	1	0.15	0.15	0.12	0.74
Day	4	8.55	2.13	1.51	0.18
Interaction	4	7.83	1.96	1.47	0.22
Residual	69	91.51	1.33		
Tubicolous					
Sediment type	1	3.08	3.08	3.5	0.06
Day	4	1.08	0.27	0.32	0.87
Interaction	4	3.53	0.88	1.03	0.39
Residual	55	46.96	0.86		

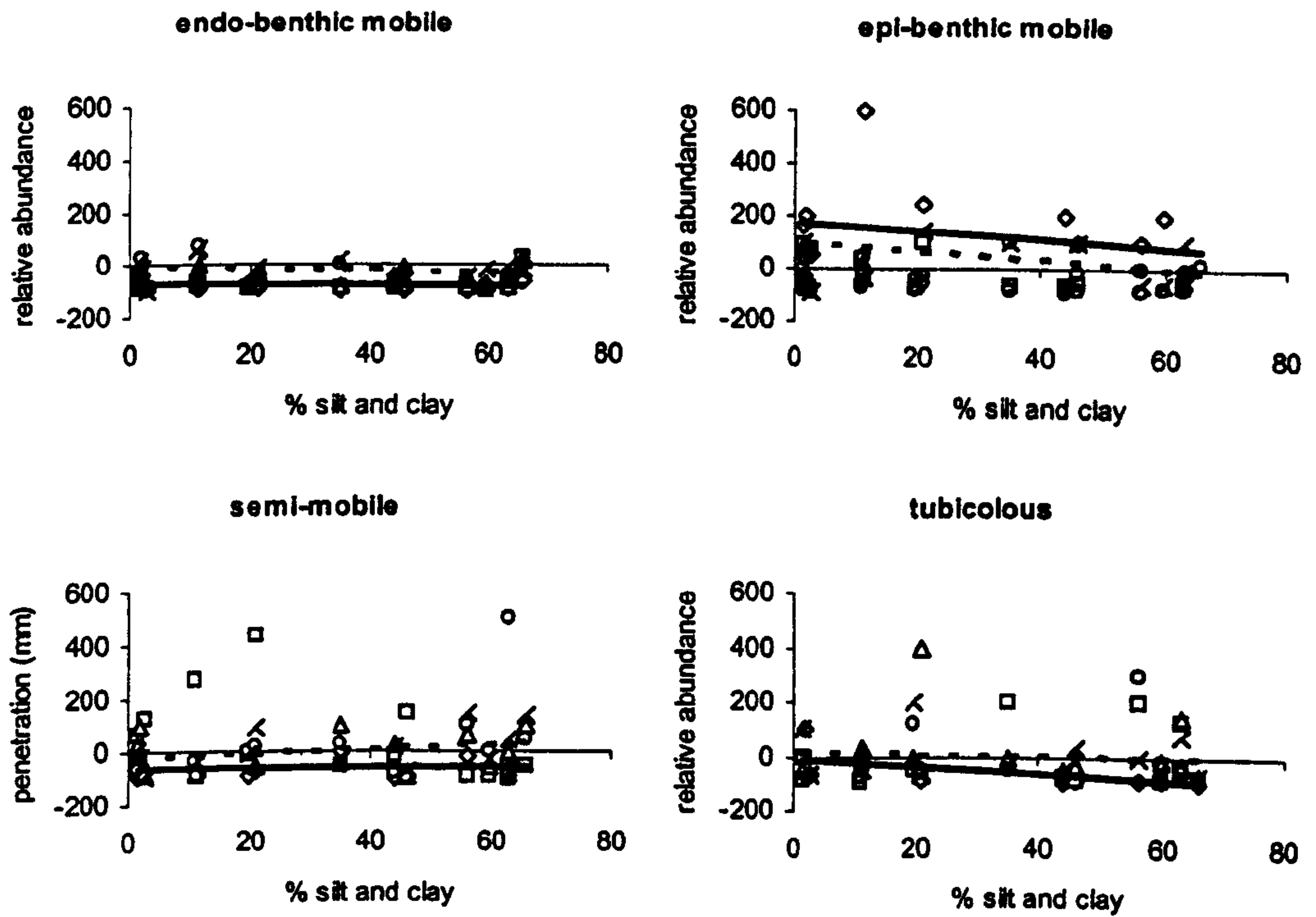


Figure 6.14: Relative response of different mobility types within disturbed plots compared to control plots on day 15 (open diamonds), 35 (open squares), 63 (open triangles), 107 (open circles) and 213 (crosses). Solid trendline = community response over sediment type on day 15, dotted trendline = community response over sediment type day 213.

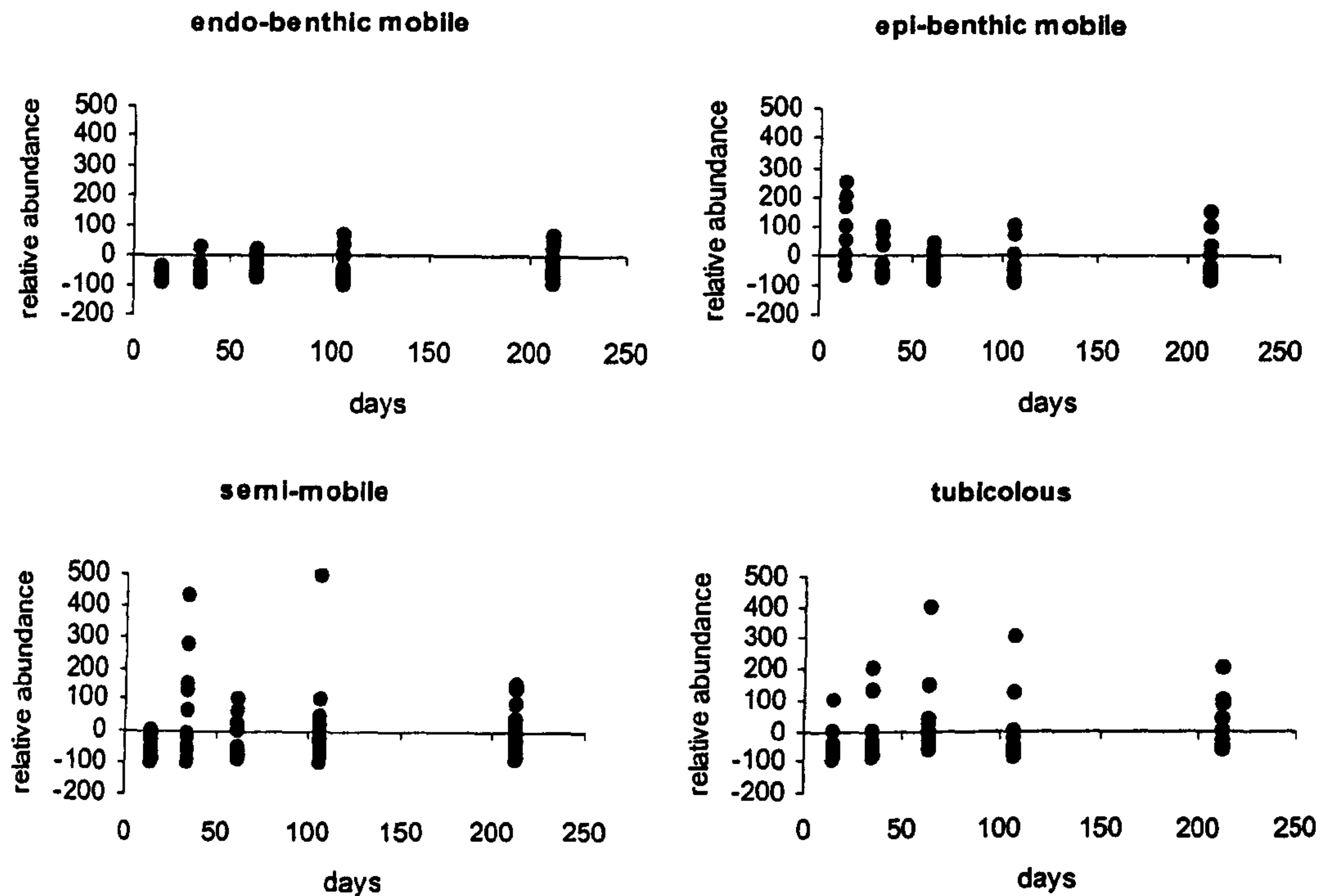


Figure 6.15: Relative abundances of mobility groupings in disturbed plots in comparison to control plots at every site over time.

Table 6.13: Spearman's rank correlation coefficients for the relative abundance of mobility groups with time (days).

<i>Mobility</i>	r_s	P
Endo-benthic mobile	0.504	<0.001
Epi-benthic mobile	-0.234	0.05
Hemi-mobile	0.242	0.032
Tubicolous	0.286	0.021

Endo-benthic mobile, semi-mobile and tubicolous groups all increased in relative abundance in disturbed plots compared to control plots over time (Table 6.13, Figure 6.15). The epi-benthic mobile group decreased in relative abundance in disturbed plots compared to control plots over the duration of the experiment although this relationship was not significant ($r_s=-0.234$, $P=0.06$). However, figure 6.15 indicates that, in comparison to other groups, the epi-benthic species were present in higher abundances within disturbed plots in comparison to the control plots at the beginning experiment, and over time there was a trend for decreasing relative abundance within

the disturbed plots as they declined to ambient levels. ANCOVA tests of the relative abundances of the endo-benthic, semi-mobile and tubicolous groups indicated that there were significant differences between the response of different groups ($F_{2,218} = 8.43$, $P < 0.001$) and a significant difference with time ($F_{1,218} = 17.67$, $P < 0.001$). There was no significant interaction for this test ($F_{2,218} = 1.21$, $P = 0.3$), indicating that the rate of change over time was similar for each group. However, when this test was performed on all the mobility groups, including the epi-benthic species, there was a significant interaction term for the test ($F_{3,288} = 3.04$, $P = 0.029$), supporting the hypothesis that there was a different response over time for the epi-benthic mobile group in comparison to the other mobility types.

6.4 Discussion

Although the total number of individuals per sampling unit rose with increasing percentage silt and clay content in a predictable manner (Rosenberg and Pearson, 1978), individual species/taxa and functional groups showed trends of both increasing and decreasing abundance across the different sediment types, while certain groups (e.g. sub-surface deposit feeders, endo-benthic mobile species) were present in equal abundance over all sites (Figures 6.4, 6.8 and 6.9 and Tables 6.1, 6.5 and 6.9). The distributions of individual species and groups of organisms were consistent with habitat ranges, behavioural and functional attributes, as reported in other benthic studies (e.g. Bonsdorff and Pearson, 1999). For example, the prevalence of surface deposit feeding became more common with an increasing percentage silt and clay content of the sediment whilst epi-benthic mobile species were more prevalent in sandier habitats. Natural disturbance levels are generally higher for sandy habitats in comparison to muddier habitats, hence the former favour organisms that have a highly mobile existence that reduces vulnerability to mortality from disturbance events (Gorzelany and Nelson, 1987).

The relative response of the total number of individuals was consistently more negative in sites with a higher percentage of silts and clays throughout the duration of the experiment. Thus the community response to a uniform disturbance is not consistent across different sediment types. Collie et al., (2000) undertook a meta-analysis of numerous fishing impact studies and found a trend for an increased severity of the initial effects of disturbance in muddy sands in comparison to clean sands, although mud sediments were the least negatively affected of all the habitats studied. However, these results were not significant, possibly due to low statistical power (Collie et al., 2000). In the present study, when the benthic assemblage was broken down further into individual species, taxa and functional groups, it was no longer possible to detect any trend of relative response with respect to variation in percentage silt and clay values. The exception to this was the tubicolous species, which were found in significantly lower relative abundances within sediments that had high percentage silt and clay content. However, this outcome was influenced by the presence of high abundances of *Myriochele* spp., a surface deposit feeding tube worm, within control plots at one mud site. The trend was no longer significant when this data was removed from the analysis and should be interpreted with caution.

The lack of any trend for a differing response from individual taxa from different sediment types makes intuitive sense given the design of the experiment as the

depth to which the sediment was disturbed was held constant irrespective of habitat type. In other studies, differences in the responses of individual taxa may be attributed to differences in the intensity of the initial disturbance, for example with respect to fishing gear type (Collie et al., 2000). The impact (in terms of physical penetration of the seabed) of the gear on each habitat and hence the biota will differ according to the physical properties of the seabed (see Collie et al., 2000; Kaiser et al., 2002). Thus, in the current study there is a disparity between the observed response of the total numbers of individuals over different sediment types and the response of individual functional groups and taxa. The less negative response of the community observed in habitats with the lowest percentage silt and clay habitats will be at least partially attributable to the increased abundances of epi-benthic mobile species present in the disturbed plots in these habitats in comparison to the muddier sites. However, this result might also indicate that the treatment of subsets of the data decreased the power of the analysis such that any patterns in relative response of individual taxa were not detected since these data were more sporadic over different sites, treatments and times. The rate of recovery of total abundances of organisms at individual sites could be predicted based on the rate of habitat restoration at each site in this experiment (Dernie et al., (2003b); Chapter 5). However, it was not possible to derive accurate estimates of the rates of recovery of individual taxa and functional groups in the current study, due to the variability of the data for individual components of the community.

Significant differences were found between the responses of the different functional groups to the physical disturbance treatment. The abundance of most groups was negatively impacted by the disturbance. The exception to this was the epi-benthic mobile group, which occurred in the disturbed plots with a 150% higher abundance than in control plots at the beginning of the experiment. Presumably their mobility above the sediment surface facilitates recolonisation into disturbed areas in comparison with less mobile groups. The formation of pits in the surface sediment can result in the increased deposition of fine material (e.g. organic particles) as a result of an altered hydrodynamic regime (Savidge and Taghon, 1988). Other studies have detected very significant increases in the numbers of mobile species in response to the reported increase in food resources within a disturbed area (e.g. Oliver and Slattery, 1980; Ramsay et al., 1997). However, there was no increase in organic content of sediments within the plots in the present study (see Chapter 5), nor was there an increase in the relative abundance of any functional feeding group that might have indicated a response to an increase in a particular food resource. In

addition, these results contrast directly with the findings of a previous experiment on a sheltered sand flat (see Chapter 2) where epi-benthic mobile crustaceans clearly avoided disturbed plots of a similar size up to 32 days following the initial disturbance (Dernie et al., 2003). Avoidance of disturbed areas by mobile crustaceans has been noted in other studies, and may be related to changes in habitat stability (Cook, 1991; Ferns et al., 2000). The likely explanation for the observed differences between this and other studies is that the epi-benthic mobile group in the current study consisted not only of crustaceans, but also included several polychaetes and the gastropod *Hydrobia ulvae*. The latter was found in very high numbers within disturbed pits in a previous experiment (Dernie et al., 2003) and is likely to have influenced the results in the present study. This disparity highlights the limitations of combining different species within one functional group, when individual taxa may exhibit different responses to the same treatment. Nevertheless, no significant differences were observed in the responses of the six key taxa, which were all present in reduced abundances within disturbed plots.

The use of functional groups in the present study provided a useful method for the examination of community responses to the physical disturbance. Since few individual taxa were uniformly abundant over the variety of sediment types included within the experiment, analyses of single species and taxa produced less definitive results. There are limitations to the applicability of using the functional group approach (Posey, 1990; Pearson, 2001). In particular, there is a lack of detailed information pertaining to behaviours and life history characteristics of soft sediment invertebrates, which at any rate may differ considerably depending on the prevailing conditions (Posey, 1990). For example, many benthic organisms are known to change feeding modes in response to differing flow regimes (e.g. Miller et al., 1992). In the context of this study, it would have been of interest to investigate differences in responses of invertebrates grouped based on reproductive strategy since the supply rate of larvae and seasonal production of gametes may be a key factor in determining recovery rates (e.g. Beukema et al., 1999). However, information on the reproductive strategy of individual species is limited and the developmental modes of different species may differ considerably even within a restricted taxonomic group (Giangrande, 1997). Moreover, a number of studies have highlighted that post-larval settlement processes (active migration and passive dispersal of juveniles and adults) may have a more critical influence on benthic community structure than larval recruitment (Olafsson et al., 1994; Norkko et al., 2001). The functional groupings that characterised the relative mobility of the species inhabiting the different sediments

revealed the most interesting relationships with the recovery rate of the physical habitat. This is perhaps not surprising, since adult migration is an important source of recolonisation of benthic habitats (Beukema et al., 1999; Thrush et al., 1991; Savidge and Taghon, 1988).

Several previous studies indicate that communities from muddy habitats recover more slowly from physical disturbance than those from sandy habitats (e.g. Schratzberger and Warwick, 1998; Collie et al., 2000). In the present study, the abundances of individuals associated with muddy sediments remained at lower levels in disturbed plots for a longer period than those found in sandy sediments. However this was not attributable to any difference in the rate of responses of the same taxon in different sediment types. Bed load transport and water currents supplying adult infauna, juveniles and larvae to the sea bed may be important mechanisms for the recovery of assemblages following disturbance (e.g. Peck et al., 1999; Beukema, 1999). However, if recovery rates were causally related to hydrodynamic regime, it would be predicted that organisms of the same species might return to ambient levels at sandy sites more rapidly than in muddy sites. The results from these analyses suggest that biotic factors such as mobility are relatively more important than physical factors such as the local hydrodynamic factors at a site in determining recovery rates. In addition, the proportional abundances of some individual species and functional groups differed over the range of sediment types (e.g. epi-benthic mobile species). If those species that are least vulnerable to disturbance events make up a higher proportion of the assemblage in areas that are subject to a naturally high disturbance regime, as is indicated in this study, then the adaptations of the community will confer a resistance to any further disturbances.

The analyses presented in this chapter contrast with the findings of Chapter 5, where rates of community recovery could be predicted based on the infilling rate of disturbed pits. This strongly suggested that there was an important influence of the local hydrodynamic regime controlling both physical and biological recovery of the system. Although no formal test of the power of this experimental design can be performed, it is intuitive that as the total number of individuals is broken down into constituent species and function groups, power will decrease as variability increases (Cohen, 1977). Thus, although the investigation described in this chapter cannot provide any evidence that recovery rates of individual species differ over sediment types, this may be as a result of a low power to detect any patterns in the data.

Further work that explicitly tests the recovery rates of individual taxa from different habitat types is required to investigate this further.

6.5 Conclusions

The results presented in this chapter indicate a disparity between the response of whole community attributes (i.e. total number of individuals) and individual components of the community including single species and functional groups. The responses of individual taxa, which may differ greatly from one another, are lost when amalgamated data are used. This is particularly pertinent where some components of the community exhibit a positive response whilst others exhibit a negative response, since such opposing responses will be cancelled out when the whole community is considered and thus the impact of a perturbation may be underestimated. Analysis of individual taxa and functional groups revealed no difference in the initial impact of the disturbance treatment over different sediment types, and no indication that recovery rate of individual taxon proceeded at a different rate in different sediment types. However, due to the reduced power of the experiment to detect patterns in the data as the community was separated into different components, no firm conclusions can be drawn from these findings. Further experimental work will be needed to explicitly test the relative importance of abiotic and biotic factors controlling the recovery rates of infaunal invertebrates following disturbance.

Chapter 7

General Discussion

7. 1 The aim of the study

The main aim of the research presented in this thesis was to examine the use of physical characteristics of soft sediment habitats to predict the recovery rates of marine benthic assemblages. This would be useful to managers of the marine environment when faced with the need to assess the long-term impact of activities that cause disruption to the sea bed. The preliminary investigation of the recovery trajectory of the benthic community at Traeth Melynog (Ch 2) indicated that the depth of water in disturbed plots was strongly correlated with community structure as they changed over time. None of the other sediment parameters correlated with recovery of the benthic assemblage, yet these are the parameters that often are most often measured in ecological studies (e.g. Yates et al., 1993; Eleftheriou and Basford, 1992; Warwick et al., 1991). A further field experiment undertaken across a range of sediment habitats demonstrated that a significant relationship existed between the rate of physical recovery (or infilling rate) of disturbed plots and the recovery rate (of total numbers of individuals) of the associated benthic assemblage (Chapter 5). Hence, measurement of the recovery rate of topographical features altered by a physical disturbance represented a more rapid and amenable method to assess the longevity of the effects of a disturbance on general community attributes rather than the detailed analyses of changes in the benthic community that are normally undertaken (sorting and identification of individual taxa in individual samples). Such an approach could become a useful management tool that could be used for rapid assessment of the potential biological recovery rate in a particular habitat.

No *a priori* prediction of recovery rates of the benthic assemblage could be made from measurements of sediment parameters alone such as the percentage silt and clay content of a sediment. Yates et al., (1993) presented data that indicated that the numbers of shore birds found feeding on invertebrates in different areas of the Wash could be predicted based on granulometrically derived sediment parameters, due to the close relationship between sediment characteristics and the densities of the associated infaunal invertebrates. Interestingly, sediment characteristics alone were not significantly related to community recovery rates in this study. Rather, measurement of the rate of habitat restoration (Chapter 5) encapsulated a number of important variables that may influence biological recovery that included structural and biological (e.g. mucous binding of particles) properties of the sediment and the local hydrodynamic regime, and was therefore more meaningful when used to predict the recovery rates of the associated assemblage.

7.2 Limitations of the work – the importance of scale

There are a number of caveats to the use of this method to predict benthic community recovery rates. Clearly, the measurement of the rate of infilling of a disturbed pit is reliant on the formation of such a topographical feature as a result of disturbance. This may not be the case for all perturbative impacts that affect benthic communities, e.g. storms or large-scale anoxic events (e.g. Santos and Simon, 1980b). The work detailed in this thesis is based on experiments applied at a relatively small-scale, (disturbed plots of 2 m x 2 m and 1 m x 4 m) and thus caution should be used in extrapolating the results from this study to predict the recovery rates of communities following disturbance impacts at larger scales (see Thrush et al., 1997a,b). Nevertheless, in a meta-analysis of over 40 fishing impact studies undertaken over a range of scales, Collie et al., (2000) found that the initial impact was more negative and recovery rate longer for muddy sand communities affected by disturbance compared with assemblages that inhabit mud or sand habitats, which concurs with the current study. The findings of the present study also concur with the findings of Hall et al., (1994) and fit the trend of recovery times required for impacts of different scales outlined in Fig. 1.2 of this thesis (p6), being of a similar magnitude to foraging pits and hydraulic dredging disturbance. The disturbance treatment applied in the experiments detailed here occurred at a similar scale to a number of anthropogenic disturbances that occur in intertidal areas, including bait digging, the hand collection of shellfish species, hydraulic and tractor dredging activity. Such activities also result in the formation of pits and furrows. Thus the findings from this study are directly applicable with respect to the sustainable harvesting of wild resources in soft-sediment intertidal habitats. Further work is needed to test this predictive technique in relation to disturbances that occur over a broad range of scales and habitats (i.e. sublittoral areas). Presumably as the scale of individual impacts and cumulative impacts increases so recovery rate will decrease given the mechanisms of recovery of the physical and biological components of the habitat.

The mechanisms by which recovery occurred were not explicitly tested as part of this work. However, it is likely that post-larval immigration was the primary means by which organisms recolonised the disturbed pits, as this has been observed in other studies investigating disturbances on a similar scale (e.g. Thrush et al., 1991; Savidge and Taghon, 1988). The importance of different modes of recolonisation may vary depending on the scale of the disturbance (Gunther, 1992), with post larval immigration a relatively more important mechanism for small disturbed areas and larval settlement the dominant recolonisation mechanisms for disturbances that occur at a larger scale (Smith and Brumsickle, 1989). This has implications for the determination of the recovery rate

benthic assemblages following small and large-scale disturbances. For example, when larval recruitment is the primary source of recolonisation, seasonal variations in larval supply will be a significant factor in determining the structure of the recovering assemblage, in addition to the rate at which recovery can occur. Where recolonisation by adults is the main source of recolonisation the relative mobilities or rates of passive dispersal (presumably controlled by local hydrodynamics, (e.g. Commito et al., 1995)) of the local fauna will largely control recovery rate.

The increased length of time required for the eventual recovery of the benthic assemblage reported in some large-scale studies has been attributed to the shorter edge-to surface ratio of the disturbed patch (Beukema et al., 1999). Many of these studies describe the recolonisation of defaunated patches following an anoxic event (Beukema et al., 1999; Santos and Simon, 1980a,b). This type of disturbance is not comparable to the work described in this thesis since no physical disruption to the seabed occurs. In addition to this, defaunation is usually complete and larval settlement is the major mode of recolonisation (Santos and Simon, 1980a). However, many physical disturbances that cause disruption to sediments (and are thus more comparable to the current study), even when they occur over large scales, are not uniformly distributed over the seabed. Rather they are a mixture of intensively impacted areas, low impacted areas and areas that remain undisturbed (see Illustr. 7.1). Thus, there will be an increase in the edge to surface ratio of the disturbed patch and recolonisation by post larval stages will remain an important mechanism for biological recovery.

The effects of the disturbance treatment were similar over all habitats. The experimental approach was to exert a uniform disturbance over all habitat types, by systematically removing all sediments up to a depth of at least 10 cm. Thus, all organisms inhabiting this upper layer (the majority of infaunal species) should have been removed from the immediate habitat. This differs substantially from other disturbances, (e.g. the passage of towed bottom fishing gear) that will not exert the same level of physical disruption in all habitat types. For example, otter trawl boards sink into muddy sediments, whilst only scraping the surface of coarse sand and gravel sediments (Kaiser et al., 2002). Thus, the vulnerability of infauna exposed to the same source of physical disturbance may differ considerably between different habitats. This results in different initial responses to the disturbance and will consequently affect subsequent recovery trajectories in different habitats. Nevertheless, this may be reflected in the differential infilling rate of the disturbed areas, where a significant topographical feature results from the disturbance, and thus may still be amenable to the prediction method outlined in this thesis.

Recovery of an assemblage has been defined herein as having occurred when the disturbed community structure, or a univariate measure of community such as the total number of individuals, is no longer significantly different from that of an adjacent, undisturbed community (control). This is the premise of many other studies that have investigated the recovery of benthic assemblages (e.g. Hall and Harding, 1994; Zajac and Whitlatch, 1982a,b; Thrush et al., 1991,1996). However, an important aspect of an assemblage is the biomass supported by the community. Beukema et al., (1999) studied the recovery trajectory of benthic communities in the Wadden Sea following defaunation of large areas (120 m²). The authors observed that the recovery of abundances of benthic communities occurred well in advance (approximately one year or less following disturbance) of recovery of the biomass of the community (which took up to three years to reach ambient levels). This study investigated recovery following an anoxic event where larval settlement was the major source of recolonisation and thus differences in biomass between the disturbed assemblage and adjacent undisturbed communities would have been most pronounced. However, the work highlights the importance of biomass in defining the temporal extent of community recovery, and this should be taken into account when assessing the ecological significance of disturbances. Nevertheless, the current study did not aim to investigate the ecological significance of physical disturbance but instead to provide a rapid and amenable method for assessing the length of time for recovery of defined attributes of benthic community structure.

7.3 Responses of different components of the benthos

The prediction of benthic community recovery rates based on rates of habitat restoration relates to the macrofaunal community. This work also included a comparison of meiofaunal and macrofaunal recovery following physical disturbance in a sandflat system (Chapter 3). Whilst the macrofaunal community is known to have recovered 63 days following the disturbance treatment, the point at which eventual recovery of the meiofaunal community occurred is unknown and may even have exceeded that of the macrofaunal community, although this is unlikely. While significant differences occur between ambient and disturbed macrofaunal assemblages, differences in the concomitant meiofaunal communities may be maintained purely as a result of this difference, since the effects of the activities of macrofauna on meiofaunal community structure is well-documented (Austen et al., 1998; Warwick et al., 1986; Widdicombe et al., 2000). Although this study has highlighted the importance of understanding the effects of disturbance events of other components of the benthic community (meiobenthos, micro flora and fauna), investigating the recovery rates of macrofaunal

communities is likely to remain the focus of scientific studies due to the conservation importance of this component.

7.4 Using physical properties as a proxy for disturbance

Understanding the relationships between benthic communities and physical processes is currently hampered by a lack of techniques available that can easily be deployed in the field to quantify physical parameters. In order to undertake statistically rigorous experiments, a high level of replication is required and many techniques that measure physical properties of the sediment are not amenable to such studies. There is a pressing need for this problem to be addressed with the development of *in situ* techniques to measure sediment characteristics, such as the cone penetrometer described in Chapter 4. Significant advances have been made in this area over recent years, for example with the development of the Cohesive Strength Meter (CSM) (Tolhurst et al., 1999), which measures *in situ* erosion shear resistance of intertidal sediments and the sublittoral shear vane device discussed in Chapter 4 (Hauton and Paterson, 2003). These techniques should be applied more widely by ecologists undertaking studies in the field.

Benthic ecologists have measured disaggregated sediment properties (i.e. grain size distributions obtained through granulometric analysis) since they provide a good indication of the 'average' hydrodynamic regime of a particular area. However, these properties rarely reflect temporal fluctuations in the hydrodynamic processes that are likely to significantly affect recolonisation processes and may explain, for example, differences in recovery rates observed at different times of year. The use of granulometric techniques to describe sediment characteristics has a number of limitations when applied to ecological studies. The disaggregation of the sediment to describe the primary grain size distributions may not well describe the natural habitat encountered by organisms. Further techniques exist that allow the measurement of the proportion of faecal deposits and other natural aggregates in sediments and thus provide a better description of the habitat. However, the length of time taken to process samples (usually several days per sample) often precludes this type of analysis from experimental studies, such as described in the present study, where a very high level of replication is required. Whilst most ecological experimental studies occur at scales of <10m (Hall et al., 1994), studies of physical processes tend to focus on measurements at much greater scales (Hall, 1994). In the current study it was not possible to obtain detailed information concerning the currents in the Menai Strait despite the concentration of studies

investigating physical processes in this area for the past 30 years. Nevertheless, the infilling rate of disturbed pits will be significantly influenced by local fluctuations in the hydrodynamic regime and thus may reflect differences in recovery rate where disturbances occur at different times of year.

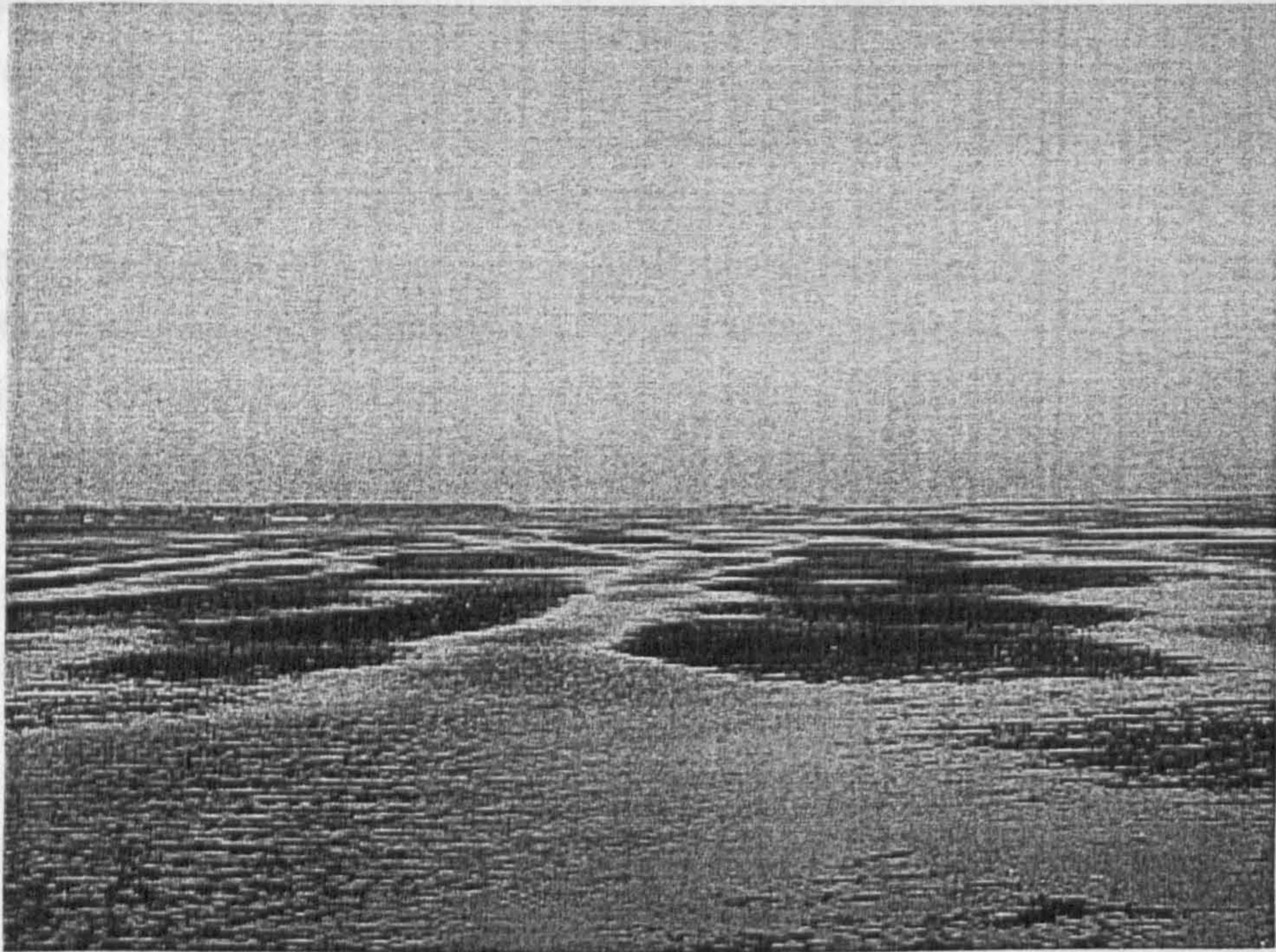


Illustration 7.1: Cockle dredge tracks in the Wadden Sea

7.5 Management options

The work presented in this thesis has practical implications for the management of perturbative activities in intertidal benthic environments that result in topographical changes to the substratum, for example the formation of pits or furrows. Such activities include, for instance, hydraulic dredging (see Illustr. 7.1). However, it is not possible to make an *a priori* assessment of the length of time for biological recovery of the community at a specific location based on physical parameters at the site. Nevertheless, the rate of infilling of disturbed areas was sufficiently related to biological recovery that managers of intertidal areas could use the eventual recovery of the dredge tracks, for example, as a surrogate for the recovery of the benthic community. Any management strategy that employed this technique to predict the recovery rates of infaunal communities in intertidal areas should adopt a precautionary approach, incorporating

additional time allowances to increase the confidence that biological recovery had truly occurred. An appropriate method for adopting the precautionary approach would be to predict recovery rates based on the length of time taken for the recovery of the visible manifestation of the disturbance plus an additional 15% of this time. This approach would take into account the large fluctuation in recovery rates in different habitats and would maximise the possible use of benthic resources over a range of sediment types.

7.6 Future Work

Further work is required to explicitly test the relative importance of adult/post-larval immigration and larval recruitment to disturbed patches of different sizes. Furthermore, the relative importance of active swimming/burrowing and passive movement related to local hydrodynamics are important factors in determining recovery rates and require further testing. The results from this work would seem to indicate that those processes controlling the infilling rate of disturbed areas are closely related to those controlling recovery rates of benthic infauna, which suggests that local hydrodynamics play a key role. The use of the rate of habitat restoration to predict the recovery rates of benthic assemblages following physical disturbance should now be tested over a broad range of scales and habitats to investigate the applicability of this technique to a wider range of anthropogenic impacts.

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Journal of Applied Ecology **30**: 599-614.

Appendix 1: Species list: Traeth Melynog

Mysta picta

Anaitides maculata

Glycera alba

Microphthalmus

sczelkowi

Exogone hebes

Hediste diversicolor

Nephtys hombergii

Scoloplos armiger

Aricidea roberti

Polydora ciliata

Pygospio elegans

Spio martinensis

Magelona alleni

Chaetozone setosa

CAPITELLIDA

AMPHARETIDAE

OLIGOCHAETA

Tubificoides benedii

Bathyporeia sarsi

Gammarus salinus

Corophium arenarium

Crangon crangon

Carcinus maenas

Hydrobia ulvae

Retusa obtusa

Mysella bidentata

Cerastoderma edule

Spisula subtruncata

Macoma balthica

Scrobicularia plana

Appendix II: Species list and functional groups – Menai Strait soft sediment habitats

	Mobility	feeding
<i>Myriochele</i> spp	tubicolous	surface deposit feeder
<i>Sphaerodopsis baltica</i>	endo-benthic mobile	sub surface deposit feeder
<i>Malmgrenia arenicolae</i>	epi-benthic mobile	active carnivore
<i>Pholoe baltica</i>	epi-benthic mobile	active carnivore
<i>Mysta picta</i>	endo-benthic mobile	active carnivore
<i>Eumida sanguina</i>	endo-benthic mobile	active carnivore
<i>Eteone</i> spp	endo-benthic mobile	active carnivore
<i>Phyllodoce</i> spp	endo-benthic mobile	active carnivore
<i>Glycera</i> spp.	endo-benthic mobile	active carnivore
<i>Micronephtys</i>	endo-benthic mobile	active carnivore
<i>Hesionidae</i>	endo-benthic mobile	active carnivore
<i>Gyptis</i> spp.	endo-benthic mobile	active carnivore
<i>Exogone hebes</i>	endo-benthic mobile	omnivore
<i>Hediste diversicolor</i>	endo-benthic mobile	omnivore
<i>Nephtys</i> spp.	endo-benthic mobile	omnivore
<i>Scoloplos armiger</i>	endo-benthic mobile	sub surface deposit feeder
<i>Aonides</i> spp.	semi-mobile	surface deposit feeder
<i>Polydora horseshoe</i>	semi-mobile	surface deposit feeder
<i>Polydora straight</i>	semi-mobile	surface deposit feeder
<i>Pygospio elegans</i>	semi-mobile	surface deposit feeder
<i>Laonice</i> spp.	semi-mobile	surface deposit feeder
<i>Streblospio benedictii</i>	semi-mobile	surface deposit feeder
<i>Spiophanes bombyx</i>	semi-mobile	surface deposit feeder
<i>Spio filicornis</i>	semi-mobile	surface deposit feeder
<i>Scololepis</i> spp.	semi-mobile	surface deposit feeder
<i>Spio martinensis</i>	semi-mobile	surface deposit feeder
<i>Paraonidae</i>	semi-mobile	surface deposit feeder
<i>Malacoceros</i> spp	semi-mobile	surface deposit feeder
<i>Magelona filiformis</i>	semi-mobile	surface deposit feeder
<i>Tharyx</i> spp	endo-benthic mobile	surface deposit feeder
<i>Capitomastus</i>	endo-benthic mobile	sub surface deposit feeder
CAPITELLIDA	endo-benthic mobile	sub surface deposit feeder
TEREBELLIDAE	tubicolous	filter feeder
<i>Eupolymnia</i>	tubicolous	filter feeder
AMPHARETIDAE	tubicolous	filter feeder
<i>Amphicteis</i>	tubicolous	filter feeder
<i>Pectinaria</i>	tubicolous	filter feeder
<i>Lanice conchilega</i>	tubicolous	filter feeder
<i>Owenia fusiformis</i>	tubicolous	filter feeder
<i>Sabellidae</i>	tubicolous	filter feeder
OLIGOCHAETA indet.	endo-benthic mobile	sub surface deposit feeder
<i>Tubificoides benedii</i>	endo-benthic mobile	sub surface deposit feeder
ENCHYTRAEIDAE	endo-benthic mobile	sub surface deposit feeder
<i>Bathyporeia sarsi</i>	endo-benthic mobile	sub surface deposit feeder
<i>Gammarus salinus</i>	epi-benthic mobile	omnivore
<i>Corophium arenarium</i>	endo-benthic mobile	surface deposit feeder
<i>Corophium volutator</i>	endo-benthic mobile	surface deposit feeder
<i>Crangon crangon</i>	epi-benthic mobile	active carnivore
<i>Eurydice pulchra</i>	epi-benthic mobile	sub surface deposit feeder
<i>Carcinus maenas</i>	epi-benthic mobile	omnivore

<i>Hydrobia ulvae</i>	epi-benthic mobile	sub surface deposit feeder
<i>Retusa obtusa</i>	epi-benthic mobile	sub-surface deposit feeder
<i>Mysella bidentata</i>	semi-mobile	surface deposit feeder
<i>Cerastoderma edule</i>	semi-mobile	filter feeder
<i>Spisula subtruncata</i>	semi-mobile	surface deposit feeder
<i>Macoma balthica</i>	semi-mobile	interface feeder
<i>Scrobicularia plana</i>	semi-mobile	surface deposit feeder
<i>Juv. Bivalve indet.</i>	semi-mobile	surface deposit feeder
<i>Abra alba</i>	semi-mobile	surface deposit feeder
<i>Fabulina fabula</i>	semi-mobile	surface deposit feeder