2008

Linking biotic activity to ecosystem functioning

Sanders, Jeanette Louise

LINKING BIOTIC ACTIVITY TO ECOSYSTEM FUNCTIONING

JEANETTE LOUISE SANDERS, M.RES., B.SC. (HONS.)

A thesis submitted to the University of Plymouth

in partial fulfilment for the degree of

DOCTOR OF PHILOSOPHY

School of Biological Sciences

Marine Ecology Research Centre

In collaboration with

Plymouth Marine Laboratory

October 2008

Linking biotic activity to ecosystem functioning

Abstract

Jeanette Louise Sanders

The central theme of this thesis was the search for ecologically meaningful ways to quantify the relationships between the biota and ecosystem processes. This thesis investigated whether a "functional group" approach, that characterised the fauna according to similarities in their activities, could be successfully employed to quantifiably link species' performance to important ecosystem processes.

Initially the abilities of traditional "trophic" and "bioturbatory" categories to characterise the estuarine macrobenthic fauna and discriminate between estuarine sites were examined. This thesis determined that the perceived inter-site similarity within an estuary varied according to the function being investigated and that the apparent associations between abiotic factors and biotic assemblages were also heavily influenced by the choice of functional classification.

This study provided strong evidence that links between the macrobenthos and abiotic factors were most easily detected if the species were grouped according to their bioturbatory abilities. Thus, attempts to model the contribution of the estuarine macrofauna to sediment mixing throughout an estuary were pursued in preference to modelling trophic group distribution.

This thesis identified limitations of existing "bioturbation" categories and hence, developed a novel classification system that incorporated species' activity rates, magnitude and location within the sediment.

Strong evidence was found that estuarine macrobenthic communities should be treated as two separate assemblages: one shallow assemblage occupying surface and near surface layers, and one deep assemblage with the ability to exploit the sediment at greater depths. The two separate assemblages displayed different associations with the environmental factors examined in this study.

By developing new functional groupings of species' behaviour, and treating shallow and deep assemblages as separate entities, this thesis was able to estimate the contribution of the biota to sediment mixing and successfully develop and validate generic predictive models of functional group distribution within the Tamar/Plym estuarine system. Since the functional groups themselves convey information about the magnitude of their effect and the sediment horizons impacted, this thesis represents an important advance in our ability to predict biological contribution to sediment mixing processes in estuarine ecosystems.

CONTENTS

TABLES

Table 5.10 The observed and predicted abundance, s.e and 95% confidence intervals for each sediment disturbance group at St. John's Ford in the Tamar estuary. 207

FIGURES

Acknowledgments

Firstly I wish to thank my supervisors Mike Kendall, Tony Hawkins and John Spicer for all their support, patience and encouragement throughout the time I have taken to complete this thesis. They have all provided invaluable support and guidance in their very different ways. In particular the willingness to read and comment on various manuscripts and posters that were inevitably "late" and needed "tomorrow"! They surely thought this day would never come.

I must thank NERC for providing the funding for this thesis and PML for the provision of boats, equipment and a boat crew.

In undertaking the studies described in this thesis I have been fortunate enough to meet and be helped by an amazing array of people and I only hope that someday I can repay them for their kindness.

I must start with Bob Clarke who has spent hours discussing my "latest plan", only to then be presented with another! He has been so helpful, thoughtful and clear in his explanations.

John Widdows and Tony Bale provided data, advice and practical support. They were kind enough to allow me to use their flume and sample alongside their own surveys, which saved vast amounts of time and effort. They also provided good company at conferences!

Data were also supplied, although not all used, by many other people: Amanda Prior from the Environment Agency, Astra Zeneca supplied data for the Tees and also the BELLPLUME model output thanks to the late Roy Lewis and his associates.

Several people helped with processing samples: Erica Keppel, Utra Mankasingh, Angela Raffo, Kev Solman (although some were recompensed for their expertise in chemistry and faunal identification). One who was not recompensed in any way (except chocolate) but spent many hours helping me improve my identification skills was Louis McNeill, without whose help I would probably still be looking at cirratulids!

In the final stage several people have helped me complete this thesis: Kirsten Richardson read and commented on several drafts, Utra Mankasingh provided comments on one chapter and a great deal of support, friends took children out, and in-laws cooked tea!

I have left until next to last those people who cheerfully crawled and dragged buckets across mud without whom I would have no thesis: Sarah Dashfield, Andrea McEvoy,

Sally Marsh, PB, Carolyn Harris, John Stevens, Erica Keppel, Hazel Needham and of course, Mike Kendall, whose eagerness to get wet and muddy is legendary.

That leaves the most important people to thank: my husband David and our two wonderful children Aaron and Owen. They have always supported and encouraged me and I am grateful that after all this time they are still here!

AUTHOR'S DECLARATION

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award without prior agreement of the Graduate Committee.

This study was financed with the aid of a studentship from the Natural Environment Research Council and carried out in collaboration with Plymouth Marine Laboratory.

The work described in this thesis was conducted by the author under the supervision of M. Kendall, Dr. AJS Hawkins and Prof. J.I. Spicer.

This research has used data sets not collected by the candidate (1992 SWW Tamar Estuary and Sublittoral Sediment Survey, 1986 OPRU HRE Plymouth Harbour and Yealm Estuary Survey, routine monitoring data from the UK Environment Agency and data on the distribution of the macrofauna of the Molenplaat, Westerschelde, collected as part of the ECOFLAT campaign). Consequently, these data have previously been used in publications and theses. The macrobenthic survey of the Tamar and Plym undertaken in spring 2005 was conducted by the author and the data has not yet been published. The processing, application and interpretation of the data within this thesis is completely the work of the author and is to the best of the author's knowledge, completely original. Throughout the thesis all sources of information have been specifically acknowledged by means of reference.

Courses Attended:

PRIMER-E (Plymouth Routines in Multivariate Ecological Research) 3-7 February 2003, Plymouth, UK.

ECRC Short course: Numerical analysis of biological and environmental data. Environmental Change Research Centre, UCL, London, 9-20 May 2005.

Presentation and Conferences Attended:

Oral Presentations:

Sanders JL, Kendall, MA, Hawkins AJS, Spicer, JI (2005) Vertical distribution of macrofauna plays an important role in estuarine site classification. British Ecological Society (BES) Annual Meeting 5 - 7 September 2005, Hatfield, UK

Poster Presentations:

Sanders JL, Kendall MA, Hawkins AJS, Spicer JI (2003). Macrobenthic biodiversity of British estuaries. Poster presentation: Estuarine Coastal and Science Association (ECSA) Conference: Recent developments in estuarine ecology. Scarborough, UK. 27-28 August 2003

Sanders J, Kendall M, Hawkins A, Spicer J (2004) Can functional groups be used to indicate estuarine ecological status? Estuarine Coastal and Science Association (ECSA)-Seine-Aval Changes in land use: consequences on estuaries and coastal zones. Rouen, France 13-17 September 2004

Sanders JL, Kendall, M, Hawkins, A, Spicer, J (2005) Linking biological activity to measurements of function at the ecosystem level in the Tamar estuary? Estuarine Coastal and Science Association (ECSA) Symposium: Estuaries of South West England, 6-8 April 2005, Plymouth.

Sanders JL, Kendall, M, Hawkins, A, Spicer, J (2005) Defining the potential of macrofaunal species to promote bioturbation in estuarine environments. British Ecological Society (BES) Special meeting: Body size and the organisation and function of aquatic ecosystems. 2-4 September 2005, Hatfield, UK

Delegate:

Climate change and aquatic system: past, present and future. University of Plymouth, 21-23 July 2004, Plymouth UK

Publications:

Sanders JL, Kendall MA, Hawkins AJS, Spicer JI (2007) Can functional groups be used to indicate estuarine ecological status? Hydrobiologia 588(1):45-58

Word count of main body of thesis: 58,438

Signed

.....Jeanette Sanders.....

Date

.....2 October 2008.....

CHAPTER 1

General Introduction

"The universe is like a safe to which there is a combination. But the combination is locked up in the safe."

Peter de Vries (1910-1993)

1.1 Why link biological activity and ecosystem function?

The adverse effects of human activity upon *human* health have long been a cause for concern, for example a "smoke abatement" law was introduced in London in 1273. It was not, however, until the middle of the twentieth century that concerns about man's influence upon the *environment* and the wealth of resources provided by that environment were brought to a wider audience, e.g. the seminal book "Silent Spring" by Rachel Carson (1962) did much to raise public awareness of the pernicious effects of pesticide use. In the last few decades a multitude of studies have reported detrimental impacts of man's activities upon many different ecosystems (see review by Chapin et al 2000 and the references therein) providing the impetus for the UN Millennium Ecosystem Assessment, the findings of which were published in 2005. Awareness has now risen of both the importance of *ecosystem health* to human health (Rapport et al 2003, Millennium Ecosystem Assessment 2005) and of the global impact of combined human exploits upon the environment and climate (Parry et al 2007).

The Intergovernmental Panel on Climate Change (IPCC) report, "Climate Change 2007" (Parry et al 2007), provided a synthesis of current knowledge on the manifestation of climate change and consequent effects upon ecosystems, their goods and services. The report provided strong evidence that anthropogenic activity is driving climate change and will have far reaching consequences in terms of the availability and distribution of resources, with associated economic costs (Parry et al 2007). According to the findings of the IPCC, the changes in climate will be sufficient to alter the structure and functioning of many ecosystems. The IPCC recommended that researchers turn their attention to, among other things, understanding and modelling the role that biota play in the function and structuring of ecosystems (Fischlin et al 2007). Determining the influence of the biota upon

ecosystem functioning, should lead to better assessment of the consequences of species extinctions and migrations upon the provision of ecosystem services and goods (Fischlin et al 2007).

Ecosystems are complex structures and elucidating all the links between every species and its ecosystem is virtually impossible (Smith et al 1997, Gitay and Noble 1997). Increasingly attempts to link biota to ecosystem processes have focused on grouping the biota into "functional groups" according to similarities in traits or activities (Pianka 1978, Simberloff and Dayan 1991, Gitay and Noble 1997, Schwartz et al 2000, Pearson 2001, Blondel 2003 and references therein, Norberg 2004). By characterising the biota in terms of functional groups, researchers are able to investigate relationships between the environment and the functional group (which is treated as a single entity) rather than studying relationships for every single species. Thus, researchers aim to reduce the levels of complexity that must be investigated and hence, permit generalisation and modelling of associations between the biota and the overall ecosystem functioning (Padilla and Allen 2000, Pearson 2001).

The use of the term "functional group", however, is not consistent throughout the literature (see reviews by Gitay and Noble 1997, Blondel 2003); for example, it has been applied to species that are "ecologically equivalent", that exploit the same resources using the same mechanisms or that demonstrate similar responses to environmental variables (Blondel 2003). Within the estuarine environment species have been variously grouped according to their feeding preferences, life history strategies and ability to alter sediment properties (de Sylva 1975, Elliott and DeWailly 1995, Elliott et al 2007a, Mazik et al 200) to list but a few examples. In this thesis, however, the term "functional group" is employed to describe *any group*

of species that have been combined as a single biological unit according to their similarity in one or more of their traits or activities.

1.2 What is an ecosystem?

Man has a long history of fascination with the natural world and the entities contained therein. This "Biophilia" (Wilson 1996) can be traced back thousands of years to the Greek philosophers e.g. Aristotle and Theophrastus. As man explored further from his home shores, he reported on species occurrences from around the globe. With increasing numbers of observations came increased theories, and some notable advances in our conceptual understanding of the natural world, for example, von Humboldt's (von Humboldt and Bonpland 1807) theories of climatic zonation of plants and Darwin's (1859) theory of natural selection of species.

As interest grew in interactions between species themselves terms such as "biocoenosis" were introduced to describe biological communities. Suess (1875) focussed on the interplay of environmental forces and coined the phrase "biosphere" to describe the "envelope of life". The term biosphere was championed by Vernadsky (1926) who proposed the existence of several biogeochemical cycles in his work linking biology with the physical and chemical environment. The term ecosystem was introduced in the 1930's by Tansley who considered an ecosystem to comprise:

"the whole system (in the sense of physics), including not only the organism-complex, but also the whole complex of physical factors forming what we call the environment of the biome....."

More recently the Millennium Ecosystem Assessment (2005) produced its own definition of an ecosystem that was applied in a global assessment to "map the

health of our planet":

"An ecosystem is a dynamic complex of plant, animal, and microorganism communities and the nonliving environment interacting as a functional unit."

1.2.1 Using the ecosystem concept in environmental studies.

Although studying individual species responses to environmental forcing can be very informative, such studies are costly, time consuming and rarely reflect the environmental conditions truly experienced in the field. In reality species existence and activity is determined not only by intrinsic ability to respond to environmental conditions but also by interactions with other members of the biocoenosis. Hence, environmental managers often seek ecosystem-level studies that provide information about overall structure and functioning of ecosystems.

Much of the recent focus on ecosystem-level processes in ecology has been driven by concerns about the detrimental effects of human activity upon the environment (Naeem et al 1994, Chapin et al 2000, Houghton et al 2001, Reiss and Kröncke 2005, Tett et al 2007). To assess how anthropogenic exploits might alter the structure of ecosystems, one needs to consider many factors such as the geology, hydrology, chemistry and biota.

Both Tansley's original definition and that of the Millennium Ecosystem Assessment (2005) can easily be applied to a multitude of scenarios, for example the study of sea grass meadows (Ziegler and Benner 1998), terrestrial habitats (Weltzin et al 2003) and tundra (Forget and Lebel 2001). The ecosystem concept has been employed extensively in estuaries, for example to study the effects of non-native species upon productivity (Ruesink et al 2006), the influence of changing geomorphology on biota (Smaal and Nienhuis 1992) and the impact of pesticides upon the biocoenosis (Phillips and Spies 1988).

It is the lack of scale and complexity in the above definitions of "ecosystem" that allows flexibility in use of the concept. For example, both the "biosphere" and a lone rock pool could be regarded as ecosystems. This flexibility, however, presents problems for ecologists seeking a unifying theory of ecology and attempting to compare patterns observed across different ecosystems. What is the influence of an individual rock pool upon the functioning of the biosphere? Not only are the scales of measurement different within each ecosystem, but also the intrinsic nature of the components will vary. Interactions within ecosystems will be driven in part by the nature of the components and hence are unlikely to be directly comparable in the above two examples of ecosystems. Consequently, ecologists need to define their ecosystem further for each separate study (Jax 1998), which detracts from the goal of identifying processes and interactions that are evident both within and between ecosystems.

The spectre of climate change hangs over environmental managers but *exact* predictions as to the full extent of altered climatic regimes upon any ecosystem are still generally lacking (Sagoff 2003, Hooper et al 2002, Gessner et al 2004) although possible climate "scenarios" have been predicted for the United Kingdom by UKCIP02 (Hulme et al 2002). Producing predications and explanations that help environmental managers has not proven easy yet many feel that preservation of ecosystems is one of the most important challenges facing today's scientists (May 1995, Millennium Ecosystem Assessment 2005).

1.2.2 The Ecosystem Approach to environmental management

In recent years environmental managers have advocated an "Ecosystem Approach", that considers how anthropogenic activity and aspirations impact upon the other components of ecosystems, with the eventual goal of promoting

sustainable management of resources (Elliott et al 2006, CBD 2000). The Convention for Biological Diversity (CBD 2000) has defined principles and outlined steps to be undertaken in implementing such an approach. The CBD emphasises the need to identify human interests and objectives as well as requiring the structure and function of the ecosystem to be characterised: after careful consideration of ecosystem structure, functioning, relationships with other systems and benefits provided to man, a monitoring strategy and management plan can be implemented.

1.3 Structure and Functioning of Ecosystems

Whether for management or academic purposes, it is clear that a thorough understanding is required of the internal structures and functions occurring within ecosystems at many different scales and with many feedback loops, before progress can be made to elucidate how human activity truly affects the biosphere (Reynolds 2001, Margalef 1997).

The *structure* of an ecosystem refers to the components that unite to create the ecosystem. At the broadest level there are two components of ecosystem structure – biotic and abiotic (Mathews et al 1982, Elliott et al 2006). The *functioning* of ecosystems refers to the processes that occur both within the components and between them. Functions occur as a result of biological, physical and chemical processes, for example the cycling of carbon and fluxes of nutrients between compartments or the oxygenation and destabilising of soft sediments. Ecosystem functioning can be regarded as the net result of all these processes (Norberg 2004).

1.3.1 The abiotic component

Principally, the abiotic component comprises sources of energy (e.g. solar radiation, wind and wave energy), nutrients, space (substratum) and water, i.e. the basic chemical and physical factors needed to support life. The form taken by these resources and the subsequent environmental conditions will vary according to location and the scale of interest. For example, in an arid environment it may be that the amount of rainfall is an important factor, whilst within a lake ecosystem it may be the chemical nature of the water that is influential upon ecosystem structure and function.

Abiotic factors can have direct effects on the biocoenosis but may also combine with other environmental factors to produce joint effects. For example, climate can influence the biota directly through levels of illumination or precipitation. In addition, altered rainfall can impact organisms indirectly by causing leaching of minerals or weathering of habitat (Weltzin et al 2003).

There have been numerous attempts to predict the structure of the biocoenosis from knowledge of environmental factors (Dolédec et al 1999, Statzner et al 2001, Lavorel and Garnier 2002, Ysebaert et al 2002, and review by Guissan and Zimmermann 2000 and references therein). One abiotic component that has received much attention is the availability of nutrients, in particular nitrogen and phosphorous. Researchers have shown that nutrients are assimilated and later released by the biocoenosis in a cyclic manner, leading to the identification of biogeochemical cycles. Biogeochemical cyclic events are the basis for some of the processes thought to be key to ecosystem functioning and development (Loreau 2002). Within estuaries the erosion-deposition cycle has been shown to greatly influence nutrient cycling and the benthic community structure (Elliott et al 2006). Hence, many researchers have sought links between benthic community

structure and the physico-chemical nature of the sediment within which they reside (Rhoads 1974, Aller 1982, Hall 1994, Pearson 2001, Mazik et al 2008,).

1.3.2 The biotic component

The biota can be divided into many sub-units, for example individual species, species populations (i.e. all individuals of the same species), communities, groups based upon functional attributes or groups defined by molecular similarity. The term *community* encompasses all the biota that live and interact within a habitat or specified location. Thus, in defining a group of co-occurring species as a community there is an inherent assumption that interactions occur between community members. To avoid making any such supposition, and to recognise that choices of field sampling methodology limit the extent to which the entire community is sampled, the term *assemblage* will be used throughout this thesis to indicate a group of species found at the same location during the field sampling, and *community* will be reserved for theoretical discussions that pertain to the entire biocoenosis.

Within the biocoenosis, interactions can occur at many scales and in very different ways (Connolly and Roughgarden 1999, Levin et al 2001b). Mutualism, competition for resources, predation and complementary resource use are all examples of well-studied biotic interactions (Nybakken 1993, Doncaster et al 2003). Lawton (1994) suggested that the multitude and magnitude of potential interactions should theoretically result in many varied community structures. However, Peterson et al (1998) proposed that there is convergence, not divergence, of community structures, with similarity in structure being driven not by the presence or absence of individual species, rather by the trait composition of the functional groups present (Norberg 2004).

Whilst some researchers have proposed equal importance to every species, for example Ehrlich and Ehrlich's (1981) analogy with rivets holding a structure in place, others (Walker 1992) suggest that the loss of certain species may have a disproportionate influence on overall structure. Still others maintain that communities are idiosyncratic and their responses are not easily predicted from knowledge of individual species (Emmerson et al 2001). The extreme null model suggests that no species is important (Lawton 1994).

Species composition will determine which biotic traits are present in a given community and define the potential interactions that can occur. Thus many consider that species diversity plays an important role in determining biotic structure (Tilman 1996, Levin et al 2001b).

Diversity can be measured in many ways (Purvis and Hector 2000). For some researchers it is simply the number of species in the system, whilst other ecologists combine species richness with a measure of how evenly individuals are spread among the different species, and yet others try to include a measure of "disparity": assessing how similar in morphology or activity species may be (Gray 2000, McCann 2000).

Although evidence has been found to support relationships between diversity and ecosystem functioning in recent years (Tilman 1996, Levin et al 2001b, Gerino et al 2003) there is still much debate as to whether it is species diversity itself, diversity of species traits (including life history) or diversity of functional abilities that drives such relationships (Hooper et al 2002, Lawton 1994, Norberg 2004). In addition, Elliott and Quintino (2007) suggest that it is the characteristic low biodiversity of estuaries that actually promotes natural ecosystem functioning within estuarine systems.

Reynolds (2001) stated that "the prominent species are not necessarily the best

fitted" i.e. the species exploiting a location are not necessarily ones for which existing conditions are optimum but rather Reynolds (2001) suggests that sorting pressures select for species whose *traits* allow them to tolerate conditions. Norberg (2004) also asserts that it is diversity of species *traits* and not diversity of species *per se* that will influence ecosystem functioning. Indeed Norberg was critical of laboratory manipulations that examine the role of biodiversity in ecosystem functioning. If the biocoenosis is indeed a random, emergent community, as Norberg (2004) and Reynolds (2001) propose, the selection of a small sub-sample cannot replicate the true level of interactions occurring in the field. The sequence of species introductions cannot be identified from field assemblages since this has occurred under past interactions. Thus, laboratory based experiments may introduce species into the system in an order never experienced in reality. The past evolutionary filters may have produced trait distributions very different to those simulated in manipulative experiments. Trait distribution in reality may not follow species diversity patterns and Norberg (2004) recommends that efforts be re-focussed on examining *trait diversity* and the role of sorting on *trait* selection.

Hooper et al (2002) assert that it is diversity of functional abilities of organisms that determines the scale and intensity of ecosystem processes. This begs the question "Are species sufficiently different in terms of function to be the unit of functional investigation?" Alternatively, "are only a few limited functions performed to which species contribute at different levels?" In the latter case changes in species numbers will not automatically alter the number of functions performed but may influence the level of performance. Identifying the functions to which species contribute and the spatial and temporal extent of contributions must be addressed in order to decide the unit of functional investigations.

Early work on functional groupings arose from niche theory and the idea that there was competition for resources, be they food, substrate, hosts etc (Pianka 1978, Blondel 2003). Such groupings of intense competitors were termed *guilds*. Later the term *functional group* was coined, referring to species that performed similar roles within the ecosystem, rather than being associations arising by competition (Blondel 2003). The concept of classifying species according to their role in processes occurring within the ecosystem has developed to provide many different modes of classification. Each definition is usually applied independently of others and the choice of category reflects the researcher's focus of interest, for example the "bioturbatory" ability of species to mix and disturb sediment (Pearson 2001), "trophic groups" that incorporate feeding activity (Hulot et al 2000), or species activities that influence soil processes (Lavelle et al 1997), to name a few.

1.3.3 The organisation and regulation of ecosystem components

To understand processes and structure in the ecosystem, questions such as "How are components organised", "Is there a hierarchical structure?" and "How is regulation imposed, if any exists at all?" need to be addressed (Jorgensen 1994, Belyea and Lancaster 1999, Rojo 2000, Levin et al 2001a, Reynolds 2001). Understanding the ways in which the internal complexes of the system are linked allows questions of function and value to be addressed. It also allows predictions of changes arising from human activity to be made.

There has, however, been debate as to whether these processes are merely collections of random events or whether information transfer truly occurs within the system (Engelberg and Boyarsky 1979). Evidence of feedback was cited by Jordan (1981) from among the many mutualistic associations known to exist and

which support the view that the biotic and abiotic complexes are subject to diffuse co-evolution (Levin et al 2001b, Ehrlich and Raven 1964).

Both Reynolds (2001) and Lavorel and Garnier (2002) proposed that abiotic filters act at the broad and local scale, and act on abiotic and biotic factors simultaneously. Equally the biotic structures interact with each other and the environment to provide feedback throughout the ecosystem. Species' trait heterogeneity combined with abiotic heterogeneity allows the filters' influence to vary across the system. The end point is a self-organised, complex adaptive system, which Reynolds (2001) described as an "emergent high-order structure". Thus, heterogeneity within the system maintains species variety and promotes diversity, maintaining the gene pool for flexible species responses to filter variation (Norberg 2004, Lavorel and Garnier 2002).

Some researchers consider ecosystems to be open systems that interact with others, allowing interactions across boundaries (Levin et al 2001b, Norberg 2004). This hierarchical approach allows the world to be viewed as a set of interconnecting components that are constantly exposed to interactions between groups. The balance of these interactions at any one time drives the state of the system. However, the challenge remains not just to identify processes and interactions but also to quantify rates and net effects.

Sagoff (2003) and Pickett and Cadenasso (2002) suggested that modelling could be a useful tool if supported by empirical testing. Sagoff (2003) criticised ecologists for retaining too many potential models, theorising about ways to link them all together rather than testing their usefulness.

If modelling studies are combined with testing of field data, then the causes of the ecosystem organisation can be investigated and ecological theories rigorously tested. Thus, to progress beyond theory it is not enough simply to identify

ecosystem structures and theorise about potential interactions. To truly assess the importance of each component, interaction strengths and contribution to ecosystem performance need to be quantified. This requires a detailed knowledge of links between the abiotic and biotic elements and the unification of biology, ecology, chemistry, physics, geology and an appreciation of human activity and aspirations.

Thus, whilst it has gradually been accepted over the past century that the existence of a particular species is dependent upon the system within which it resides (Vernadsky 1926, Elton 1933), consensus as to *how* the species and system are interrelated and organised has not yet been achieved. The system and species are inextricably linked through a past history and a future to be determined by interactions as yet unknown. As Wilson (1996) observed "*The true frontier for humanity is life on earth – its exploration and the transport of knowledge about it into science, art and practical affairs*".

1.3.4 Exploring links between biotic and abiotic components

Traditionally estuarine scientists have worked in isolation, biologists studying species, chemists describing nutrient fluxes in and out of systems, physicists modelling sediment movements and hydrologists studying water flows. Thus, there has been a rift between these traditional foci of research. Environmental managers can obtain small-scale (often laboratory derived) data about biotic activity on the one hand and large-scale physical and chemical measures of mechanisms driving the abiotic conditions on the other. Elucidating links between components of intrinsically different nature that act on different temporal and spatial scales however is difficult. Ideally researchers seek to merge knowledge obtained from "bottom-up" and "top-down" studies (Elliott et al 2006).

According to Hooper et al (2002) this can be achieved by studying functional attributes of the community. Sagoff (2003), however, claimed that few studies have truly linked top-down and bottom-up approaches or produced general theories that are transferable between ecosystems. Sagoff (2003) attributed this lack of success to heterogeneity of ecosystem components, scales and interactions.

To link top-down and bottom–up approaches one needs to overcome two major difficulties. The first is to identify and quantify the functions to be investigated. The functions measured at the ecosystem scale may in fact represent a composite effect of many processes at the species scale. This mismatch of scale is the second problem. It is key that not only can we identify to which processes species contribute, but also that we can measure the amount of contribution and relate it to measurements of the same function at a different scale

As shown in Figure 1.1, links need to identified that can relate contribution occurring on different scales to overall ecosystem function. The search for such links is central to this thesis and poses subsequent questions:

- Is the scale at which we have the technical ability to measure the ecosystem function relevant to the scale at which an organism is active?
- Is the scale at which the animal's activity is measured relevant to the ecosystem?

It is also important to remember that if a species does not appear to have a direct effect upon a specified function, it may influence overall function indirectly, e.g., Purvis and Hector (2000) point out that a species may be important for reasons other than the function under investigation, or on different time scales. Thus the researcher's main focus may obscure the true overall functioning of that community

SPECIES

Activities commonly used to classify species include:

ECOSYSTEM

Measurements often made:

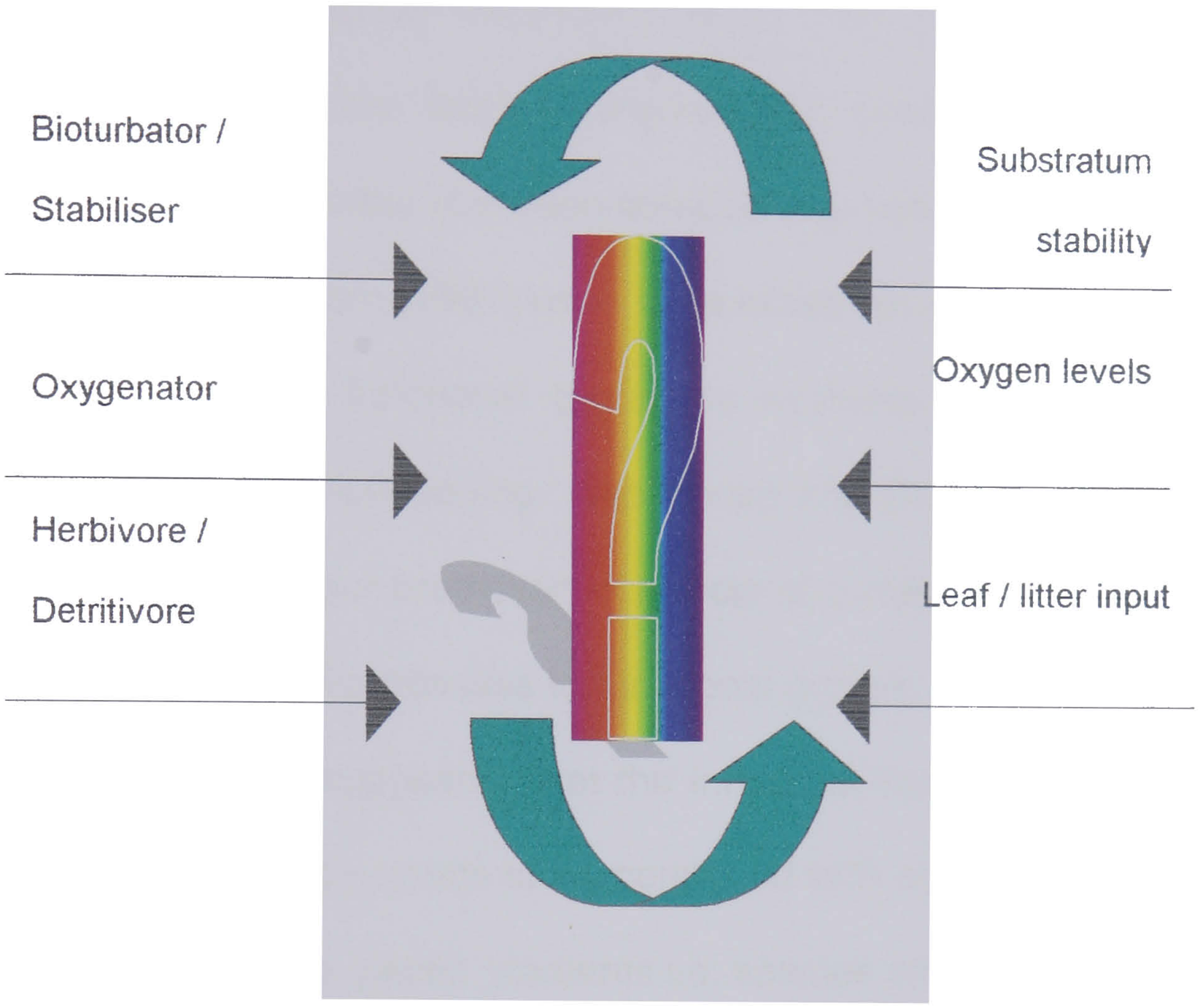


Figure 1.1. The problem of identifying the function under investigation: both species and ecosystem approaches are considering the same processes but from different perspectives, thus it should theoretically be possible to elucidate the links (represented here by the question mark) between them e.g. the decomposition of detritus will be influenced by the occurrence of species capable of degrading organic matter. Linking activities will only be possible, however, if the activities of species are truly known, the conceptual model of the relationship is valid and the functions can accurately be defined and quantified.

To progress with understanding we need to be able to :

- identify and quantify what a species does,
- be able to attribute this activity to the overall processes in the ecosystem,
- be able to determine whether the sum activity of the biocoenosis is detectable at the coarse estimates of ecosystem level and

- remind ourselves that we have focused on only one or a few function(s) out of many possible and often unidentified activities.

If we are able to accurately quantify the species activity and the overall amount of the process occurring at ecosystem level then we might be able to start understanding how one level of organisation (within complex e.g. within an estuary) relates to another (between complex e.g. between estuary and sea).

Woodward and Diament (1991) used traits of fire-resistance, drought survival and salinity tolerance as functional groups to examine how climate change could influence ecosystem functioning. Woodward and Diament (1991) proposed that one way to improve our prediction of effects of climate change would be to scale down from ecosystem processes to functional groups.

Hooper et al (2002) suggested that the influence that functional groups have on the ecosystem function needs to be combined with other functional traits that link species distribution to abiotic gradients i.e. species should be grouped into:

(i) functional *effects* assemblages according to how they influence ecosystem processes, and

(ii) functional *response* assemblages according to how they are distributed in the ecosystem along environmental gradients.

The effects groups could be derived by a top-down approach whilst the response groups would be addressed using a bottom-up approach. To truly understand ecosystem processes we need to understand species distributions in response to abiotic factors and the impact of biotic activity on the abiotic environment. Thus both top-down and bottom-up approaches and better links between the two methods are required in order to reduce the problems associated with scaling from one level of investigation to the other.

1.4 How do we decide if ecosystems are the "same"?

When assessing the likely impact of human activity upon the environment, managers and theoreticians need to ask, "How stable is the ecosystem structure?" (Tilman 1996, McCann 2000). According to Sagoff (2003), a major hurdle in being able to answer this lies in being able to quantify what is the *same* ecosystem. For environmental managers it is important to be able to assess what is the expected status of the ecosystem and how much variability can be accommodated before ecosystem functioning is affected. When does a lake stop functioning like a lake? Is it when it dries up totally, or when all the fish die, or when plants occupy a certain percentage of the ground? This raises the questions "What is stability?" and "Are any ecosystems truly stable if a long enough period of evolutionary history is considered?"

The ability of an ecosystem to return its previous state after a period of perturbation is referred to as *resilience* (Elliott et al 2007, Tett et al 2007). To be an ecosystem there must be a degree of resilience so that the ecosystem remains in evidence long enough to be observed! Indeed, early researchers viewed ecosystems as constant in nature. Whilst disturbance could perturb the abiotic and biotic conditions at any one time, the interactions would always lead to an ordered, predictable pathway of "succession", i.e. a progression from one biotic community to another, until a terminal and permanent biotic structure is achieved – the climax community (Clements 1916, Sanders 1968, Odum 1969, McIntosh 1985).

Whilst support for this successional view has been found in ecology (Pearson and Rosenberg 1978, Bonsdorff and Ősterman 1985), there is also evidence of non-equilibrium systems, where perturbation can lead to an altered "climax" scenario. In particular, it has become increasingly obvious that anthropogenic activity has

the potential to push ecosystems into altered states from which there is no natural return (Wilson 1996, Woodward and Diament 1991)

Like a spring that is stretched, removal of the disturbing force can lead to oscillations in form around the original, these gradually diminishing as the spring regains its original form. The ease and speed with which original form is obtained is termed resilience. Alternative views suggest that the return to the original state can occur via a different pathway, rather than as a series of successively dampened oscillations. However, in many instances, like a material stretched beyond its elastic limit, the original form may never be regained, or only be achieved at a very slow rate – a phenomenon known a "hysteresis". Many ecologists believe that, whilst ecosystems do demonstrate degrees of resilience, it is possible to perturb systems sufficiently to create an altered state (McCann 2000).

There is also another view, that although the perturbations may not produce a permanent new state, disturbance can occur with sufficient frequency to prevent any dampening or return to the *status quo*. Odum (1969) viewed this as a way in which an ecosystem could remain at an early stage of succession. An alternative interpretation (Levin et al 2001b) views this more as a way in which an ecosystem remains in flux, with heterogeneity of components. The distinction is subtle, Odum's (1969) view implies that the ecosystem state is fixed but if the perturbation is removed, an ordered journey will be resumed. The second view sees the ecosystem state varying as a result of perturbation with many possible states. Removal of the perturbation could have many pathways depending upon the point in space and time that the perturbation is removed.

The idea that perturbation can increase heterogeneity within ecosystem components is consistent with Connell's "Intermediate Disturbance Hypothesis"

(Connell 1978). Connell proposed that where disturbance occurs at intermediate strengths, the system maintains a greater level of species diversity than when disturbance is greater or lower. Greater levels of perturbation may be sufficient to alter the biocoenosis (removing less tolerant species), whilst low levels of disturbance may allow a less diverse community to become established according to competitive interactions.

To achieve sustainable management of resources, managers need to understand how ecosystems have been, or will be, altered by disturbance and whether natural recovery is likely within an acceptable time frame (Elliott et al 2007b). Armed with this information, managers can assess whether restorative measures are needed or indeed likely to succeed. Informed decisions can only be made, however, if underpinned by a solid appreciation of the structure and functioning of the system: to evaluate lost resources and restorative measures, managers must be able to identify and quantify ecosystem processes.

1.5 The estuarine system as a test-bed for ecological theory

The estuarine ecosystem provides an ideal test-bed for studies linking biotic communities and ecosystem functioning. The number of species within estuaries is greatly reduced compared to terrestrial, freshwater and marine environments (McLusky and Elliott 2004, Barnes 1974). As a result, the number of species traits and activities that need to be identified is also reduced. Estuaries are better known and in general easier studied than some other marine environments such as deep-oceans (McLusky and Elliott 2004). Historically, estuarine species have been well studied, as have sediment movements and water flows, since these sites have long been of commercial interest (McLusky and Elliott 2004).

Estuaries are often classified as "stressful" environments (but see Elliott and Quintino 2007) due to salinity gradients, tidal regimes, and periods of aerial exposure and hypoxia. Thus, for any given abiotic factor, a large range of values may be experienced along an estuary producing very variable selective pressures within a relatively small geographic region for many estuaries. Thus the changes in ecosystem processes can be compared at many locations, and the effects of biotic and abiotic heterogeneity assessed (Levin et al 2001a).

1.5.1 The drivers

In recent years, international and national legislation has been a principal driver in estuarine research, with the main focus within the European Union now being on the obligations placed upon signatories by the Water Framework Directive (Directive 2000/60/EU) that requires *good water status* for all waters by 2015.

This directive introduces the term *transitional water* to replace the descriptor *estuary* that has itself many definitions (Perillo (1995) lists over 40). For the purposes of the Water Framework Directive (WFD), transitional waters are defined as

"..bodies of surface waters in the vicinity of river mouths which are partly saline in character as a result of their proximity of coastal waters but which are substantially influenced by freshwater flow" (Article 2.6 WFD)

In order to meet their obligations to achieve *good water status*, member countries must decide what is the expected standard for good water status and how this can be measured.

To decide what is the expected standard, member states are being asked to predict, for a given suite of physical parameters, which biological communities and chemical levels would be expected. The realisation of a defined *pristine*

community or *baseline* data has proved elusive and alternative methods such as comparisons with historical data, similar systems, use of indicators of ecosystem health or model outputs are being investigated (A. Prior pers comm). The WFD, however, focuses on measures of species diversity and taxonomic identity ("*composition and abundance of fish/benthic invertebrate fauna*") as indicators of environmental change. It is becoming increasingly apparent that the natural variability of environmental conditions occurring in estuaries leads to communities of low biodiversity, comprising tolerant species, but with high degrees of natural variability in abundance and community structure (Elliott and McLusky 2004). The structural characteristics of natural estuarine communities often mimic those found in water bodies suffering from anthropogenic organic enrichment and hence, Elliott and Quintino (2007) advocate that researchers develop separate methodologies for estuaries. Elliott and Quintino (2007) recommend placing greater emphasis upon functional characteristics of the biota than traditional structural attributes of the biocoenosis, although this would be in contravention of the specific requirements of the WFD.

1.5.2 The estuarine macrobenthos

There are many assemblages within an estuary that could be studied because they are known to contribute to ecosystem function. One of the best-studied assemblages is the benthic macrofauna, which has been shown to play an important role in nutrient transfer through the estuarine system (Nybakken 1993). There are many advantages in focussing functional studies on this part of the biocoenosis:

- the macrobenthos are relatively less mobile than fish and bird communities: thus they are less likely to demonstrate rapid migration from the ecosystem in response to abiotic changes:
- the macrobenthos are relatively well studied and the taxonomy of the species better known than many other parts of the community (McLusky and Elliott 2004);
- due to the lower levels of motility, the macrobenthos can be easier to sample quantitatively than fish and bird populations;
- there is a large body of literature on estuarine species' traits and life history that can be applied in functional group analyses;
- studies on microbial and meiofaunal communities are more recent and thus less is known about species diversity and traits; and
- many estuarine studies have already addressed the relationship of species distribution to abiotic factors.

The estuarine macrobenthos can comprise many taxa with many different life strategies. The sediment is not merely a two dimensional resource for the biota. Whilst the sediment-water interface plays an important role in biophysical processes, many species do exploit the vertical structure of the substratum (Nybakken 1995, Peterson 1977).

It has been suggested that space is a limited resource for benthic fauna (Peterson 1977, Whitlach 1980, Josefson 1989). However, most macrofaunal species require periodic contact with the sediment-water interface via some means, principally to obtain oxygen. Thus it is unlikely that the entire substratum is truly available for exploitation by fauna. Many researchers have reported that most species and individuals are found in the uppermost 10cm and propose that various forms of biotic interactions lead to a structured community pattern (Whitlach 1980,

Johnson 1967, Myers1977). Understanding this pattern can help to explain the functional contribution of species to ecosystem processes.

Firstly, the vertical distribution of species will influence our ability to effectively sample the community (Hines and Comtois 1985). Peterson (1977) found some species below 50cm in the sediment, whilst Hines and Comtois (1985) recorded species to 35cm below the sediment surface. Thus, studies that only investigate the top few centimetres of sediment risk ignoring some community members, depending upon the nature of the sediments.

Secondly, the depth occupied by a species will determine its ability to interact with other species and partake in ecosystem processes. Depth in the sediment may impact upon processes such as energy transfer, nutrient uptake and sediment stability. Thus depth should be taken into account when considering both the type of functional traits demonstrated and the strength of contribution to overall process. For example, consider hypothetical species that both move similar horizontal distances over a period of time but at different sediment depths. The influence of the two species on sediment disturbance should be different. One species will disturb the upper layers. The uppermost layers are interacting with the overlying water and abiotic factors above the sediment. The upper layers are also where most individuals and species occur. Hence, it could be hypothesised that the shallower species will have more interactions with other biota and the abiotic factors, thus their functional contribution will be very different. Any investigation into the functional contribution of macrobenthos to ecosystem functioning should consider vertical, in-sediment distribution when defining the function categories and when assigning strengths to the interactions.

Within the estuarine benthic community most studies have focussed upon trophic and "bio-engineering" functions, although other categories could be developed

(Pearson 2001). The former aggregates species with similar feeding strategies, and facilitates studies on nutrient and energy flows around the system. The bio-engineering classifications consider the way in which species alter the physical environment within which they reside (Jones et al 1994).

Trophic studies have been used to produce food webs and species fall into broad categories such as primary producers, herbivores and omnivores (Pearson 2001). The use of such broad categories allows connections to be made to other ecosystems and consequently linking the flows of nutrients and energy between very different ecosystems is theoretically possible. Within the broad categories many sub-divisions are possible, for example based upon the mechanism by which food is captured.

The majority of bio-engineering functional groups have been developed by considering "bioturbation" processes i.e. how the animals disrupt the sediment and promote mixing of particles (Pearson 2001, Jones et al 1994). Species have been placed into broad categories of stabilisers and destabilisers, or into groups defined by how the animal's activities move sediment particles. For example, François et al (2002) proposed that there were five main categories: biodiffusers, gallery diffusers, regenerators, upward conveyors and downward conveyors. Other researchers have investigated how deposit-feeding fauna influence sediment mixing by ingestion and defecation of particles (Wheatcroft et al 1990, Swift et al 1996) or by a range of activities such as motility and burrowing (Swift 1993, Solan 2000).

Rather than addressing energy flows, these "bioturbatory" groupings aid investigations into processes such as sediment stability, nutrient transfer and oxygenation of the substratum.

The species' traits used to delineate the functional groups differ according to the classification applied, so that species can be aggregated very differently according to the focus of the investigation.

There have been attempts to examine how human activity can influence the distribution of functional groups (Woodward and Diament 1991, Chapin et al 2000, Naeem et al 1994). If human activities influence energy input to systems, then trophic groups would be the favoured functional unit of investigation. If, however, human activity results in species removal, both approaches would have merits depending upon the ecosystem processes being examined.

1.5.3 Attempts to link estuarine species activity to abiotic factors

Many studies have demonstrated that the abiotic variables within an estuary influence the community structure at any one location (Wildish 1977, Warwick et al 1991, Ysebaert et al 2002, Forster et al 2006). The principal factors identified are salinity, sediment characteristics, tidal regime and elevation (Warwick and Uncles 1980, Warwick et al 1991, Anderson et al 2004, Thrush et al 2005).

There have been many attempts to model species distributions in estuaries with some limited successes (Ysebaert et al 2000, Attrill 2002, Ysebaert et al 2002, Ellis et al 2006). These successes, however, have yet to provide generic predictions that can be transferred between estuarine systems. Thus whilst the general principles of which factors play a role are widely understood, practical algorithms to translate generality into specific predictions are still lacking.

Models based on species' distributions are costly in time and effort and so functional models have great appeal to environmental managers. Whilst estuarine species have been well studied the links between those species and estuarine processes have received less attention. It is imperative that attention is now

focussed on determining the critical processes and associated functional groups (Bonsdorff and Pearson 1999).

Elliott and Quintino (2007), recommend that, for management purposes, links be sought between the environmental status of estuaries and functional attributes of species. According to Elliott and Quintino (2007) the naturally stressful conditions that exist in estuaries are only stressful to non-tolerant species and produce an *Estuarine Quality Paradox* i.e. methodologies used to detect anthropogenic impacts upon other ecosystems will indicate low environmental status even in pristine estuarine environments

1.5 Aims and objectives of this study: linking ecosystem processes and biotic activity

This thesis sets out to address the major hurdles to improving our understanding of the role macrobenthic species play in estuarine functioning. This study investigates ways to define and quantify the contribution of the macrofauna to processes occurring in, or associated with, estuarine soft sediments. To achieve this aim, the following objectives are pursued:

- assess how effectively sites are differentiated at the ecosystem level according to patterns in the distribution of the biota, when the latter are characterised by either feeding or bioturbatory functional characteristics;
- explore whether species' body size could be used as a means of weighting species abundance to indicate the relative contribution of each species to a specified function;
- evaluate the role that species' spatial distribution, both vertically within the sediment and horizontally through the system, plays in determining that

species' effect upon ecosystem processes and its relationships with environmental factors;

- develop new theoretical functional groups that reflect the magnitude of the biotic contribution to processes occurring in the estuarine ecosystem; and
- develop a predictive model of the distribution of the new functional groups based upon abiotic characteristics of a given estuary.

1.6.1 Organisation of the Thesis and hypotheses tested

Chapter 1 provides a review of some of the extensive literature relating biotic activity and community structure to ecosystem health and functioning. It also introduces some of the estuarine-specific literature and outlines the reasons for focusing the thesis upon the estuarine macrobenthos.

Chapter 2 addresses the first of the thesis objectives by examining whether ecologically-meaningful site classification could be achieved by grouping the biotic assemblage in terms of functional traits, rather than using taxonomic identity alone. The chapter questions whether inter-site similarity according to environmental factors could be matched to patterns in the distribution of functional groups. In addition, the second chapter also considers whether apparent patterns in functional group distributions, and any matches between abiotic and biotic patterns, are altered if species' body size is used to weight the abundance of each species included in the different functional groups.

The hypotheses are:

- *There is no difference in the patterns of similarity between estuarine benthic assemblages according to whether species abundance or various functional groups are considered.*

- *There is no difference in the strength of relationships between the biota and abiotic factors according to whether species abundance or various functional groups are considered*
- *There is no difference in the strength of relationships between the biota and abiotic factors if species abundance and the various functional groups are weighted according to the body size of component species.*

Chapter 3 addresses the third objective by investigating relationships between abiotic factors and the horizontal and vertical, in-sediment distribution of estuarine benthic macrofauna. In particular, the chapter focuses on whether macrobenthic species living at different depths in the sediment have different responses to environmental forces and potentially different impacts upon ecosystem processes. The hypothesis tested are:

- *There is no difference in the structure of assemblages from different sediment depth horizons*
- *There is no difference in the nature of the abiotic factors shown to have relationships with the biota according to the depth range at which the benthic assemblage is found in the sediment.*

Chapter 4 combines the findings of Chapters 2 and 3 to develop new functional groups, according to the impact of any species' activities that promote sediment disturbance. The decision to focus on sediment disturbance is driven by the conclusions of Chapter 2 and also by the strong relationship that sediment mixing has upon other ecosystem processes, such as nutrient cycling and sediment erosion. This chapter explores a novel approach to functional classification and then tests the following hypotheses:

- *There are no relationships between the various abiotic parameters used to characterise the sediment*

- *There is no relationship between the distribution of the different functional groups within the estuary and the abiotic characteristics of the sediment*
- *There is no relationship between measures of total biologically-mediated sediment disturbance and the abiotic characteristics of each site.*

Chapter 5 applies statistical modelling techniques to develop predictive models of the distribution of the new functional groups within an estuary in response to abiotic variables. The models are validated using an independent dataset and the application of the models in studies of sediment dynamics is discussed.

The hypothesis tested is:

- *There is no significant association between total abundance in any SDE group and one, or a combination, of the abiotic factors.*

The final chapter, Chapter 6, reviews the results of all the preceding chapters and provides a synthesis of the findings of this thesis. Chapter 6 discusses some of the limitations of this study and also the benefits that could be obtained by the application of the approach of quantifying function contribution, as presented here, to future studies of species distribution, ecosystem health, ecosystem functioning and forces driving community organisation.

CHAPTER 2

Can Functional Groups be used to indicate estuarine ecological status?

Aspects of this chapter are included in:

Sanders JL, Kendall MA, Hawkins AJS, Spicer JL (2007) Can functional groups be used to indicate estuarine ecological status? Hydrobiologia 588:45-58

2.1 Introduction

This chapter compares the ability of different functional group approaches to discriminate between separate estuarine sites, whilst linking biotic data with abiotic factors

There is increasing awareness that anthropogenic effects can have lasting impacts upon our environment (Carson 1962, Wiesner 1995, Wright 2000, Levin et al 2001). This has led to a variety of initiatives to develop ways of quantifying impacts of human activities upon ecosystem status (Gergel et al 2002). There have been studies on the use of sentinel species (the "bioindicator" approach of Hilty and Merenlender 2000), attempts to measure water and air quality to determine their suitability for sustaining life (Matthiessen and Law 2002) and modelling studies that attempt to predict species assemblages (Emlen 2003).

Environmental managers seek methods, which are not specific to one location or time and which are cheap and easy to both apply and interpret. This has often led to a search for a set of broad scale physical parameters that will predict an expected community assemblage in the absence of anthropogenic influences (Wright 2000, Skriver 2001, Austin 2002). Theoretically, this would then allow interpretation of the presence or absence of community members in terms of ecosystem health. Many countries and international bodies are introducing legislation that places a legal requirement upon signatories to define such "reference conditions" (Simboura and Zenetos 2002). One example is the European Water Framework Directive (Directive 2000/60/EC), which stipulates that ecological quality will be decided according to the relationship between observed biological elements and the relevant reference condition for those biological elements.

Definition of reference conditions for estuarine waters is proving problematic, as is the prediction of the associated macrobenthic assemblages (A.Prior pers. Comm). Estuaries are naturally stressful environments for organisms to inhabit, due to the range of hydrodynamic and chemical conditions that can prevail (Ysebaert et al 2002). Approaches based upon predictive modelling often fail at the initial attempt to predict the community assemblage (Hols 1996). One principal reason for this failure is insufficiently robust relationships between broad scale, physical parameters and species distributions (Attrill et al 1999, Austen 2002, Emlen et al 2003). For example, the lack of a mathematical, hydrodynamic model prevented Warwick et al (1991) from making specific predictions of species' distributions in response to proposed changes to the physical environment of the Severn estuary. Failure to develop models may also be due to the large range of biotic variation, both spatially and temporally, within and between estuaries (Platell and Potter 1996, Hagberg et al 2003).

There have been some successful attempts to model estuarine species distribution patterns, as predicted by abiotic variables (Ysebaert et al 2002, Attrill 2002). The most notable feature of such attempts is the vast amounts of fine-scale biotic and abiotic data required to produce predictions. For example, Attrill (2002) successfully used "mean salinity range" as a predictor of alpha diversity (number of species at each site) in the Thames estuary, but the salinity values were predictions from an estuary-specific model of salinity. In a similar way, the logistic regression employed by Ysebaert et al (2000) also had input from estuary-specific models capable of fine-scale predictions of salinity and tidal currents. The time and effort frequently required to produce detailed hydrodynamic models deter attempts to apply this elsewhere (Attrill et al 1999). Thus, although there is often

general consensus as to which abiotic factors are most influential, algorithms that truly represent the relationships across all estuaries are still not available.

In an attempt to reduce the effects of variability within the biological data, some researchers have considered grouping species into functional groups, rather than analysing simple species abundance (Pearson 2001, Lavorel and Garnier 2002). This approach appeals to environmental managers since, from their perspective, it is not the species that is important, but the overall "status" of the ecosystem. The presence or absence of a species may not be as easy to interpret as changes in occurrence of functional groups (Pearson 2001). However, Snelgrove and Butman (1994) emphasise the need to choose functional definitions with care to avoid loss of information that results from no longer identifying individual species. Within the coastal and estuarine environments, examinations employing functional groups have mainly focussed on the traditional areas of trophic or bioturbatory activities (Dauwe et al 1998). Early work by Pearson and Rosenberg (1978) demonstrated a change in trophic diversity and in the predominant group (based upon feeding and motility attributes) along a depth gradient, as organic enrichment increased. To differentiate between coastal sites according to their bioturbation potential, Swift (1993) proposed a system of scoring species. Mazik and Elliott (2000) combined both of these approaches, with work by Gerino et al (1993), Wheatcroft et al (1994) and Dauwe et al (1998), to examine relationships between functional groups and sediment dynamics along a pollution gradient. They successfully demonstrated changes in function with distance from a pollution source. None of these studies set out to *quantify* the relationships between changes in functional groups and either the physical environment or ecological status. Thus, whilst such studies advance our conceptual understanding of ecosystem function, they have not addressed the need for a predictive

management tool to aid in the determination of "ecological status". To date, none have investigated which method provides the best match to a given set of environmental variables. Until this has been addressed, interpretation of the changes between relative abundances of each functional group remains qualitative rather than quantitative.

This present study sought to redress this shortfall by examining how two functional groups may be linked to the physical environment. The work presented here assessed how changing the way in which the biota were classified altered the match of biological and abiotic data, and the implications this has for our understanding of ecosystem health. Mazik and Elliott (2000) demonstrated that the bioturbation potential scores of Swift (1993) and trophic groups both altered with increasing pollution levels. This present study extends their work by examining how well each category differentiated sites along natural environmental gradients and how easily the results could be interpreted.

However, the presence or absence of a functional group may be too coarse a measure upon which to base ecosystem management decisions. This current study assessed whether a more sensitive approach should be taken, measuring variation in amount of "function" to help identify more subtle fluctuations and act as an early warning indicator of change to status. Swift's method (1993) went some way to differentiating between the contributions of component species, awarding a score to each species, according to that species' ability to promote bioturbation. The score was the sum of values allocated according to three activities: burrowing, motility and feeding. This was an attempt to place relative numeric values on bioturbatory activity, and which highlighted coastal site associations according to values of bioturbation potential. However, the system assumed that any two species with the same potential score are active at the same scale and level of

intensity, i.e. they have equal potential to cause displacement of sediment particles, but no consideration was taken of how far those particles might be moved or how often. Mazik and Elliott (2000) pointed out that bioturbation scores could have greater ecological significance if biomass, abundance and body size were also considered.

Each species will contribute to any given function on the scale at which its activities occur (Peterson et al 1998). Thus consideration must be given to assessing which species do in fact contribute at the scale at which the manager wishes to investigate and predict. Thayer (1983) proposed ways to calculate individual sediment disturbance rates, but in general there is insufficient knowledge of each species' activities to apply this measure (Snelgrove and Butman1994). Whilst sediment turnover rates have in the past been described (Hall 1994) no attempt has been made to use these to apportion species contribution to bioturbation. Hall (1994) showed that turnover rates do not vary greatly according to trophic group, reworking mode or sediment type classifications, and concluded that characteristics, which are specific to a species, for example body size and burrowing depth, did merit consideration.

This study expanded Swift's (1993) work by weighting the relative contribution of each species to its functional group according to its body size. The same approach was applied to both trophic groups and abundance data, thereby turning theoretical grouping according to function into a more integrated measure of functional performance. Under such a scheme, where two species contribute to a single function at similar levels of activity, then greater ecological importance would be accorded to the larger species.

Thus, in this study, the aim has been to determine which functional group approach provides the best correlations with abiotic data, and how such

relationships are influenced by introducing body size weightings to the calculations of overall function.

The null hypotheses were:

- *the way in which the biological data are classified will not alter the way in which the estuary sites are grouped by multi dimensional scaling (MDS) and cluster analysis;*
- *weighting the biological datasets according to the body size of component species will not alter the way in which the estuary sites are grouped by MDS and cluster analysis; and*
- *weighting the biological data classification methods, according to the body size of component species, will not alter the relationships between the biological classifications and the abiotic data.*

2.2 Methods

2.2.1 Biological Dataset

To test the hypotheses, data were obtained from the JNCC Marine Recorder Database, for a survey carried out on the Tamar Estuary in Devon, UK in 1992 (1992 SWW Tamar Estuary and Sublittoral Sediment Survey). The data used were derived from Day grab samples collected at 17 locations along the main channel of the River Tamar into Plymouth Sound (Figure 2.1). Each sample was sieved (mesh size = 0.5 mm) and the number of individuals and the number of species were recorded together with sediment particle size analysis (fractions retained on sieve meshes of 8 mm, 4 mm, 2 mm, 1 mm, 500 μm, 250 μm, 125 μm, and 63 μm) (see Data CD).

The biotic data were then transformed to produce functional group datasets based on the bioturbation score proposed by Swift (1993) and trophic feeding guilds

(Fauchald and Jumars 1979, Barnes 1987), with species being assigned to one of five trophic categories: omnivores, surface deposit feeders, sub-surface deposit feeders, suspension feeders and generalists/carnivores.

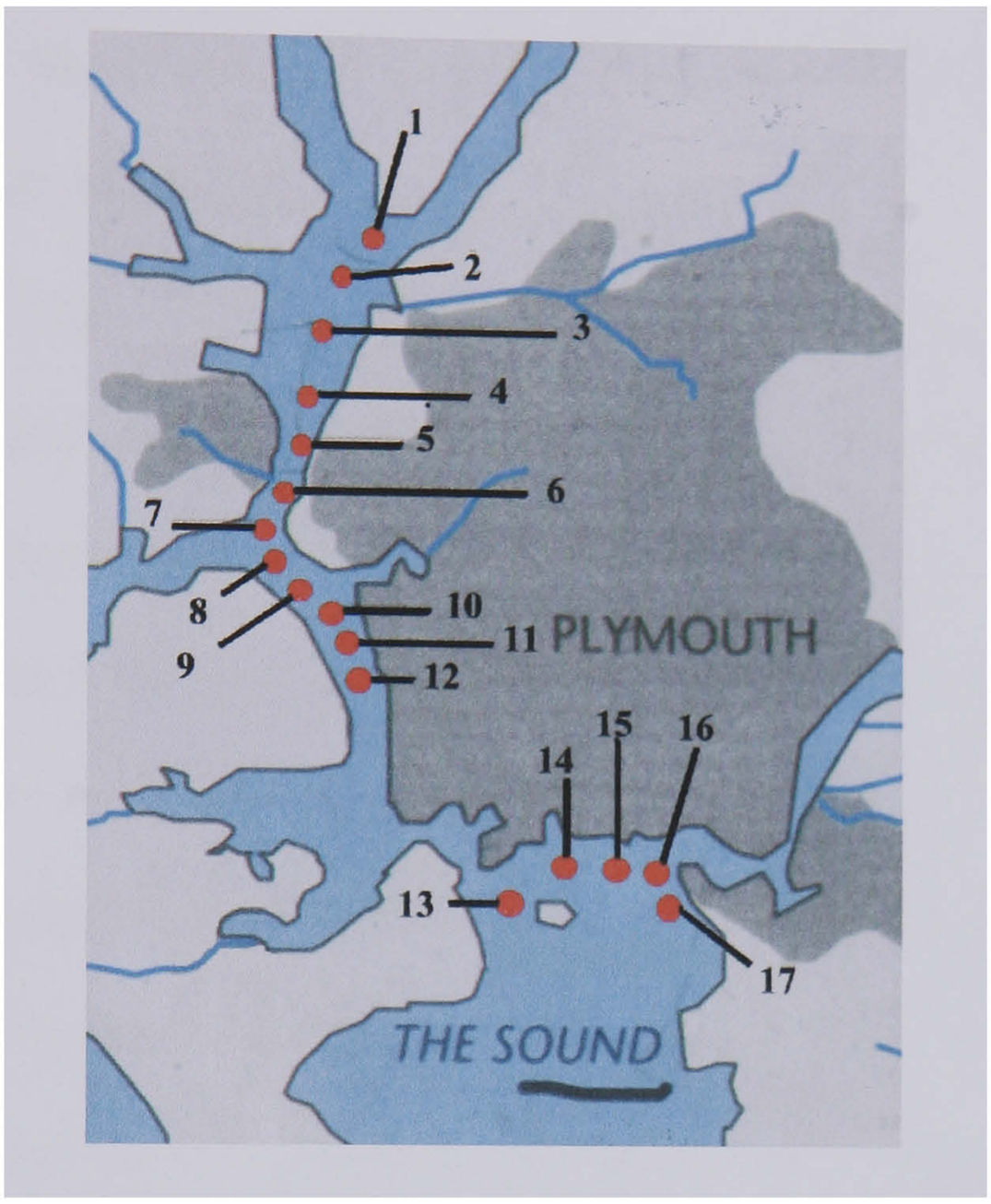


Figure 2.1. Location of sample sites for 1992 SWW Tamar Estuary and Sublittoral Sediment Survey

A literature search was undertaken to obtain sufficient information for each species to be allocated into the appropriate functional categories and for maximum adult body size (length) to be estimated (see Appendix 1). All of this information was then combined to produce six separate classifications of the biotic data to be used in analyses (see Data CD), these being:

- Abundance dataset: raw species abundance data.
- Bioturbation dataset: each species was allocated a score using the method of Swift (1993) and this score was multiplied by the number of individuals for each site.

- Trophic Group dataset: the total number of individuals in each trophic group.
- Weighted Abundance dataset: each species' abundance multiplied by body size for that species.
- Weighted Bioturbation dataset: each individual species' value in the Bioturbation dataset multiplied by its body size.
- Weighted Trophic Group dataset: each species' abundance multiplied by its body size and values summed into respective trophic groups.

All statistical procedures and analyses were performed using PRIMER-E 6 software (Plymouth Routines in Multivariate Ecological Research).

For each dataset non-metric multi-dimensional scaling (MDS) plots, based on Bray-Curtis similarity (Field et al 1982), were produced over which results of cluster analysis (hierarchical agglomerative method with group-average linkage) were overlaid. The latter cluster analysis were also based upon the same Bray-Curtis similarity matrices used for MDS plots and were merely included to aid visualisation of the ordination. Clusters were grouped using a cut off of 40%.

For sites that changed their association according to classification method, a SIMPER test was used to investigate which species were driving the dissimilarity between clusters. For each species, this test calculates its overall percentage contribution to the average dissimilarity between two groups, which enables species to be listed in order of importance (Clarke and Gorley 2001).

2.2.2 Physical Data

Sediment particle size analysis data were available for all sites and were used to calculate four parameters from the grain size frequency distributions: median grain size; sorting (second moment of frequency distribution); skewness (third moment

of frequency distribution) and kurtosis (fourth moment of frequency distribution) (Folk and Ward 1957).

Since no other physical data were available from the 1992 SWW survey, interpolation from other sources was necessary. Another set of survey data was obtained from the JNCC Marine Recorder database: the "1986 OPRU HRE Plymouth Harbour and Yealm Estuary Survey". This 1986 OPRU study contained categorical data, based upon methodology from the MNCR monitoring programme (Connor 1999), for salinity, wave exposure and tidal currents for many sites along the estuary. To check the validity of interpolation from the 1986 OPRU data, salinity profiles were also obtained from the UK Environment Agency (EA), for stations along the estuary. For each point the maximum salinity range was calculated from the EA data and compared to categorical interpolations based upon the OPRU dataset. These two datasets concurred for similar sites and hence were used to estimate categorical salinity values for the sites from the SWW Tamar survey. Data from the Tidal Stream Atlas for Plymouth Harbour and Approaches (1991) were used in a similar way, to validate interpolations based upon tidal current categories in the "OPRU" dataset. Wave exposure was based purely on interpolation of the OPRU dataset, whilst depth was estimated from Plymouth Harbour and Rivers Chart (Imray Chart C14) (Table 2.1).

The abiotic data was normalised, an MDS plot (based on the Euclidian distance similarity matrix) was produced and cluster analysis was again superimposed on the ordination to aid interpretation. A comparison of the underlying similarity matrices (used in the production of the MDS plots) was then undertaken to

Table 2.1. Environmental values used (Category and actual as appropriate) for each survey site. Categories: **salinity** 2=Reduced/low (0.5-30), 3=Variable (18-35); **exposure** 2=extremely sheltered, 3=very sheltered, 4=sheltered; **tidal stream** 2 is <1knot, 3 is 1-3knots; **median Φ** is the obtained from a plot of % mass retained by each sieve mesh size against sieve mesh size expressed in Φ units, where $\Phi = -\log_2$ (sieve mesh diameter in mm). Median Φ is read as the value of Φ corresponding to 50% the sediment mass being retained by sieves (as the grains become coarser so their phi value becomes smaller/negative); **sediment sorting** (the second moment of the grain size frequency distribution) 4=moderately sorted, 5=poorly sorted, 6= very poorly sorted; **sediment skewness** (third moment of the grain size frequency distribution) 1=very fine skewed, 3=symmetrical, 4=coarse skewed, 5=very coarse skewed; **sediment kurtosis** (fourth moment of the grain size frequency distribution) 1=very platykurtic, 2=platykurtic, 3=mesokurtic, 4=Leptokurtic, 5=Very leptokurtic; **depth** 1 is <5m, 2 is<10m, 3 is <15m and 4 is ≥15m.

SWW Site	Salinity	Exposure	Tidal Streams	Median Φ	Sediment Sorting	Sediment Skew	Sediment Kurtosis	Depth
1	2	2	3	2.14	5	4	3	1
2	2	2	3	3.13	5	5	4	1
3	2	2	3	3.37	4	5	4	1
4	2	2	3	3.42	5	4	4	1
5	2	2	3	3.82	4	4	4	1
6	2	2	3	-0.3	6	1	2	3
7	2	3	3	3.27	5	5	5	2
8	2	3	3	2.25	6	5	1	2
9	2	3	3	4.1	6	5	1	3
10	2	3	3	1.1	5	3	2	3
11	2	3	3	2.7	6	5	1	3
12	3	3	3	1.4	6	5	1	3
13	3	3	3	-2.13	5	1	4	4
14	3	3	3	0.36	5	3	4	4
15	3	4	3	0.31	5	3	4	4
16	3	4	2	3.4	4	5	5	4
17	3	4	2	2.8	6	5	4	4

determine which, if any, of the biological datasets provided the best match to the environmental data. The comparison was based upon Spearman rank correlation and performed using the RELATE routine in PRIMER 6 software (Clarke and

Gorley 2001). Subsequently, a BIOENV test (based again on Spearman rank correlation but between the biotic similarity matrix and matrices derived from each of the various possible combinations of abiotic variables (Clarke and Gorley 2001), was used to investigate which of the combined environmental variables contributed most to the match between abiotic and biotic datasets.

2.3 Results

Neither "Trophic Group" nor "Bioturbation" classifications produced exactly the same cluster patterns as using "Abundance" data (Figure 2.2) although patterns were similar.

Table 2.2 shows the SIMPER results, for clusters with more than one site, for the "Abundance" and "Bioturbation Potential" datasets, detailing those species with the greatest percentage contribution to overall within cluster similarity. For "Bioturbation", dissimilarity between Sites 6, 7, 9, 10, 11 and 12 (hereafter referred to as Cluster 2) and Site 8 was characterised by Site 8 having lower abundance of *Aphelochaeta marioni* and *Caulleriella* sp. (by more than a factor of 10) and greater abundance of *Corophium sextonae*.

SIMPER analysis applied to the "Trophic Group" clusters revealed a gradient of decreasing contribution of generalists and increasing influence of surface deposit feeders (SDFs) to cluster similarities across the plot, from upstream areas (right-hand side on the plot) to downstream sites. The results are summarised in Table 2.3.

The MDS plots for the weighted groupings are shown in Figure 2.3. These plots also show a strong effect by body size producing different cluster patterns to the original raw abundance. "Weighted Abundance" and "Weighted Bioturbation" produced almost identical MDS plots and only differed in cluster analysis, when

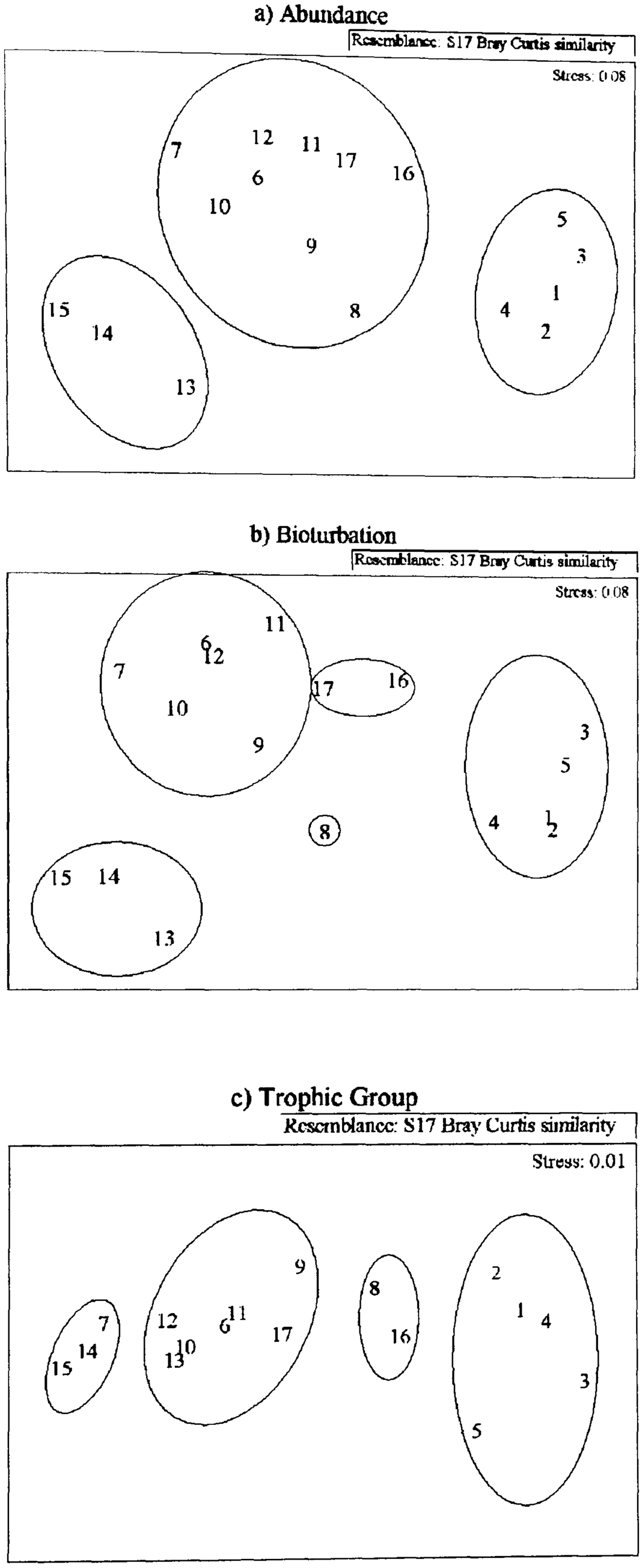


Figure 2.2. MDS plots, with significant clusters overlaid (cut off 45% similarity) for a) Abundance data, b) Bioturbation Potential, c) Trophic Groups.

Table 2.2 Percentage contribution to the within cluster similarity (four largest contributions shown in bold and underlined). Survey sites falling within each cluster are listed below corresponding "cluster number".

	Abundance Dataset			Bioturbation			
Cluster Number	1	2	3	1	2	4	5
Sites within cluster	1-5	6-12, 16-17	13-15	1-5	6,7,9-12	13-15	16,17
Species Name							
Nephtys hombergii	**63.38**	5.88		**70.6**			6.2
Streblospio shrubsolii	**15.15**			**11.23**			
Aphelochaeta marioni	**3.00**	**45.77**	1.01	**4.19**	**72.97**	1.75	
Melinna palmata		**7.98**			**2.27**		**17.78**
Corophium sextonae	2.51	3.79	**18.78**	**3.92**		**36.03**	
Caulleriella sp.	**3.03**	**14.44**	1.22	3.74	**12.44**	1.83	6.16
Tubificoides benedii		**10.97**	**8.05**		**3.62**	**9.37**	**26.2**
Apseudes latreillii			**26.52**			**18.71**	
Gammarella fucicola			**13.22**			6.1	
Nemertea indet.			4.34			4.88	
Myriochele heeri							**16.06**
Heteromastus filiformis		2.07				**7.48**	**14.72**

Table 2.3 Percentage contributions to within cluster similarity for trophic groups contributing more than 5% overall. The contribution represents the percentage of within group similarity that is due to each trophic group i.e. 87.26% of similarity in cluster 2 was due to the presence of SDFs. Although Generalists and SDF (Surface deposit feeders) contributed more to within cluster similarities than other trophic categories, the dominant group varied between clusters.

Cluster Number	1	2	3	4
Sites within cluster	1-5	6, 9-13,17	8,16	14,15,7
Trophic Groups				
Generalists	57.51	7.73	16.17	5.76
SDF	38.57	87.27	77.14	89.51

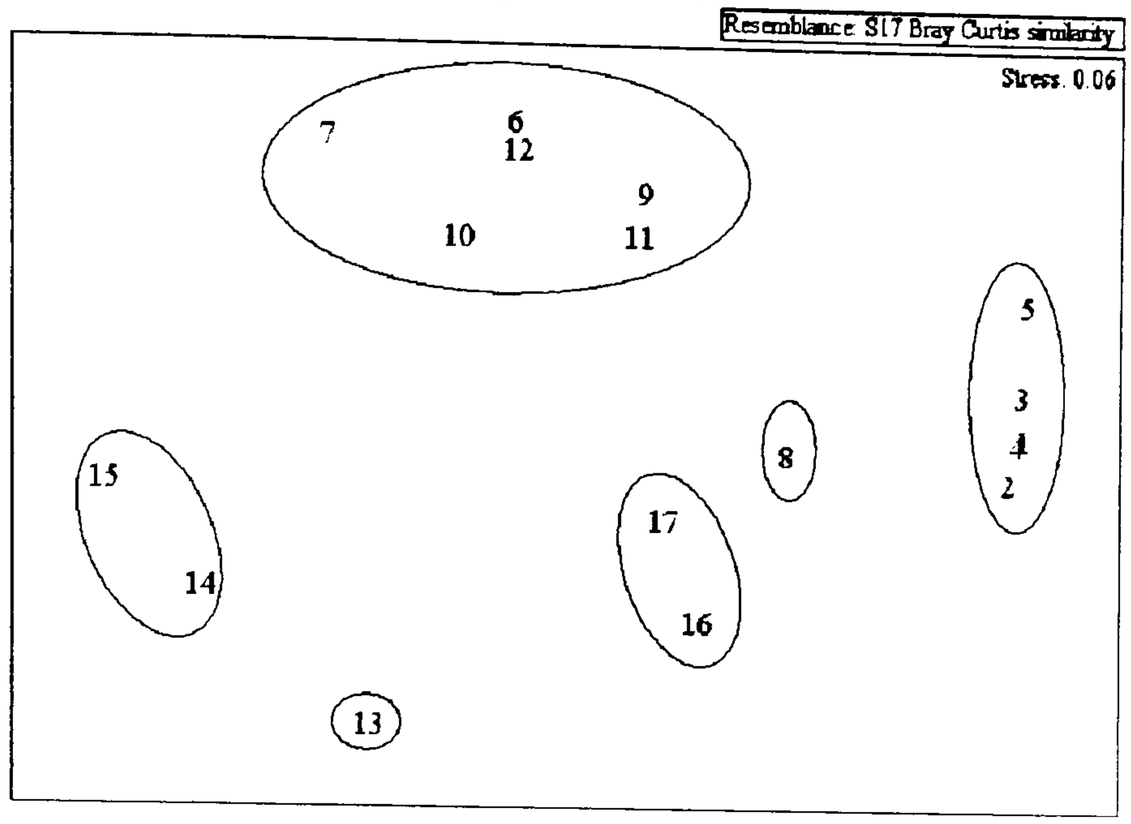
Site 13 and 15, respectively, separated out as individual clusters. A RELATE test revealed significant similarity between the two datasets (ρ = 0.966, p<0.05). In addition, the original "Bioturbation" MDS plot was significantly similar to both the "Weighted Abundance" (RELATE ρ = 0.901, p<0.05) and "Weighted Bioturbation" (RELATE ρ=0.908, p<0.05), but placed both Sites 13 and 15 in the same cluster together with Site 14.

SIMPER analysis revealed that Site 8 was differentiated from sites in Cluster 2 (6,7,9,10,11 and 12), for both "Weighted Abundance" and "Weighted Bioturbation", by a strong signal from *A.marioni* (70.8% dissimilarity for "Weighted Abundance", 77.89% for "Weighted Bioturbation") and, to a lesser extent, by *Nephtys hombergii* (4.03% dissimilarity for "Weighted Abundance", 3.38% for "Weighted Bioturbation") and *Tubificoides benedii* (9.05% for "Weighted Abundance", 6.41% for "Weighted Bioturbation"). Each of these species had a greater contribution to sites within Cluster 2 than to Site 8.

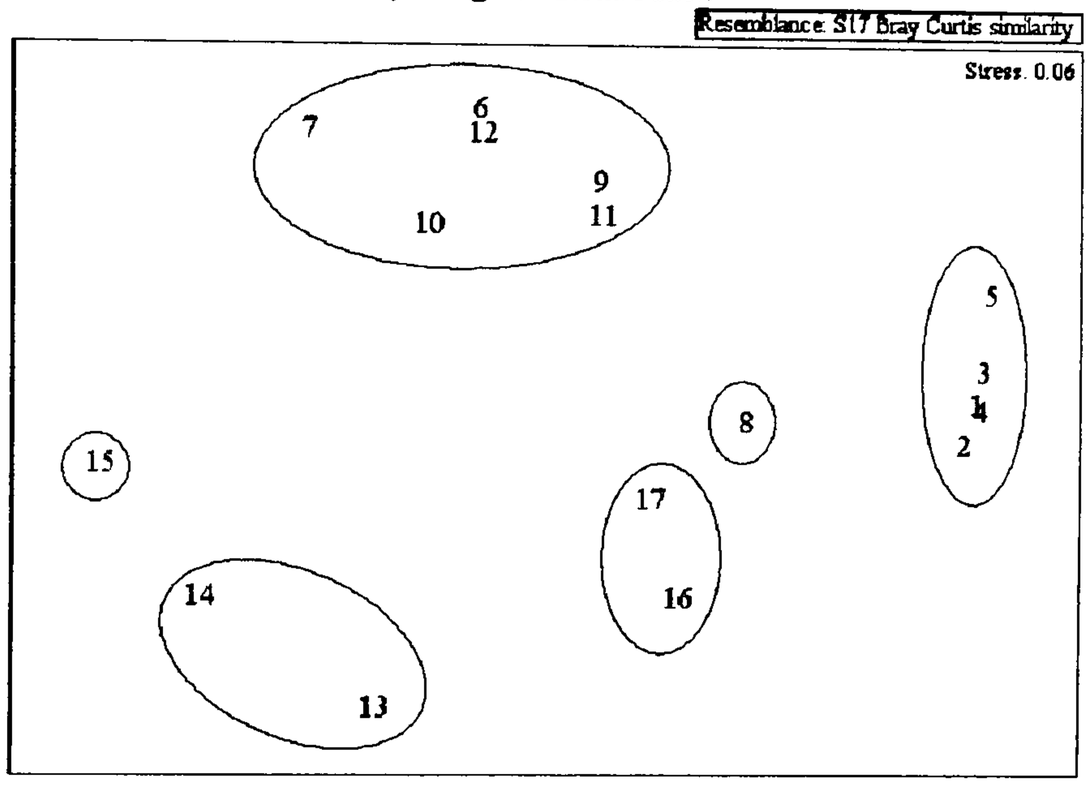
The same species also separated Site 8 from Sites 16 and 17 (Cluster 6) in the "Weighted Abundance" analysis with *A.marioni* providing a far greater contribution to Site 8, but *T.benedii* and *N.hombergii* being more important to similarities between Sites 16 and 17. For "Weighted Bioturbation", again *A.marioni* played a major role with *N.hombergii* but *Heteromastus filiformis* provided a similar strength contribution to *T.benedii.*

Site 13 was also isolated when the "Weighted Abundance" classification was employed. This separated from Sites 14 and 15 due to *T.benedii* (21.36% contribution), *H.filiformis* (16.03%) and *Nemertea* indet. (12.81%), all of which had greater contributions to similarities between Sites 14 and 15.

a) Weighted Abundance



b) Weighted Bioturbation



c) Weighted Trophic Groups

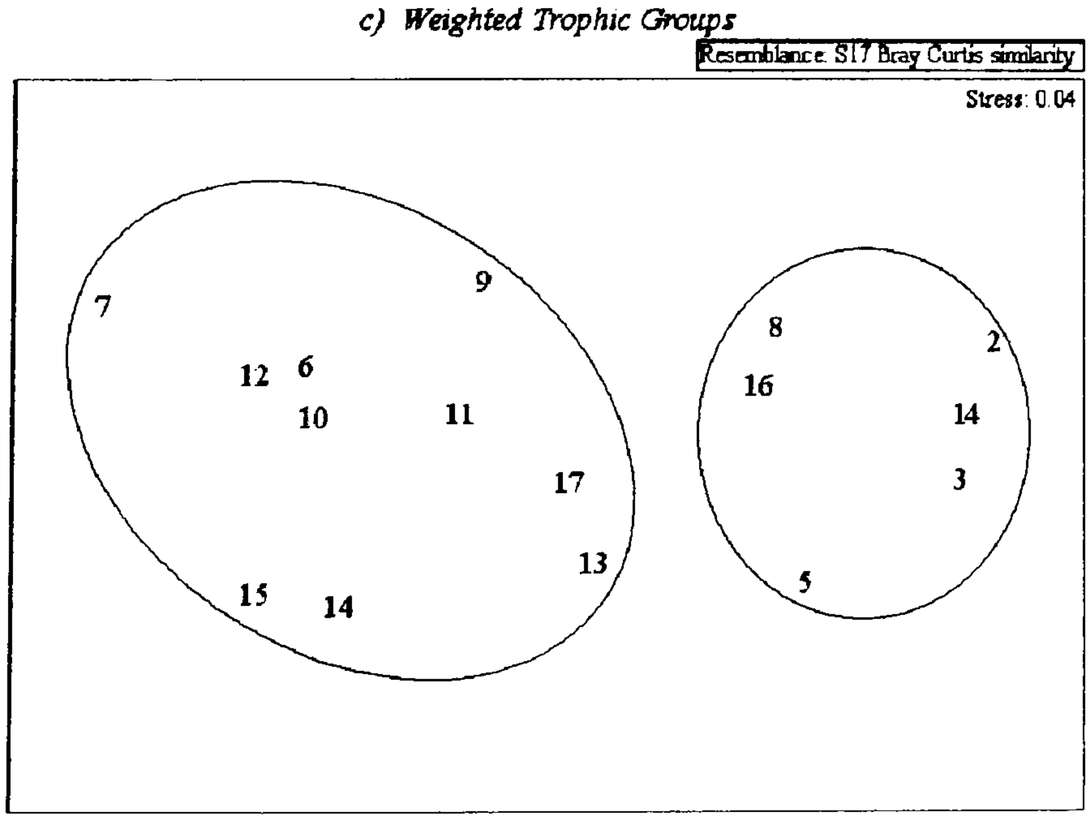


Figure 2.3. MDS plots with significant clusters (cut off at 45% similarity) overlaid for a) Weighted Abundance, b) Weighted Bioturbation, c) Weighted Trophic Group

This contrasts with "Weighted Bioturbation", where Sites 13 and 14 clustered together and Site 15 separated out. *H. filiformis* contributed most to the dissimilarity (25.48%) with much greater importance to Sites 13 and 14 than 15. *Capitella capitata* and *Platynereis dumerilii* also contributed over 16% each to the dissimilarity but with far greater contributions to Site 15.

Characterising species for clusters are summarised in Table 2.4 for clusters containing more than one site.

For the "Weighted Trophic Group" only two clusters emerged, the first characterised by generalists (83.51%) (sites 1-5, 8 and 16) and a low contribution from surface deposit feeders (11.52%). The second cluster had a much-reduced contribution from generalists (19.89%) to within cluster similarity, a small level of contribution from sub-surface deposit feeders (9.94%) and a dominance of surface deposit feeders (69.2%)

Table 2.4. Percentage contribution of major species driving within-cluster similarity. Four largest contributions are shown in bold and underlined (see Table 2.1 for full species names).

	Weighted Abundance				Weighted Bioturbation Potential			
Cluster names	1	2	5	6	1	2	4	6
Sites	1-5	6,7,9-	14-	16-17	1-5	6,7,9-	13-14	16-17
Species names								
N.hombergii	**93.0**	**1.45**		**18.22**	**93.26**	**5.36**		**19.18**
S.shrubsolii								
A.marioni		**81.22**				**85.62**	**5.28**	
C.sextone							**5.76**	
Caulleriella indet.								
T.benedii	**1.06**	**31.85**	**25.42**			3.23		**22.31**
A.latreillii		**14.44**						
G.fucicola		**8.75**						
Nemertea indet.		**22.3**					**8.19**	
M.heeri								**7.46**
H.filiformis			**11.81**				**60.0**	**22.8**
Anaitides mucosa			**12.14**					

2.3.1 Linking abiotic and biotic datasets

The MDS plot for the physical data is shown in Figure 2.4. The four clusters did not form the same site associations as any of the biotic classifications.

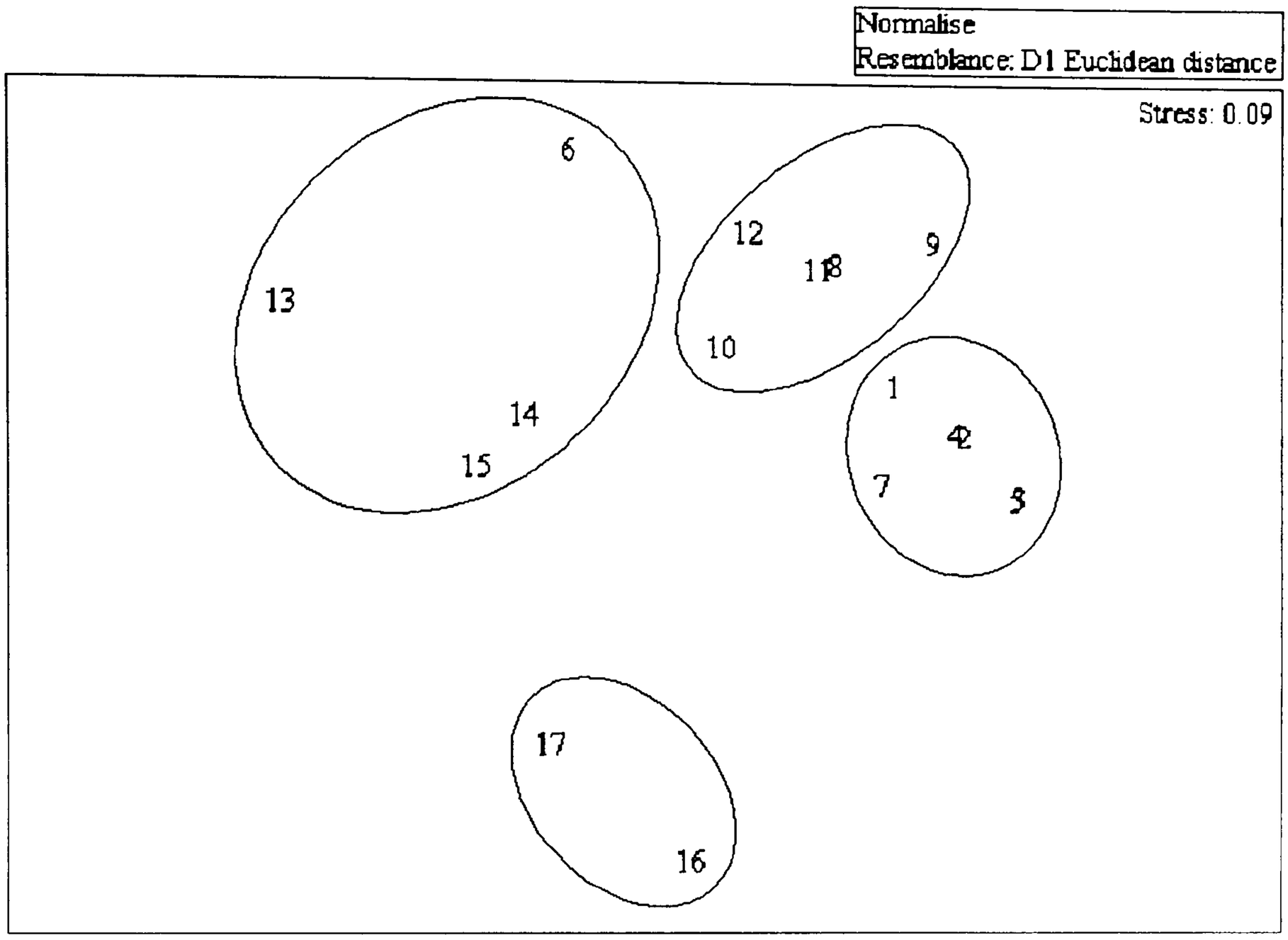


Figure 2.4. MDS plot of the environmental variables with significant clusters overlain

The results of RELATE tests (Table 2.5), revealed that the Spearman rank correlation (ρ) between abiotic variables (all combined) and biotic matrices was greatest when abundances were weighted according to body size. The use of trophic groupings resulted in decreased associations between the combined environmental variables and the biological ones.

Table 2.5. RELATE test results, giving the test statistic (Spearman rank correlation ρ) and probability (range 0-1) for comparisons between the abiotic and biotic variables from each site. A probability <0.05 indicates that similarity between the two matrices being compared is significant.

Biological Classification being compared to matrix based on all abiotic variables	RELATE Results	
	ρ	Probability
Abundance	0.37	< 0.05
Bioturbation Potential	0.369	< 0.05
Trophic Group	0.215	< 0.05
Weighted Abundance	0.386	< 0.05
Weighted Bioturbation Potential	0.371	< 0.05
Weighted Trophic Group	0.15	> 0.05

A BIOENV test, based upon Spearman rank correlation, revealed that, for all classifications of the biota, the match between abiotic and biotic variables was due to either depth alone, or to a combination of depth, median Φ and wave exposure. The correlations were greatest for abiotic data matched to Bioturbation Potential (ρ=0.649, p<0.05 n=17) using depth alone and slightly reduced for Abundance data (ρ=0.639, p<0.05 n=17) with other classifications showing correlations in the range ρ=0.543 (p<0.05 n=17) to ρ=0.593 (p<0.05 n=17).

2.4 Discussion

2.4.1 Influence of functional group classifications

MDS plots, using different schemes of classifying the biotic data, show that associations between sites vary according to the biological characteristic being considered. There was an overall consensus that sites 1 to 5 constituted a cluster,

but sites 8, 16 and 17 separated from the others on the basis of "Bioturbation", whereas the use of "Trophic Groups" produced visibly dissimilar plots.

The difference between the results of "Abundance" and "Bioturbation" classification methods was the association of sites 16 and 17, and the isolation of site 8 in the "Bioturbation" plot. Consideration of bioturbation potential scores has selectively magnified the contribution of certain species, and hence separated out the clusters. In this case, three infaunal surface deposit feeders, each with relatively high bioturbation potential scores (8 for *A.marioni*, 7 for *Caulleriella* and 9 for *C.sextonae)* have transformed an initial similarity on species abundance into a difference, due to bioturbation potential. These species are apparently doing similar things, but the overall potential for bioturbatory activity varies between clusters. Whether the perceived difference in bioturbation between these sites accurately mimics the true picture cannot be ascertained on the basis of these clusters alone.

The "Trophic Group" dataset shows a different pattern to both "Abundance" and "Bioturbation". There is a clear decrease in the contribution of generalists to cluster similarity from upstream areas on the River Tamar, to the higher salinity areas in Plymouth Sound, with a corresponding increase in the contribution of surface deposit feeders (see Table 2.3). Again, it is not possible to interpret the relevance of this gradient, without reference to the physical environment at those sites. Does the pattern truly reflect a change in overall function at each of these sites? The pattern was similar to that found by Bonsdorff and Pearson (1999) in the Baltic Sea, but they too were not able to conclusively and quantitatively link changes in trophic guilds to abiotic data.

Nevertheless, from this present work, it does seem that when attempting to interpret the biological significance of clusters, in relation to ecosystem status,

different functional groups may not be interchangeable. Each group provides different information about the area surveyed. The patterns in the distribution of trophic feeding groups throughout the estuary were not mirrored by the distribution patterns found when the biota were characterized by levels of bioturbatory activity. Each different pattern imparts information about the specific function being characterised but may not automatically provide a means to assess ecosystem status. This means that interpretation may be difficult for environmental managers who would prefer an indication of "health status" rather than function. Close attention needs to be paid to choosing the correct "functional group" with relevant links to the appropriate conditions of environmental health (Snelgrove and Butman 1994). The appropriate functional group will change according to the questions posed by environmental managers. For example, if environmental managers wish to be informed about levels of sediment disturbance, studying the distribution of trophic feeding groups may not be the best option. Equally investigating the levels of bioturbatory activity may not inform about energy flows through the estuarine system. Investigating more than one functional attribute may, however, have the potential to provide a greater understanding of combined ecosystem processes and merits further investigation.

2.4.2 Influence of body size as a method of weighting function contribution

This study hypothesised that weighting the contribution of individual species to functions according to their body size may affect the site association patterns. Indeed, weighting by body size did alter some of the site ordinations, but there appeared to be a general pattern emerging, with broad consensus between "Bioturbation", "Weighted Bioturbation" and "Weighted Abundance". The "Trophic

Group" pattern of clustering was more affected by the weighting and clusters were very different to those obtained by the other methods.

SIMPER analysis revealed that, for "Weighted Abundance", Site 8 was isolated due a change from an emphasis on abundance to an emphasis on size. Therefore, the relatively larger species now played a greater role in cluster differentiation. The same estuarine site was also isolated by the "Weighted Bioturbation" classification, but with slight changes in the species driving the dissimilarity between sites. An initial cluster of Sites 13, 14 and 15 arose using "Abundance" data. This changed when using data weighted for body size. Either Site 13 or 15 became isolated, according to either an emphasis on size or a combination of larger size and greater bioturbation potential of species. The size weighting was applied as a single factor (body length) for each species and its use does appear to have the potential to subtly alter some of the site associations.

Since actual values of bioturbation occurring at each site were not known, it was not possible to test the accuracy of these patterns in reflecting field-levels of bioturbation or indeed any other function. Thus, although there was a convergence in pattern on MDS plots for "Bioturbation", "Weighted Abundance" and "Weighted Bioturbation" there were subtle differences driven by the change of emphasis from abundance to a size and effect weighting. This is not evident from the MDS plots alone, which suggests that these changes are subtle and need a combination of methods for detection. The fact that subtle differences, in site-association patterns, can result from the application of the various weightings (according to body size or activity) also highlights the need for accurate values to be applied as such weightings. Environmental managers can only make inference about ecosystem status if the underlying data and conceptual models about individual site associations are reflecting real relationships.

2.4.3 Linking biological patterns to environmental variables

The question remains: "are observed patterns biologically relevant and can they be linked to the physical environment?" To help answer this question the biotic MDS plots were compared to the plots derived from the abiotic data alone. The latter produced four clusters. However, the resulting pattern was different from those produced using any of the six different ways of classifying the biota.

The RELATE tests (Table 2.5) revealed that the relationships between abiotic and biotic variables were greatest if the species abundances were weighted for body size. Excluding the trophic group methods, which produced very different plots, the differences between the biota and environmental variables appeared to be driven by the way in which sites 6, 7 and 8 clustered (see Figure 2.4). Unlike biological data, the abiotic variables did not isolate site 8, but rather placed it in a cluster with neighbouring estuarine sites, whilst Sites 6 and 7 were separated from each other. The abiotic data (Table 2.1) reveal little to distinguish between sites 6,7 and 8 with the differences that did exist driven mainly by the sediment characteristics of each site.

Thus, according to the physical attributes, the site ordination is not mirrored in any of the biological datasets, although an improvement in the match could be achieved by the application of weighting according to body size. This lack of agreement between the abiotic and biotic data could be due to either insufficient sensitivity in the abiotic information, leading to inability to differentiate sites, or a choice of functional grouping methods that are not truly influenced by the physical attributes selected, or both. Additionally, the choice of functional classifications may not have truly represented the species activities. Although several factors were included in the abiotic data used, the small number of sample sites has

greatly reduced variability for each parameter. For example, only two categories of salinity could be applied. In addition, only the granulometry was expressed as actual values. All other data were categorical. This will have masked some of the more subtle variations that may occur and indeed, the categories were often based upon interpolation from the nearest known data values, again introducing errors of estimation of unknown size.

Although weighting the biotic dataset by body size may improve the level of correlation with the environmental data, the RELATE results suggest that further improvements could be made. The "Trophic Group" and "Weighted Trophic Group" were less similar to the abiotic group than any of the other biological classifications employed. This may suggest that altering the "function" element of the weighting system can influence the strength of associations between the biological and abiotic data, and that links might be improved by refining the functional classification schemes.

The ability to place species into appropriate functional groups and apply a weighting also influences the usefulness of the resultant functional groups (Snelgrove and Butman 1994, Pearson 2001). For example, the method proposed by Swift (1993) requires several aspects of each species' motility, feeding and burrowing behaviours to be categorised. Consequently the "score" obtained under Swift's (1993) scheme is based on subjective categories rather than upon quantitative measures of activity. Often this information is not available, and must be extrapolated from similar species. This lack of information has started to be addressed by recent studies such as the work by Mermillod-Blondin et al (2003, 2005), in which activity rates of dominant species in assemblages are estimated. Also, new definitions of bioturbatory functional groups, e.g. gallery diffusers, erratic movers etc are being proposed (Gerino et al 2003 Francois et al 2004, Ouellette et

al 2004) which may be more useful that the schemes employed above. Recent advances in the use of micro computer tomography (microCT) also have the potential to measure the extent of species burrowing activities using undisturbed cores containing live animals (Mazik et al 2008). Such techniques will enable more accurate quantification of species' activity within the sediment.

Within the context of macrobenthic assemblages, linking bioturbation to abiotic variables holds more promise for developing predictive relationships, than does the use of trophic groupings. In this study, both weighted and unweighted trophic groupings were less related to the abiotic variables than were the other methods. This may partly be due to the nature of environmental parameters chosen. For example, no information was available for turbidity levels, suspended particulate matter or similar variables that might impact directly upon trophic function. This is supported by work of Hall (1994), who was unable to relate trophic groups to sediment turnover and Dauwe et al (1998) who found links between groupings, based on combinations of trophic and bioturbatory activities, and the quality of organic matter. This present study did indeed demonstrate changes in trophic functioning along the surveyed area. However, the inability to link this information to environmental factors limits its usefulness in the wider goal of predicting the distribution of biological activity within an estuary based on the abioitc factors investigated here. To assess the relevance of changes in function, managers need to link such changes to the expected "normal" range of "function amount" for a "healthy" location. Historically, for most estuarine locations, and indeed many ecosystems, only a limited suite of environmental variables are available upon which predictions can be based without needing to implement new sampling strategies. Further, physical data are more prevalent than are chemical surveys. This present study implies that correlations based upon the physical interplay

between species and the environment will be easier to detect than those based upon trophic interplay.

Although the differences between the results based upon simple species abundance and those based upon bioturbation or size were not large, weighting datasets for body size did subtly alter some of the cluster patterns. This has a number of important implications. Environmental managers seek methods that are based on grouping species without losing information (Snelgrove and Butman 1994). The very fact that changing the way in which the species are classified changed site associations suggests that functional groups can be used to provide more information about estuarine sites than the underlying species abundance alone. Instead of simply describing species distribution, functional groups may provide a means to assess how sites differ in their contribution to overall ecosystem functioning. Classification according to bioturbation potential and body size each produced similar patterns but with different driving species, which may inform about the relative importance of different species to different processes. The relative merits of either method were not clear, and require further investigation. It did appear, however, that body size had a more dominant effect than bioturbation potential, driving convergence of "Weighted Abundance" and "Weighted Bioturbation" datasets. This needs further investigation to determine whether the influence of body size should be scaled in some way. For example, instead of using mean body length, the surface area that a species presents to the sediment, as it goes about its activities, may be a more appropriate measure or, alternatively, species biovolume has been advocated in some studies relating benthic abundance to environmental stress (Basset et al 2004, Basset and Angelis 2007, Mazik et al 2008, Reizopoulou and Nicolaidou 2007).

This present study was limited to a very small area of one estuarine system. Its application to a broader range of estuary types, covering a wider range for each environmental variable, might improve some of the correlations and make patterns of associations clearer.

This study demonstrated that employing functional classifications of biotic data could alter our perception of site-to-site relationships. In addition, the findings showed that weighting those groups, according to the relative strength of component species, could alter the links between the physical environment and biota, and help to interpret changes in patterns of site associations.

Functional bioturbation score proved as useful as simple species abundance and weighting by body size. The benefits of one functional classification over the other are difficult to disentangle. There was no apparent loss of information when using these classifications but rather, by comparing both approaches, there was an improvement in our ability to interpret how changes in the biology reflect physical changes in the site. If such links can consistently be made, then functional groups may provide a way to improve our ability to link biotic and abiotic variables in a consistent and predictive way. If site differentiation patterns can be linked to measurable, broad scale, physical parameters, then these patterns can form the basis for future predictions of "expected function level", based upon knowledge of the physical environment alone.

The poor relationships found between abiotic and biotic datasets when employing trophic groupings suggests that efforts should be focused first upon linking bioturbatory activity to environmental driving forces. Studies wishing to predict the distribution of trophic functioning might be more productive if they investigate a different suite of environmental variables to those utilised in this study, or expand

the trophic groups to include sub-categories that might improve levels of discrimination between sites.

Although species abundance produced similar patterns in site association to those classifications based upon body size or bioturbation levels, for reasons outlined in the introduction to this Chapter, it would be preferable to search for links between the environment and functional characteristics of the biocoenosis, in order to produce generic models of function that can be transferred easily to other estuaries. The limited differences between results from simple species abundance and classifications based upon bioturbation scores suggest that future work is needed to replace Swift's scoring system with more relevant bioturbatory categories, such as those proposed by Francois et al (2002) and Mermillod-Blondin et al (2003), which are based on measured activity levels or from information derived from scanning intact cores (Mazik et al 2008). Attention also needs to be given to determining which measures of body size are most appropriate and for which species. By combining these foci quantitative values of bioturbatory contribution can be determined. These can be used to investigate links to the physical and chemical environment with greater confidence in the ecological significance of the resultant patterns.

CHAPTER 3

Differential responses of the estuarine macrobenthos to environmental factors: the role of vertical stratification within the sediment.

"It all depends on how we look at things"

Carl Justav Jung (1875-1961)

3.1 Introduction

The findings of Chapter 2 suggested that new definitions be sought for macrobenthic functional groups. Before assigning species into new categories this chapter examines whether vertical stratification of the macrofauna within the sediment influences the biotic interactions with environmental factors and hence, plays a role in determining the distribution of macrofauna within an estuary.

In estuarine regions, urban and commercial expansion, land reclamation and canalisation all contribute to an ever-increasing pressure on finite resources. Within the European Union, concerns about the ability of our waterways to cope with the demands of human activity have driven the integration of related international and national legislation into the Water Framework Directive (WFD)(Directive 2000/60/EU). The WFD requires "good water status" be achieved for all waters by 2015. To meet this target, signatory states must classify the condition of their estuarine systems in terms of their biotic and abiotic elements. The WFD requires managers to compare the actual composition and abundance of benthic invertebrate fauna with that expected to occur at a given site, under a particular suite of environmental conditions, according to either baseline community data from a pristine site, historical datasets, biological indicators or model output.

Many environmental factors have been identified as influencing estuarine macrobenthic community structure. These factors include salinity (Remane 1934, Perkins 1974), tidal stress (Warwick et al 1991) and sediment characteristics such as grain size and erodibility (Ysebaert and Herman 2002, Snelgrove and Butman 1994, Thrush et al 2003). Whilst such studies have advanced our conceptual understanding of the interplay between the biotic and abiotic factors that may

structure estuarine soft sediment communities, the incorporation of such findings into predictive models of community distributions has proved more elusive although Elliott and O'Reilly (1991) did have some success modelling biomass as a descriptor of community structure.

An alternative approach to examining benthic community structure is to model individual species distributions in response to abiotic factors (e.g. Attrill 2002, Ysebaert et al 2002, Thrush et al 2005 and Ellis et al 2006). These models, while successful at predicting local species distribution patterns within the studied area, have yet to provide generic predictions that can be easily transferred between estuaries. Locally effective models are usually underpinned by extensive sampling of the biological and physico-chemical variables within a single estuary. Separate models are then developed for every species under consideration. These are costly in time and effort, and cannot meet the needs of estuarine managers with finite resources. Models predicting the distribution of individual species may be useful to managers if key species might be linked to estuarine status. However, no such key species links have yet been identified.

Both the community and species-by-species approaches to modelling macrobenthic distribution compare biological and environmental patterns. Environmental variables are usually measured either above the sediment surface, such as water chemistry and tidal current flows, or within the top few millimetres of the sediment surface, such as grain size composition and levels of organic matter. Species abundance is estimated from counts of individuals, and is usually weighted according to the sediment surface area covered by the sampling device (Kramer et al 1994). Thus, most models of estuarine macrobenthos distribution treat the benthos as if they live in the two-dimensional world of the sediment

surface where they interact with processes occurring both within that sediment surface and at the sediment-water interface.

The sediment-water interface plays an important role in biophysical and chemical processes within the estuary (Peterson 1977). Certainly, individuals dwelling in the substratum do generally have some requirement to sustain contact with the sediment surface for feeding or respiration. To do so, they maintain permanent burrows or tubes, create temporary burrows or extend feeding or respiratory organs. Thus, it may be that all macrobenthic species compete for access to the sediment-water interface and therefore that space at the sediment surface is the most influential limiting resource for benthic fauna (Peterson 1977, Whitlach 1980, Josefson 1989). Nevertheless, many species exploit the vertical structure of the substratum to varying degrees (Nybakken 1995, Peterson 1977). In any assemblage it would be unusual for all individuals to require simultaneous access to the surface, and thus the intensity of competition for the limited surface space will vary temporally and as a function of physical form and activity.

Measurements of the physico-chemical environment of the sediment-water interface may not accurately characterise abiotic conditions deeper within the substratum. Several factors such as salinity (Bonsdorff and Pearson 1999), redox potential (Rhoads 1974, Watson et al 1985), organic carbon (Christie et al 2000), temperature (Perkins 1974), sediment characteristics (Rowden et al 1998) and water content (Christie et al 2000) are known to vary with sediment depth. Consequently, the values measured in the substratum surface for any one variable may not reflect the values experienced by deeper-living individuals that spend only a proportion of their time in the surface environment.

In addition to spending much of their time in a different physico-chemical environment to surface-living species, deeper dwellers are also substantially less

influenced by surface disturbance, erosion or deposition. Disturbances such as fish feeding activity (Thistle 1981) and tidal resuspension (Grant 1981. Paterson and Black 1999) often only disturb the upper few centimetres of the sediment. Given that ties to the surface conditions are less strong in deeper dwelling individuals than those of species obliged to live in the upper layers throughout their life, it would be reasonable to assume that the distribution of deeper living animals will be less well predicted by surface physico-chemical variables.

To date, no studies have investigated whether relationships between the macrobenthos and abiotic factors are dependent upon the depth at which the biota is found within the sediment. Whilst Guidetti et al (2000) observed that the depth at which an assemblage occurred was a more significant factor in determining community structure than pollution, they did not investigate the forces driving the vertical stratification of the assemblage. Despite several studies reporting vertical stratification of the macrofauna, with greater abundances in surface layers (Shirayama and Horikoshi 1982, Hines and Comtois1985, Grehan et al 1994, Flach and Heip 1996), little attempt has been made to answer the following questions:

- Is there a clear distinction between the assemblages living at the surface and those at greater depth?
- If a distinction between the assemblages living at the surface and those at greater depth exists, is it a universal pattern and if so which environmental variables can be used to account for the dichotomy?

In the absence of clear answers to these questions, it is hardly surprising that no attempt has been made to include information on depth related assemblages for the classification of estuarine sites.

Irrespective of whether distinctly different depth-related assemblages can be identified, the ability of some species to exploit deeper horizons has implications for all studies of estuarine macrobenthos. The vertical distribution of species will influence the ability to sample the community effectively (Spies and Davis 1979, Hines and Comtois 1985). Most studies reporting vertical stratification of the macrofauna found the majority of individuals in the top 10 cm of the sediment (Holme 1964, Hines and Comtois 1985, Josefson 1989, Guidetti et al 2000), and authors frequently quoted this finding as evidence that the majority of the community was adequately characterised by relatively shallow sampling efforts. The maximum depth of biological exploitation of soft sediments, however, can be far greater then 10 cm (Peterson 1977, Hines and Comtois 1985) albeit by far fewer individuals than occupy shallower layers. The depth range occupied by a species will determine its ability to interact with other species and its role in ecosystem processes. For example, several studies have shown that individuals living deeper in the sediment influence bioturbation and chemical fluxes within the sediment (Levin et al 1999, Gutierrez et al 2000, Mermillod-Blondin et al 2005). If these animals are not sufficiently well sampled then important elements of the biota and hence any classification of pattern or function may be overlooked.

In this Chapter, new data from studies in the Tamar and Plym estuaries, south-west England, is combined with previously unexamined data from the Schelde estuary in the Netherlands to explore:

- Whether all estuarine macrobenthic assemblages may be partitioned into a shallow assemblage and a deeper one;
- Whether, in the event that distinctions can be made between shallow and deep assemblages, deeper assemblages with greater time-averaged representation of estuarine status may have similar or weaker relationships

with abiotic variables measured at or above the sediment surface than do shallow assemblages. Deeper species tend to be longer-lived and hence have experienced local conditions over a longer temporal span than more ephemeral species. Due to their deep-living habits they may be hypothesised to obtain some degree of protection from fluctuations in abiotic factors acting at the sediment surface;

- Whether vertical stratification might be of value in classifying estuarine sites according to the characteristics of the resident macrobenthic communities.

The hypotheses tested are:

- *There is no difference in the structure of assemblages from different sites*
- *There is no difference in the structure of assemblages from different sediment depth horizons*
- *There is no difference in the nature of the abiotic factors shown to have relationships with the biota according to the depth range at which the benthic assemblage is found in the sediment.*

3.2 Methods

Data were collected from the Tamar and Plym estuaries, hereafter referred to as the Tamar/Plym, for comparison with previously unexamined data from an earlier study on the macrofauna of the Molenplaat, in the Westerscheide estuary, obtained as described in detail by Herman et al (2000), Herman et al (2001) and Widdows et al (2004), and as briefly summarised below. Abiotic data were not available for all sites and sampling occasions from the study of Westerschelde estuary and hence only biological data were included in any analysis concerning the Westerschelde.

3.2.1. Sample Collection in the Schelde Estuary

In the Schelde estuary, five sites were sampled from within a single 1.5 km^2 sandflat, the Molenplaat (51°26N, 3°57E), during June 1996 and two of those sites were revisited in March 1997. For each site, the macrobenthos were sampled using ten replicate cores, of internal diameter 11 cm inserted to depths of 30 cm in the sediment. The samples were sliced according to one of two sampling schemes, with distances measured from the core surface:

- Scheme 1. In June 1996: 0-2 cm, 2-4 cm, 4-9 cm, 9-14 cm, 14-19 cm, 19-24 cm and >24 cm
- Scheme 2. In March 1997: 0-2 cm, 2-4 cm, 4-6 cm, 6-8 cm, 8-10 cm, 10-15 cm, 15-20 cm, 20-25 cm and >25 cm

Slices were wet-sieved in the field over a 1 mm mesh and the animals transferred to 8% buffered formaldehyde for fixation. Species were subsequently identified to the highest possible taxonomic separation, being species where possible, and the abundance reported as numbers per m^2.

3.2.2. Sample collection within the Tamar/Plym system

Seven sites (see Figure 3.1) were sampled along the Tamar Estuary and a further two along the Plym Estuary during spring 2005 (see below for sampling regime). All sampling occurred on spring tides, at low water and took place at the same time and at the same sites as an independent axial study of sediment erosion along the Tamar estuary (Bale et al 2006). The latter study employed an *in-situ* flume, positioned as close as practical to the main river channel and all samples, biotic and abiotic, for the present study were taken within 2.5 m up-shore or down-shore of that flume (Figure 3.2).

Figure 3.1. Sample locations along the River Tamar (HQ to SJ) and the Plym Estuary (RD and SM). Reproduced from Ordnance Survey data by permission of the Ordnance Survey © Crown copyright 2001. HQ is Halton Quay, TP is Thorn Point, SH is Saltash, EN is Ernesettle, BP is Bull Point, LG is Looking Glass Point, SJ is St. John's, SM is Saltram and RD is The Ride.

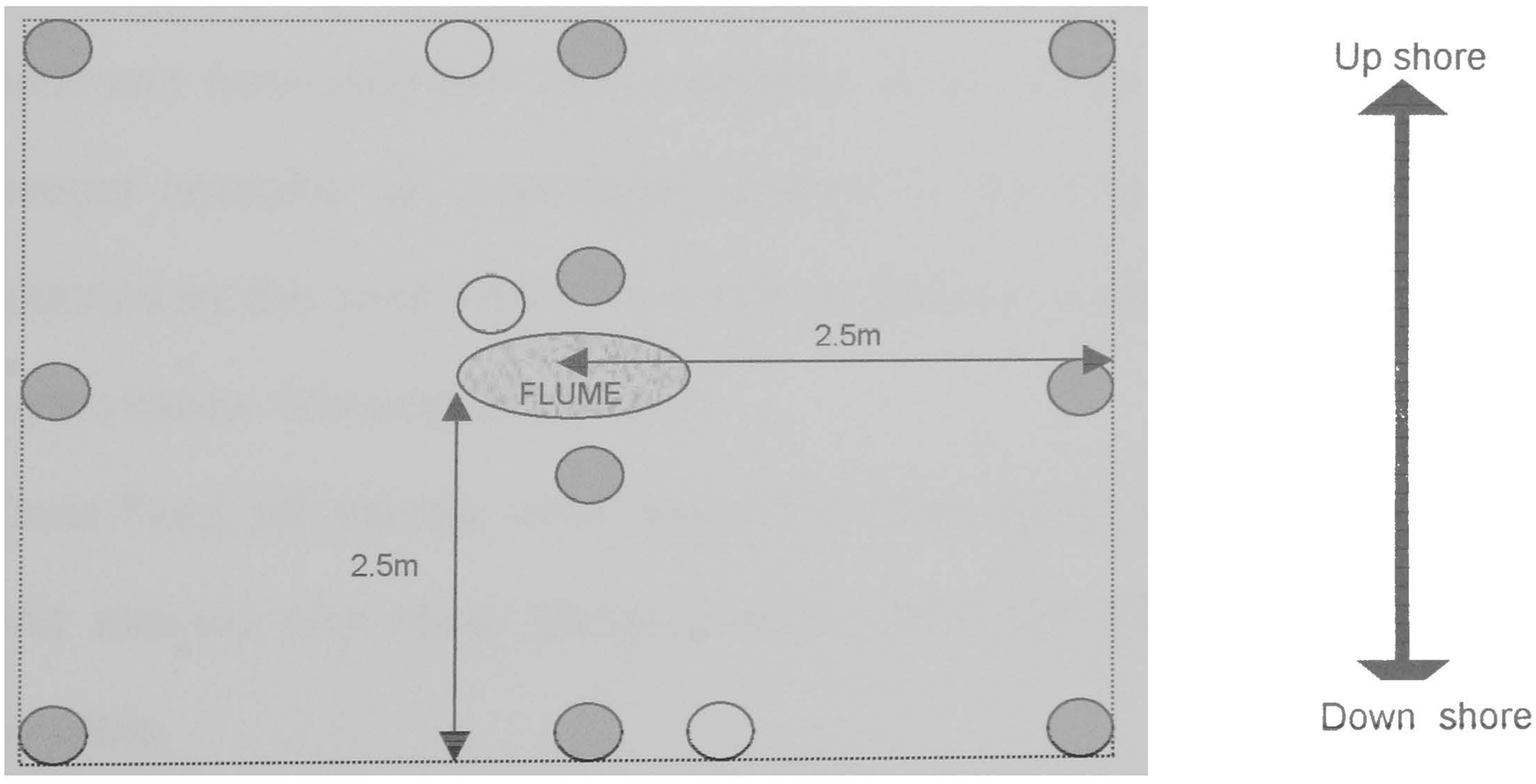


Figure 3.2. Arrangement of biological samples (filled circles) on the Tamar/Plym system. Samples were placed in a grid with three samples 2.5m up-shore of the flume. three placed 2.5m down-shore, two as close as practical to the flume and two at the same tidal height as the flume. Abiotic samples (white circles) were taken alongside the flume, at 2.5m above and at 2.5m below the flume.

3.2.2.1. Biological samples.

At each site, macrofauna were sampled using ten replicate 15cm diameter cores inserted to a depth of 30cm. Each core was sectioned into the layers according to Scheme 2 applied during March 1997 in the Schelde. 10 cores were retrieved to ensure that deeper-living organisms were adequately sampled to enable characterisation of the site rather than to be treated as replicate samples.

Prior to fixation in 10% formaldehyde, sub-samples of 7cm diameter were taken from the top two layers between 0 and 4cm from the sediment surface in each of the ten original cores at every site. The small sub-samples were sieved over a 0.5mm mesh to sample smaller-bodied animals. Sub-sampling in this way greatly reduced processing time and so effectively increased the number of sites that could be studied. The remainder of the sediment from each sub-sampled slice was sieved over a 1mm mesh to give the best practical representation of larger animals. Considerations of sampling efficiency, based on a preliminary survey also indicated that the most practical approach was to employ a 0.5mm mesh for sediment from sediment layers between 4 and 10cm and a 1mm mesh for the deeper horizons: all individuals retained by the 0.5mm mesh sieve were also retained by the 1mm mesh in preliminary studies that employed nested sieves for layers below 10cm sediment depth.

Once fixed, all animals were washed in fresh water, transferred to 70% alcohol and stained with Rose Bengal before being identified to the species where possible.

Given the differences in the volume of mud passed through the different sieve meshes used for the upper layers, all data were standardised to the number of individuals m^{-2}. While this approach had some disadvantages, particularly in considerations of diversity, it was the most practical means of bringing together

data from the two sieve meshes and core sizes. For the upper two layers where species were sampled in both the 1 mm and 0.5 mm sieves, abundances were based upon the 0.5 mm sieve. For some analyses data were transformed from number of individuals m^{-2} to presence/absence.

3.2.2.2. Environmental variables.

The abiotic variables investigated in the present study were selected because strong relationships had previously been shown with biological community structure (Rhoads 1974, Warwick and Uncles 1980, Warwick et al 1991, Hall 1994, Ysebaert et al 2002, Anderson et al 2004, Ellis et al 2006). To characterise the site, three additional cores were collected from each site as shown in Figure 3.2. The cores were not paired with any particular biota core since the aim was to characterise the sample area as a whole. The mean depth of the redox potential discontinuity (RPD) was noted in each core and the top layer (0-2cm) was divided to provide:

- one aliquot for chlorophyll *a* and colloidal carbohydrates (extracellular polymeric substances, hereafter referred to as EPS) analysis. This was stored in a dark, cool box and transferred to a –80°C freezer upon return to the laboratory; and
- one aliquot for water content, interstitial salinity, total organic carbon analysis and particle size analysis: all stored in plastic bags in the dark.

3.2.2.2.1 Sediment erosion measures.

The relative degree of cohesion and compaction of the sediment was assessed using a Pilcon 19mm shear vane to measure the undrained sediment shear strength alongside every undisturbed core (abiotic and biotic) prior to retrieval.

At each sampling site on the Tamar, measures of sediment erodibility were obtained independently as described by Bale et al (2006) using a portable annular flume within a few metres of LWS (Low Water Springs). The same methodology was employed to obtain sediment erosion measures for the Plym, using graphical plots of bed shear stress against the concentration of suspended matter, to estimate critical erosion thresholds (CET) and maximum erosion rates of the sediment surface. A temporary failure of the flume, however, at a few Tamar sites dictated that CET be derived from a strong relationship with bulk density as established for surface sediments there (Bale et al 2006). For consistency, all estimates of CET were derived from the above-mentioned relationship.

3.2.2.2.2 Sediment properties. The physical and chemical parameters of the top 2cm of sediment for each site were analysed using the following techniques: Algal pigments were extracted using 90% acetone and analysed using spectrophotometry (Welschmeyer 1994). The phenol-sulphuric method (Underwood et al 1995) was used to estimate carbohydrate concentration (EPS) following extraction from wet sediment using the method of Underwood et al (1995). A small amount of sediment was centrifuged at 4000 rpm to extract interstitial water, the salinity of which was determined using a hand held refractometer (Kyoto). Wet sediment water content was determined by measuring weight loss upon drying sediment to constant weight at 65°C. Subsequently, the Total Organic Carbon content (%TOC) of dried sediment was determined using a PRIMACS SLC Carbon Analyser, employing in-situ acidification with hydrochloric acid to remove inorganic carbon. Sediment particle size distribution was determined by combining the results of sieving dried sediment (to remove particles

larger than 2mm in diameter) and then passing the remainder through a Beckman Coulter Instruments LS230 laser counter.

3.2.2.2.3 Current Flow data.

No data were available for measured water current flows above the sediment at any of the sites. Modelled tidal current flow rates at heights of 10cm above the sediment bed were obtained from BELLPLUME, a hydrodynamic model of the Tamar and Plym estuaries developed by Astra Zenca, Brixham (Robinson and Riddle 2004). For each site, the model predicted tidal current velocities at twelve-minute intervals over the largest spring-neap tidal cycle. From this modelled dataset, the maximum predicted flow rate at each site was extracted.

Although the BELLPLUME model had previously been validated for surface current predictions at several sites along the Tamar Estuary, the lack of measured near-bed flow data and the relatively coarse resolution (50m for some sites) of the model predictions meant that the ability of the model to replicate conditions experienced by the biota sampled in the present study was uncertain. However, statistical analyses employed in the present study compared the relative strengths of current flow at each site; the relative similarity of sites according to current flows was the same whether based upon surface or near-bed predicted flows. It was therefore considered that any errors in the model predictions would have minimal effect on inter-site similarities used in the analyses employed in this present study. given that they were based upon the relative strengths of predicted tidal current flows.

3.2.2.2.4 Likelihood of tidal resuspension.

The parameters measured as proxies for sediment erodibility. as described above.

reflect the forces needed to re-suspend the sediment surface (CET). including sediment cohesion and compaction (shear stress). The spatial and temporal extents to which any estuarine intertidal site will experience resuspension and erosion, however, will also be influenced by the strength and duration of current flows across the sediment surface (Hall 1994). To assess the likelihood of tidal re-suspension at every site sampled within the present study. the amount of time was calculated during which the critical erosion threshold (CET) was exceeded by flow rates predicted just above the sediment bed.

3.2.3 Statistical analyses.

All statistical tests were performed using PRIMER-E (Plymouth Routines In Multivariate Ecological Research) (Clarke and Warwick 2001). Biological patterns were assessed by comparing rank similarities in the biological datasets based upon the Bray Curtis coefficient with datasets adjusted in accordance with Clarke et al (2006). These adjustments, which in effect add a "dummy species" to each sample, improve the stability of the Bray-Curtis coefficient in places where species abundance is sparse, as is often the case with samples from deeper layers of cores. The "dummy species" is added to every sample site and is given an abundance equivalent to the lowest (not zero) abundance actually recorded for any species in the study. This forces all sites to have at least one species in common and hence "dissimilarity" measured by the Cray Curtis coefficient becomes zero rather than undefined. Where samples have no/few species for the same reason e.g. due to a common stressor, then having a dissimilarity of zero rather than being undefined allows meaningful MDS plots to be generated. The effect of employing such a correction is more clearly explained with examples in Clarke et al (2006).

Analyses of similarity between untransformed biological datasets can be heavily influenced by the patterns of occurrence shown by a few numerically dominant species (Clarke and Warwick 2001). Many studies have shown that the majority of species and individuals are found within the upper 10cm of sediment (Hines and Comtois 1985, Josefson 1989, Guidetti et al 2000). Consequently, to assess whether any patterns observed within the biological data were driven principally by the distribution of a few species with high abundance, all analyses were also applied to transformed datasets where only presence or absence of a species was considered.

Significances of site and sediment depths as interacting factors in structuring biotic assemblages were tested using a 2-way Analysis of Similarity (ANOSIM with no replicates) on the Schelde dataset. Subsequently, a one-way ANOSIM was used to test pair-wise relationships between depth horizons within the Schelde datasets to identify potential ways to split the community into significantly different depth-related assemblages. Patterns of site associations were displayed using non-metric multi-dimensional scaling (NMDS) plots.

Using the findings from the analyses of the Schelde data, the Tamar/Plym data was split to generate new datasets, one for each of the possible groupings of significantly different depth-related assemblages as indicated by the Schelde analyses i.e. grouping data into depth layers e.g. one dataset could be 0-10cm and 10+cm assemblages. For each newly-generated dataset a one-way ANSOIM test was employed to assess significant differences between the depth-related groups. Again, NMDS plots were used to display patterns of site associations.

In addition, for each Tamar/Plym site, gradients of change in community structure with depth were analysed using RELATE seriation tests. Where a gradient of change exists within a dataset, samples might be expected to be arranged in a

linear pattern along the gradient. RELATE seriation compared the Spearman Rank Similarity between each assemblage from sampled depth horizons across a single site to patterns produced by a theoretical matrix in which each sample (depth layer) has been forced to lie along a linear gradient (Clarke and Warwick 2001).

For groupings of depth layers that produced significantly different depth-related assemblages, a SIMPER test (Clarke and Gorley 2001) was applied to identify species that contributed most to the within-depth group similarity and between-depth group dissimilarity.

To allow a visual comparison of patterns in the Schelde and Tamar/Plym data an NMDS plot was produced including all sites and depth layers across both estuary systems.

3.2.3.1 Environmental variables.

Draughtsman's plots were used to examine co-linearity between abiotic variables. Where such variables were highly correlated ($r>0.90$, $p<0.05$), only one variable was included in further analyses. Dissimilarity between estuary sites was calculated using Euclidean distance metric on normalised abiotic data to produce a correlation matrix. The latter was then employed in BIOENV tests (Clarke and Warwick 2001) that were applied to the Tamar/Plym presence/absence and species abundance data to examine relationships between the biotic variables and environmental measures. A BIOENV test seeks the combination of abiotic drivers having the best combined correlation with the community assemblages.

To aid visualisation of the relationships between the various depth groupings and the abiotic data, a 2nd Stage MDS plot was produced (Clarke and Warwick 2001). This latter plot was derived by calculating the similarity between each of the

individual depth grouping similarity matrices to produce a new, second-stage similarity matrix.

3.3 Results

3.3.1 The Schelde Estuary.

For the Schelde Estuary, biological data for the five sites representing different environmental conditions across an intertidal flat, are summarised in Table 3.1, whilst Figure 3.3 displays the relative abundances of individual species with sediment depth at each site.

Table 3.1. Summary of biological data for the Schelde. The number of species recorded and the estimated number of individuals per m^2 at each site are given for the whole depth of sediment sample, for depths below 9cm in the sediment for June 1996 and for depths below 8cm and 10cm in the sediment for March 1997. Only sites 2 and 4 were re-visited in March 1997

Site Code	1 (Jun 96)	2 (Mar 97)	2 (Jun 96)	3 (Jun 96)	4 (Mar 97)	4 (Jun 96)	5 (Jun 96)
WHOLE DEPTH							
Species m^{-2}	25	20	20	21	20	19	8
Individuals m^{-2}	23652	19086	55859	33617	10677	9604	9153
BELOW 8cm							
Species m^{-2}	-	8	-	-	11	-	-
Individuals m^{-2}	-	2261	-	-	2583	-	-
BELOW 9cm / 10cm							
Species m^{-2}	17	8	11	11	9	8	3
Individuals m^{-2}	2335	1499	1775	1008	1521	662	305

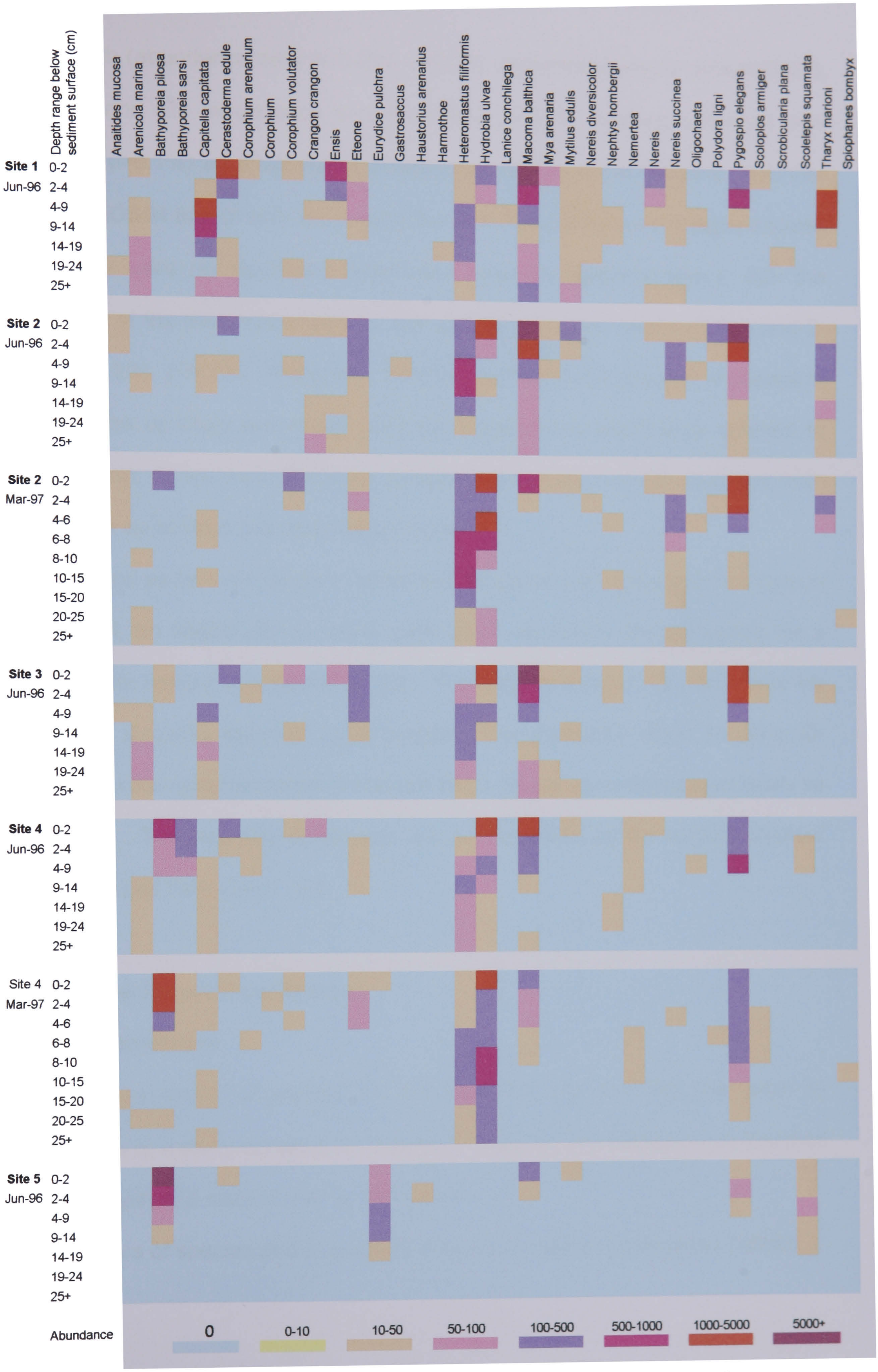


Figure 3.3. Species distribution in the sediment for the Schelde. The relative abundances (numbers m^{-2}) of each species for every depth below the sediment surface for each site in the Schelde and each sample date are illustrated.

Both depth (abundance data R=0.854, p=0.1%, presence/absence data R=0.596. p=0.1%) and site (abundance data R= 0.564, p=0.1%, presence/absence data R=0.454, p=0.1%) were significant factors in the distribution of the biota. A further 1-way ANOSIM test of only depth as a factor in structuring assemblages showed that there were no significant differences between *adjoining* layers, with the exception of the abundance data for the surface two upper layers (0-2cm and 2-4cm; R=0.231, p>0.05). There was, however, evidence of a gradient of change in assemblage structure with depth, with each layer being significantly different to more distant layers from the same sample location (i.e. layers separated from each other by at least one other depth horizon).

This general pattern of change in community structure over core depth is shown in Figure 3.4; an NMDS plot in which each point represents the community for a single depth horizon at a particular site. The distance between points reflects the degree of similarity between assemblages. The shallowest depth horizons (0-2cm) lie on the right hand-side of the plot whilst deeper assemblages generally lie to the left. The inter-site differences are demonstrated by the vertical gradient across the plot from sites 1 to 5.

3.3.2 The Tamar/ Plym System

3.3.2.1 Macrofauna

Not all cores could be inserted the full 30cm into the sediment due either to compaction or a stony substratum. Therefore, sites SJ and SM were only sampled to 25cm depth and site LG only to 20cm depth.

The numbers of species and individuals at each site are summarised in Table 3.2.

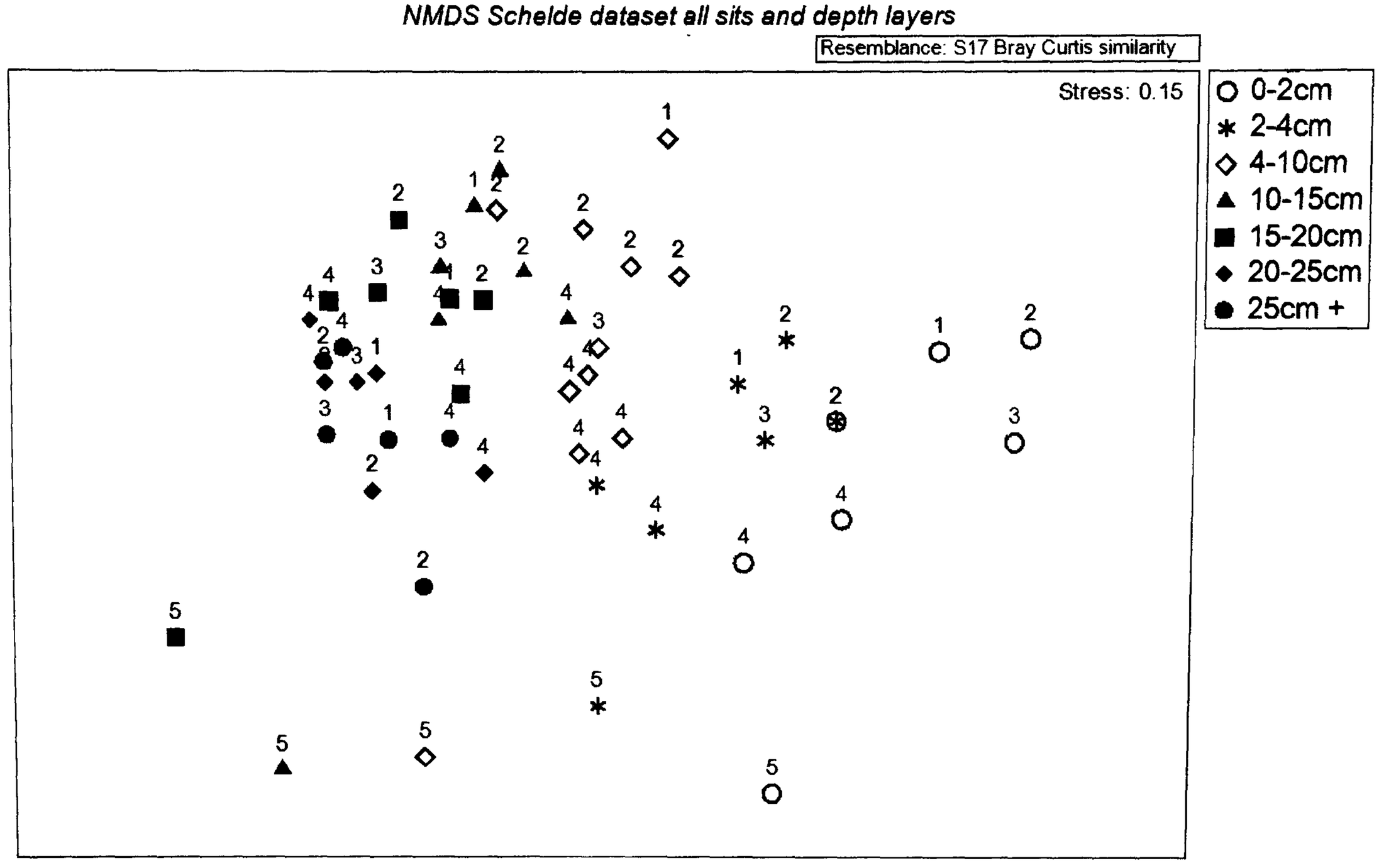


Figure 3.4. NMDS plot for untransformed data from the Schelde. Each point represents the community at a depth group for that site. Numbers refer to the site and symbol to the depth horizon of the sample

As with the Scheldt estuary, for all sites in the Tamar and Plym the majority of species and individuals were associated with the upper layers of substratum. as shown in Figure 3.5. Deeper regions were exploited at all sites but to differing degrees; for some species, maximal abundance was below 8cm, e.g. *Nemertea* and *Sipunculidae* at Site 2 (HQ) and *Scrobicularia* at Site 4 (SJ) and site 5 (SH).

Table 3.2. Summary of biological data for the Tamar/Plym. The number of species recorded and the estimated number of individuals m^{-2} at each site are given for the whole depth of sediment sample and for depths below 8cm and 10cm in the sediment.

Site	TP	HQ	EN	SJ	SH	LG	BP	RD	SM
Site Code	1	2	3	4	5	6	7	8	9
WHOLE DEPTH									
Species m^{-2}	23	15	29	46	25	31	31	23	23
Individuals m^{-2}	20645	14959	7992	18245	15356	38413	33425	25005	46192
BELOW 8cm									
Species m^{-2}	4	8	2	12	12	9	4	7	6
Individuals m^{-2}	102	1573	76	681	856	312	334	1310	1145
BELOW 10cm									
Species m^{-2}	4	3	2	9	12	9	4	4	4
Individuals m^{-2}	46	351	76	297	836	54	176	918	562

The RELATE seriation tests revealed that within the Tamar/Plym system a significant gradient of change in community structure occurred with sediment depth at all sites and regardless of transformation (rank correlation, ρ, ranges from 0.35 ($p<0.05$) to 0.874 ($p<0.05$), with the exception of the transformed assemblage data for site 6 (Looking Glass Point) ($\rho= 0.408$, $p>0.05$)

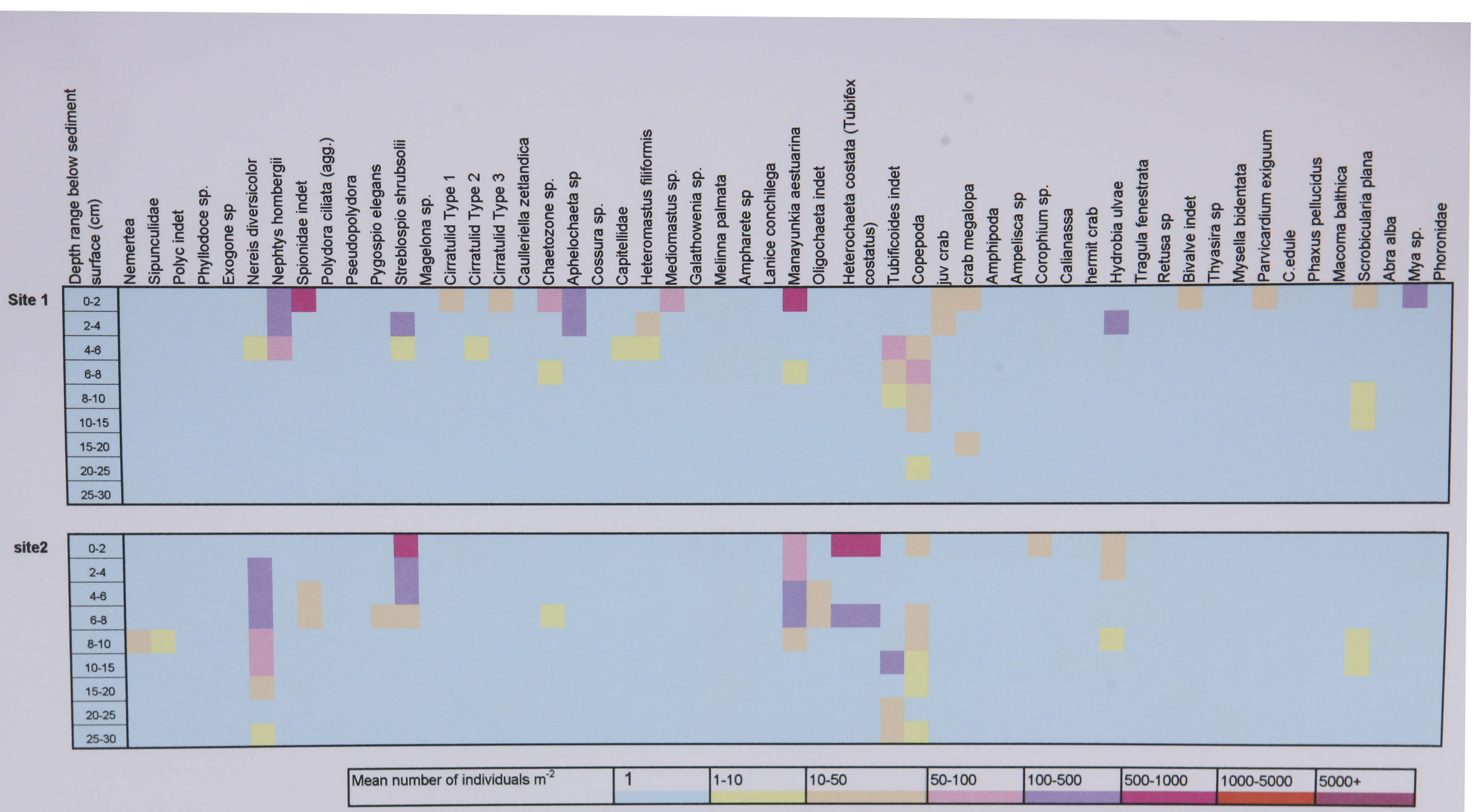


Figure 3.5. The relative abundance of the biota within the sediment of the Tamar / Plym estuary sites. The abundance at each depth is indicated by the colour as set out in the key

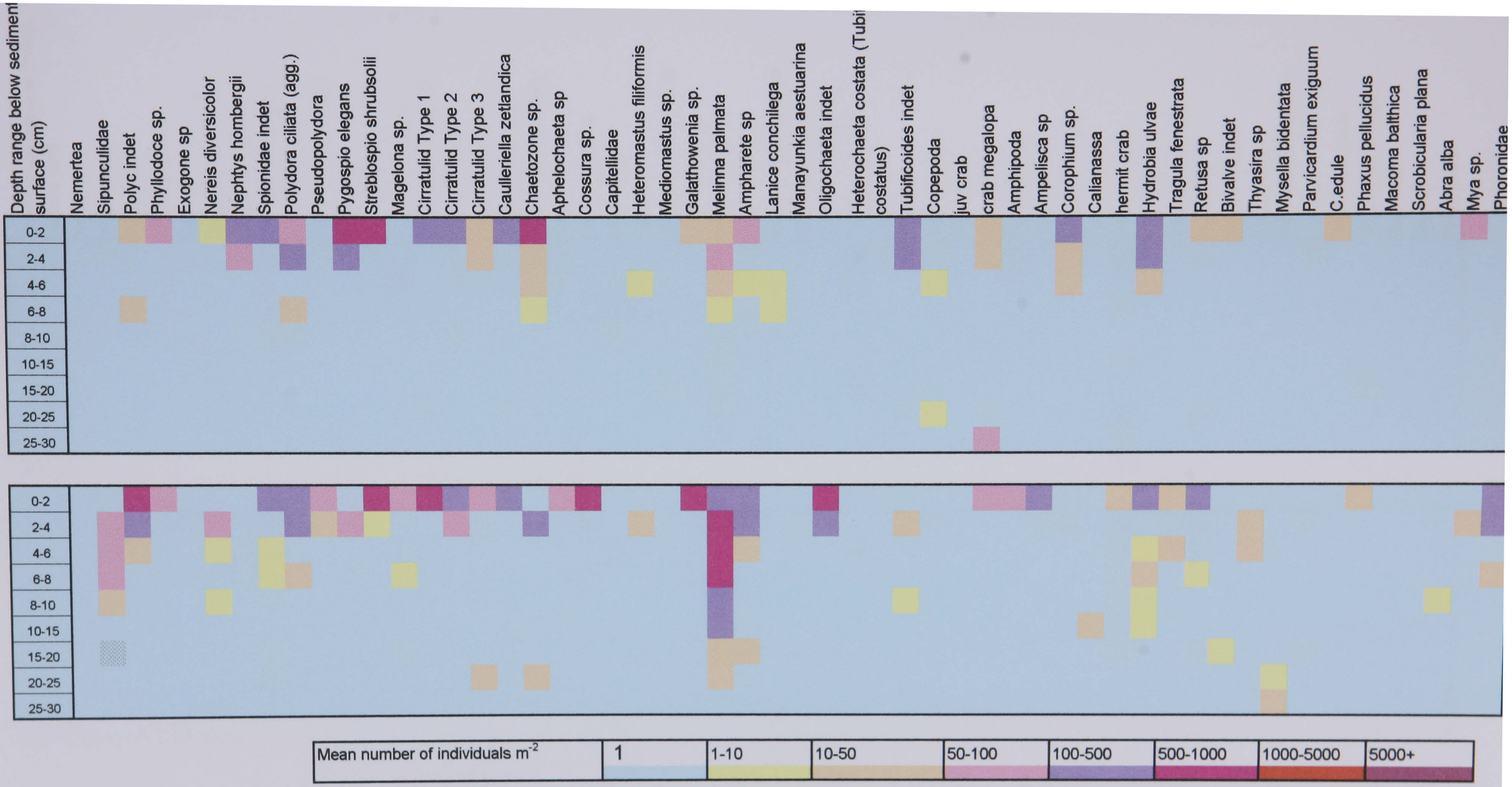


Figure 3.5. (contd.) The relative abundance of the biota within the sediment of the Tamar / Plym estuary sites. The abundance at each depth is indicated by the colour as set out in the key

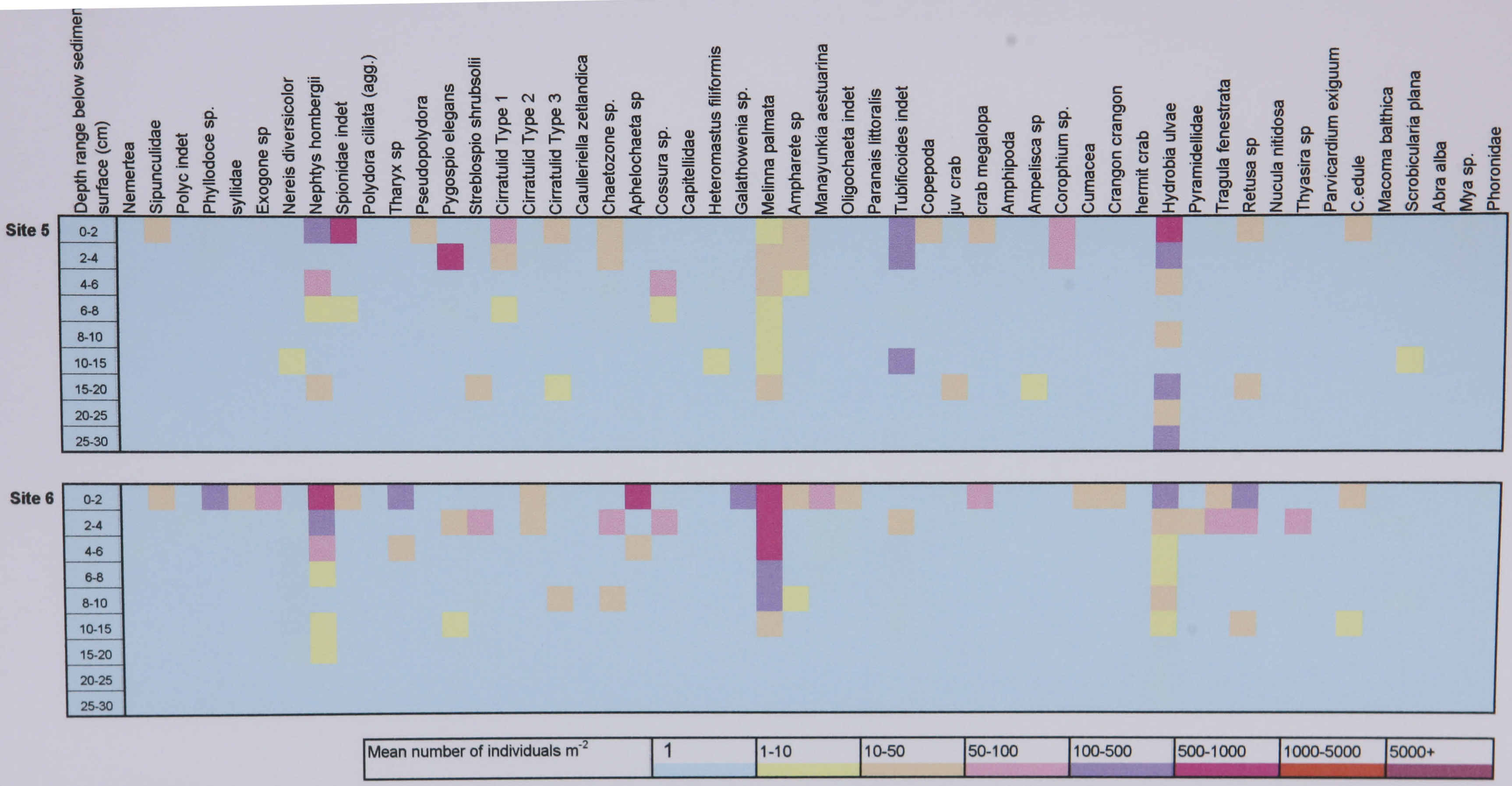


Figure 3.5. (contd.) The relative abundance of the biota within the sediment of the Tamar / Plym estuary sites. The abundance at each depth is indicated by the colour as set out in the key

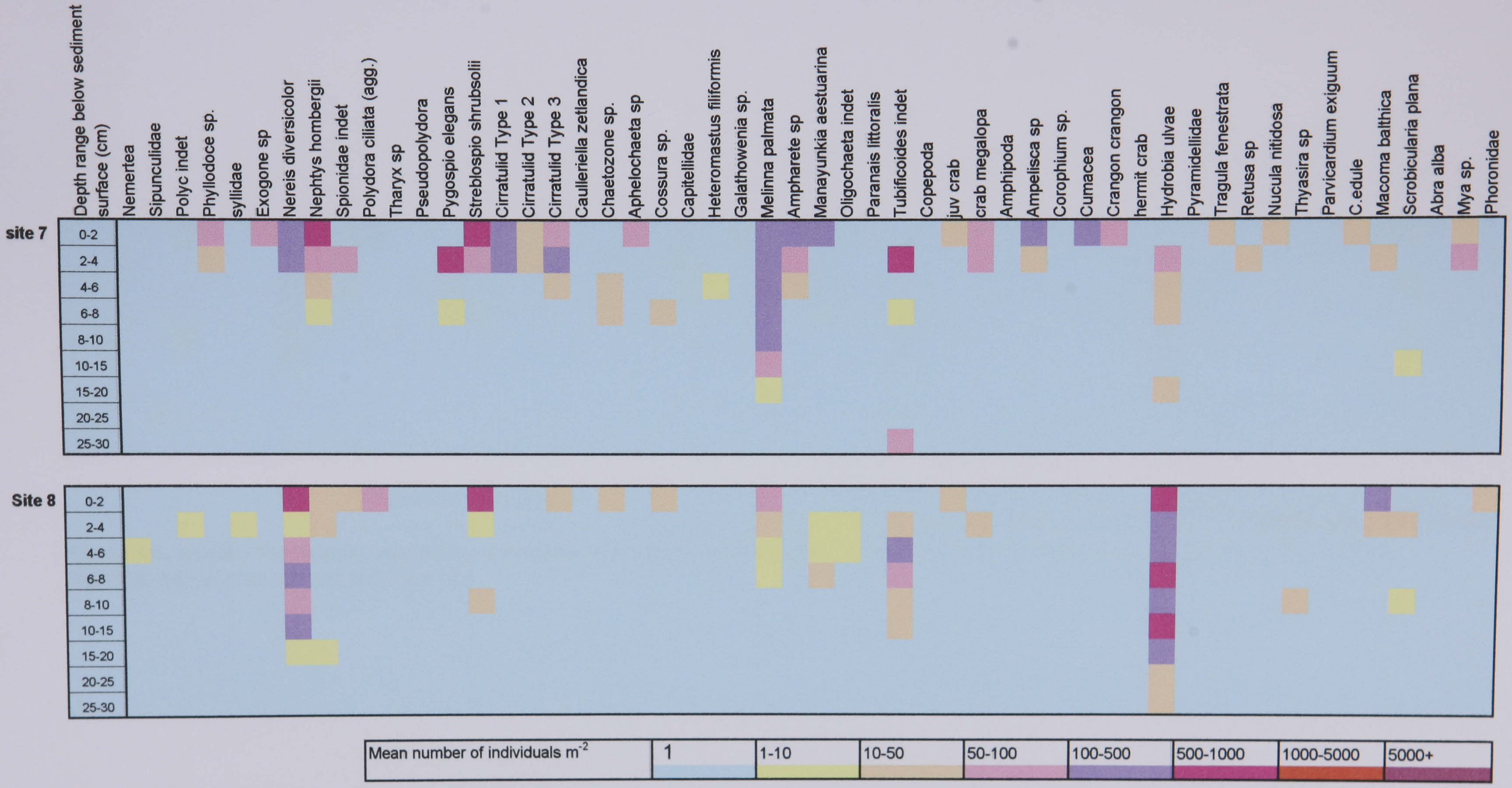


Figure 3.5. (contd.) The relative abundance of the biota within the sediment of the Tamar / Plym estuary sites. The abundance at each depth is indicated by the colour as set out in the key

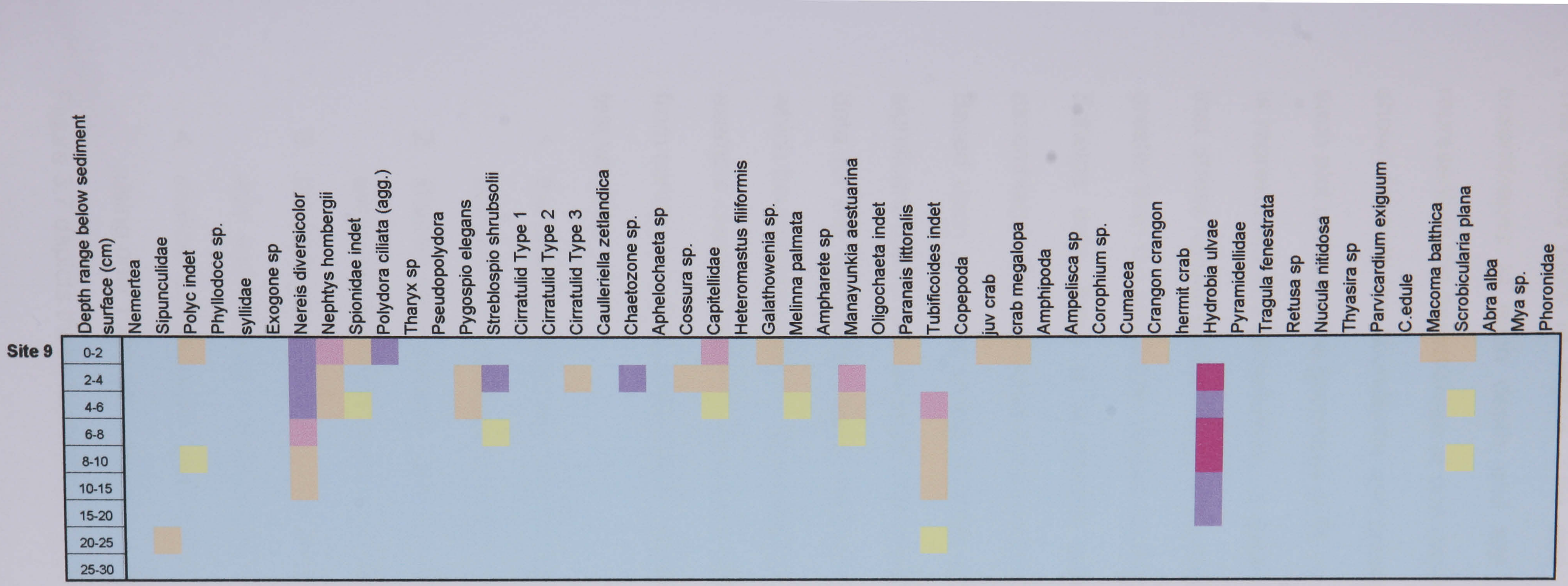


Figure 3.5. (contd.) The relative abundance of the biota within the sediment of the Tamar / Plym estuary sites. The abundance at each depth is indicated by the colour as set out in the key

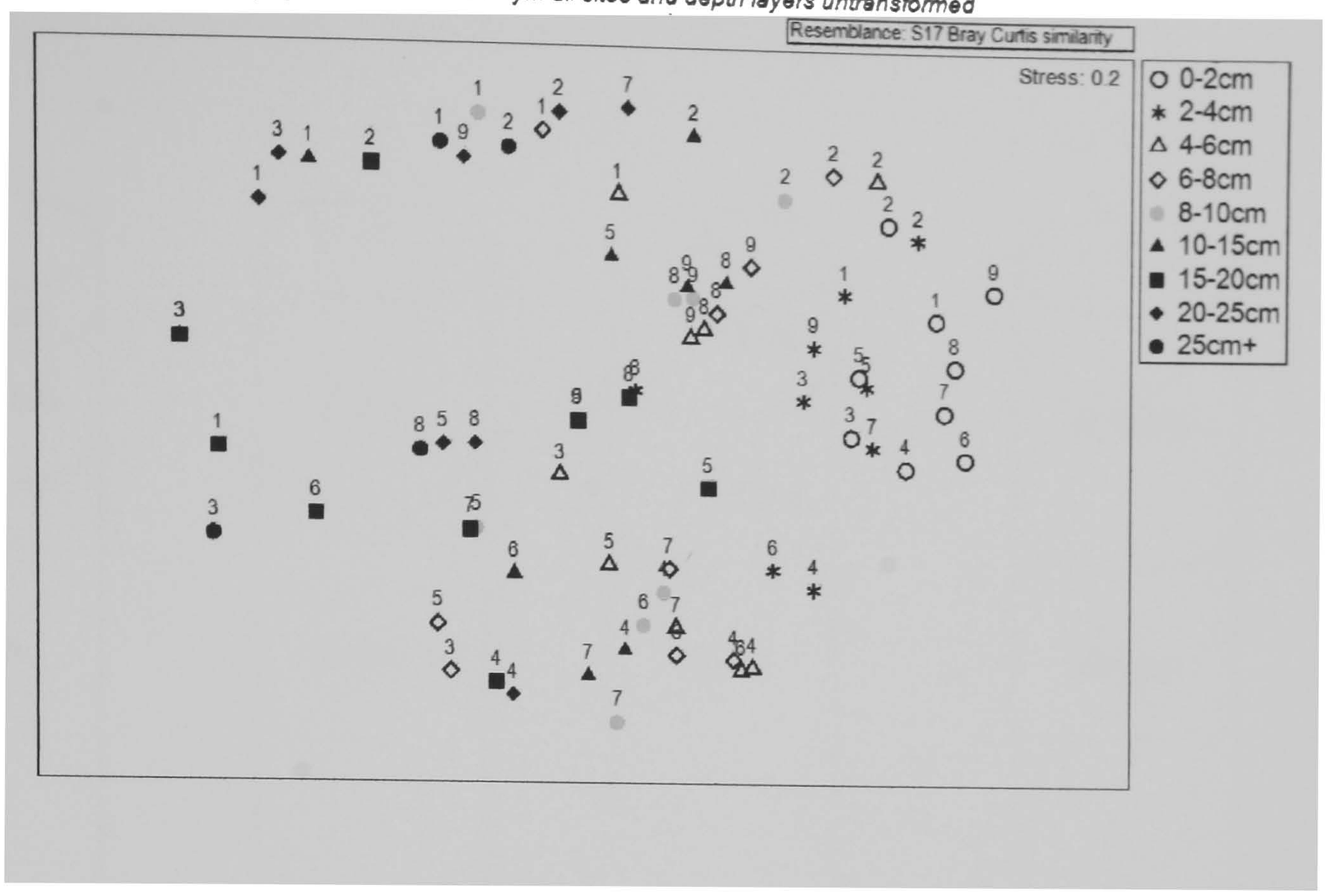
The NMDS plots in Figure 3.6a and 3.6b show the relationships between assemblages at each depth and site for the Tamar/Plym, with each point representing the assemblage at one depth horizon for a particular site. Plots are shown for both the abundance and presence/absence data. The stress value on each plot indicates the goodness of fit, i.e. how well the relationship between sites is represented in 2 dimensions. In general, Clarke and Warwick (2001) suggest that stress values below 0.2 give a useful two-dimensional picture, whilst those greater than 0.3 should be viewed cautiously especially if *n* is small. As with the Schelde data, there is a general gradient of depth across the plot, with assemblages from shallower horizons to the right and deeper ones to the left.

Based upon analyses of the Schelde data which, as outlined above, indicated significant differences between the assemblages from various depth layers, the data for the Tamar/Plym were explored to determine the most effective way in which boundaries could be set to discriminate between separate assemblages for example creating "surface", "mid" and "deep" assemblages. To this end, the data from contiguous depth layers were combined and further ANOSIM tests applied to test whether:

1. the biota could be split into three significantly different assemblages using 2cm and 8cm as boundaries between assemblages;
2. shallow assemblages were significantly different from deep assemblages using only 8cm as a boundary between the two;
3. the biota could be split into three significantly different assemblages using 4cm and 10cm as boundaries between assemblages; and/or
4. shallow assemblages were significantly different from deep assemblages using only 10cm as a boundary between the two.

Figure 3.7 depicts these four different possible groupings of assemblages

(a) *NMDS Tamar/Plym all sites and depth layers untransformed*



(b) *NMDS Tamar and Plym all sites and depth layers*

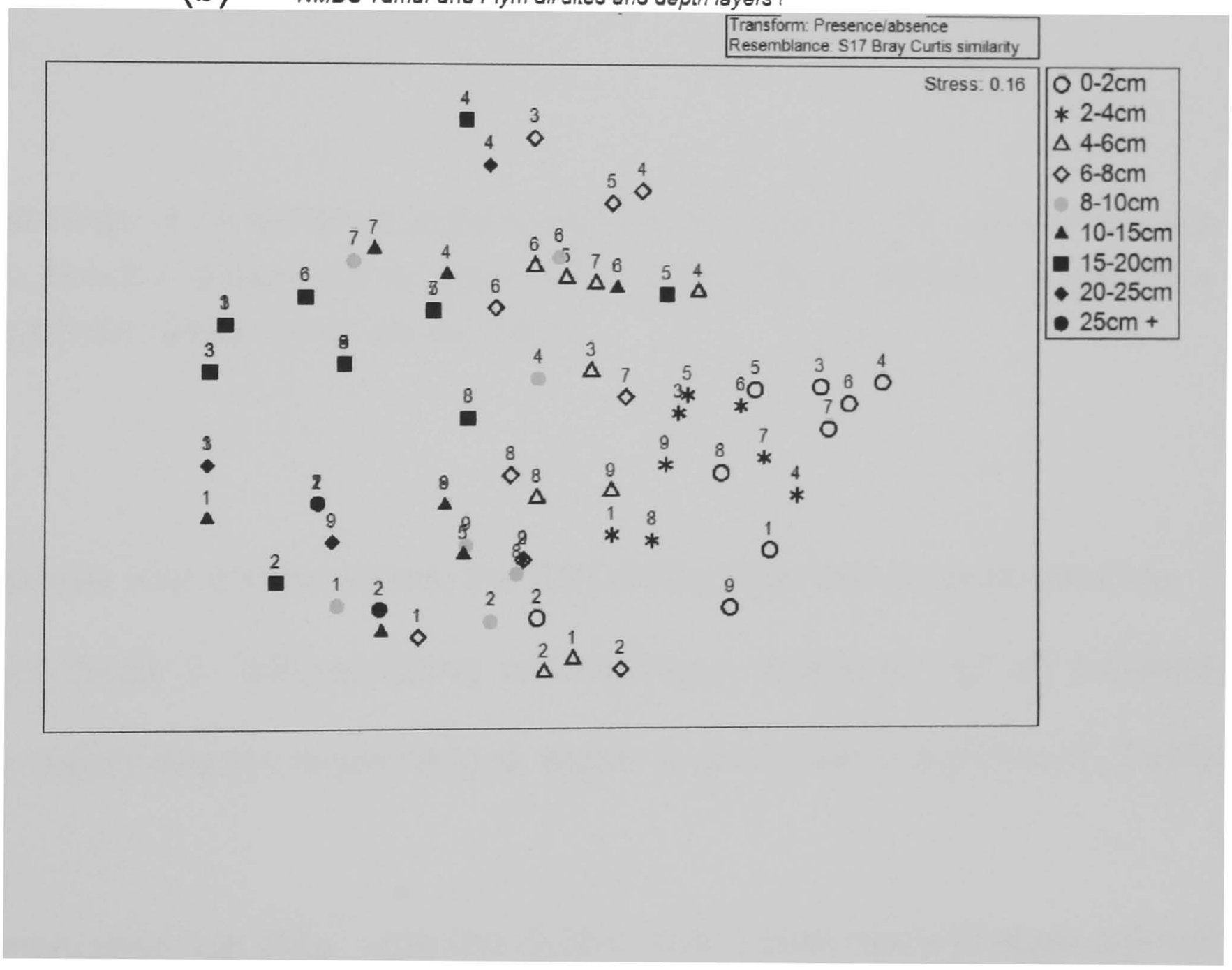


Figure 3.6 NMDS plots for abundance data (a) and presence/absence data (b) from the Tamar and Plym. Each point represents a single depth region at a site. The site is labelled by number according to site code in Table 3.2 and depth horizon by the symbol.

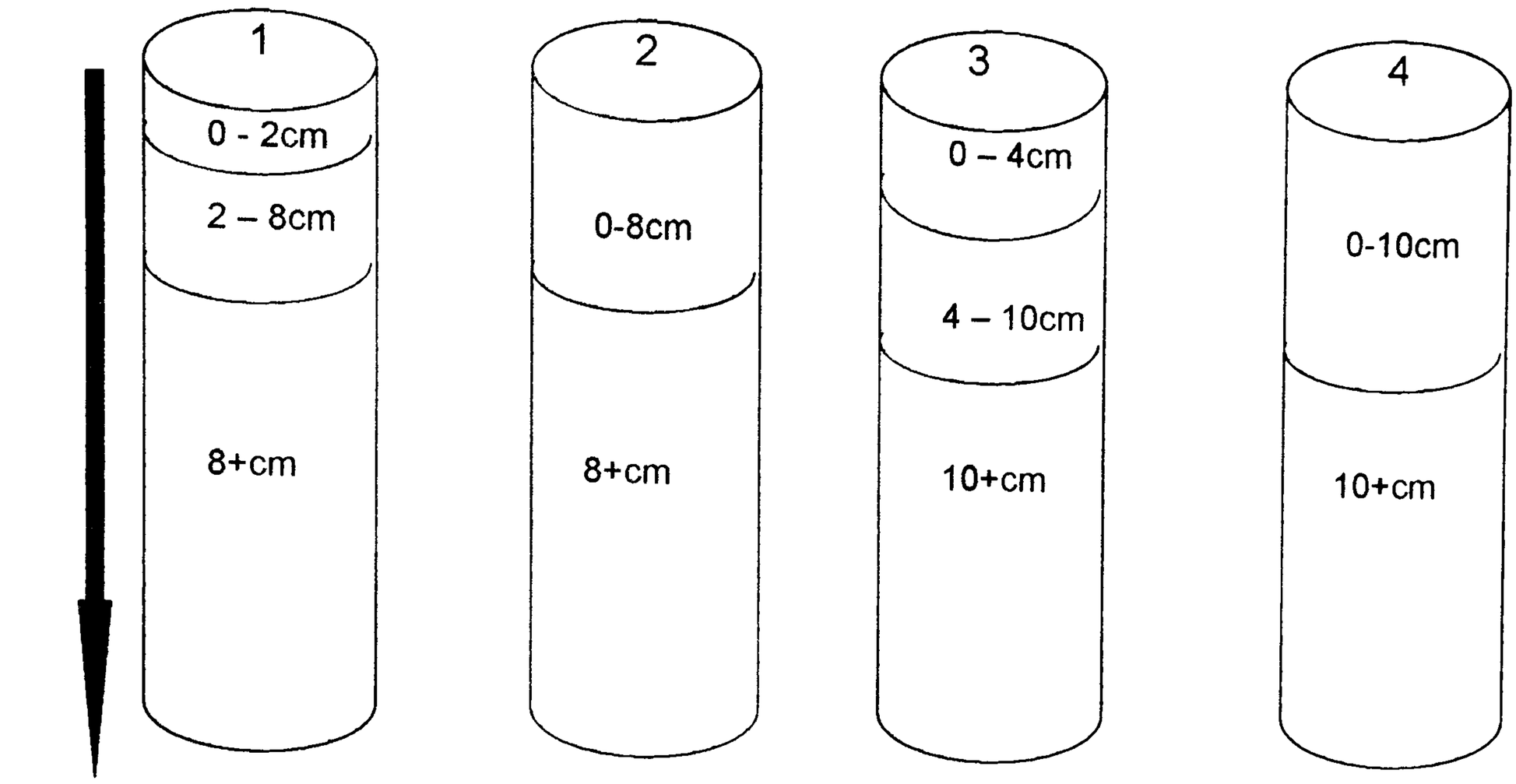


Figure 3.7. Depth range of the combined layers used in further analyses. The layers within each comparison were, Group 1: 0-2 cm, 2-8 cm and 8+cm, Group 2: 0-8 cm and 8+cm, Group 3: 0-4 cm, 4-10 cm and 10+cm, Group 4: 0-10 cm and 10+cm.

For all of the above four combinations, the ANOSIM global test showed depth to be a significant factor in differentiating assemblages. However, not all pairwise tests between depth-related assemblages within a group were significant (Table 3.3).

For the presence/absence data, only the 0-2cm and 2-8cm assemblages did not significantly differ in composition from each other, whilst for the abundance data. the 4-10cm and 10+cm layers were not significantly different from each other.

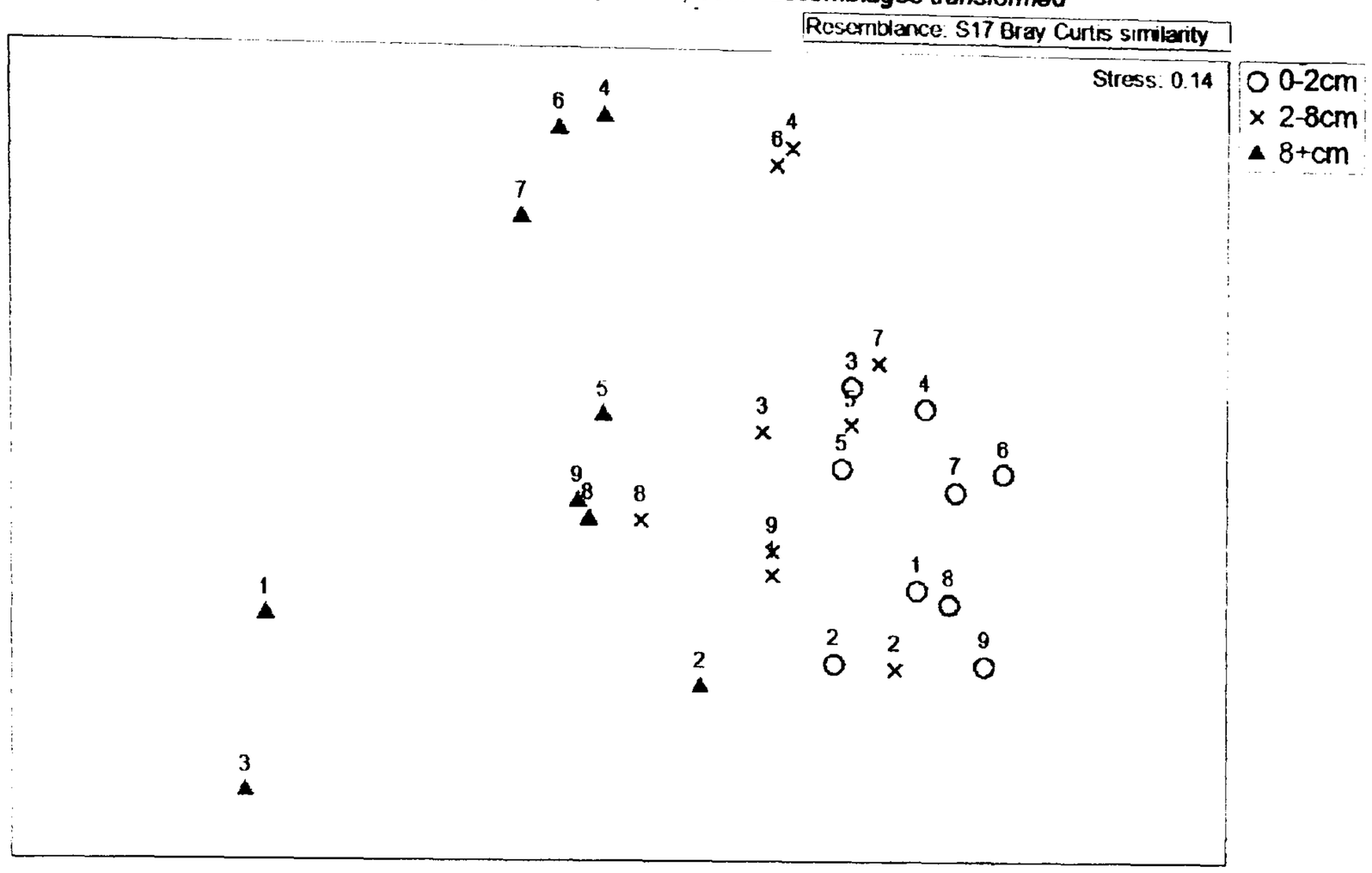
Table 3.3. Global and pair-wise ANOSIM results (R statistic) for tests of similarity between each of the assemblages contained within each group (see Figure 3.7) for the Tamar and Plym. *p<0.05, **p<0.01, ***p<0.001.

Combination Group	Global test of depth as a factor		Pairwise comparison of layers			
	Abundance data	Presence / Absence data	Layers being compared		Abundance data	Presence / Absence data
1	0.34 ***	0.31 ***	0-2	2-8	0.19	0.08
1			0-2	8+	0.57 **	0.45 **
1			2-8	8+	0.22 *	0.256 *
2	0.20 ***	0.59 ***	0-8	8+	0.20 ***	0.59 ***
3	0.44 ***	0.35 **	0-4	4-10	0.59 ***	0.256 *
3			0-4	10+	0.632 ***	0.564 ***
3			4-10	10+	0.038	0.183 *
4	0.63 ***	0.66 ***	0-10	10+	0.63 ***	0.66 ***

Relationships between sites for Group 1 and Group 4 of the potential assemblage combinations (Figure 3.7) are shown in Figure 3.8 for presence/absence data. Similar plots were obtained for abundance data and for the other combinations.

SIMPER results did not reveal characteristic assemblages for the different depth groups. However, within group similarity was higher for shallower communities (35-56%) than for deeper ones (16-33%).

A visual comparison of patterns in the Schelde and Tamar/Plym data is shown in the NMDS plot in Figure 3.9. The Schelde and Tamar/Plym sites are distinct from



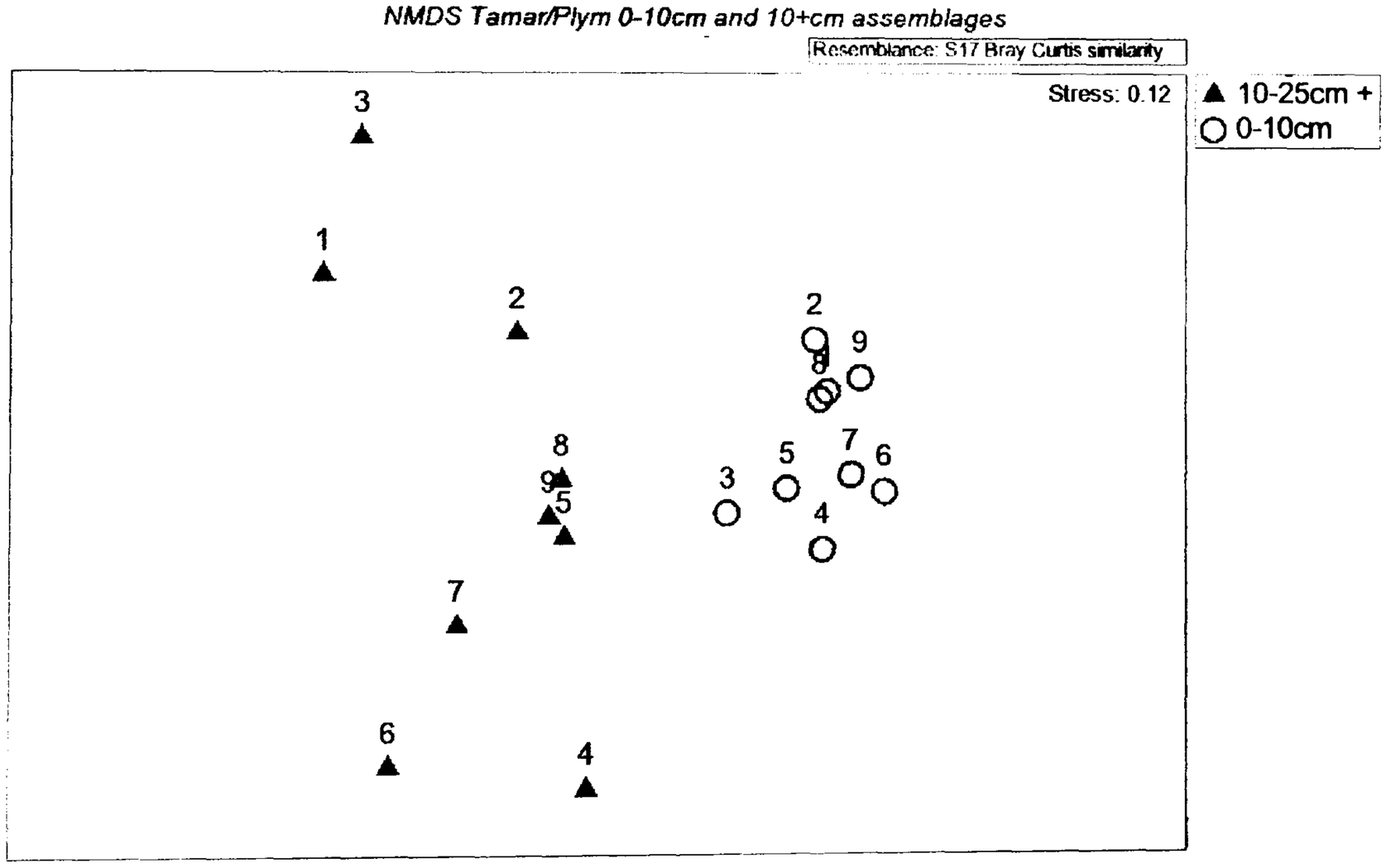


Figure 3.8. NMDS plots of Tamar/Plym presence/absence data. Each point represents the biota at a particular depth region as indicated by the symbol, and each site is numbered with the site code (refer Table 3.2).

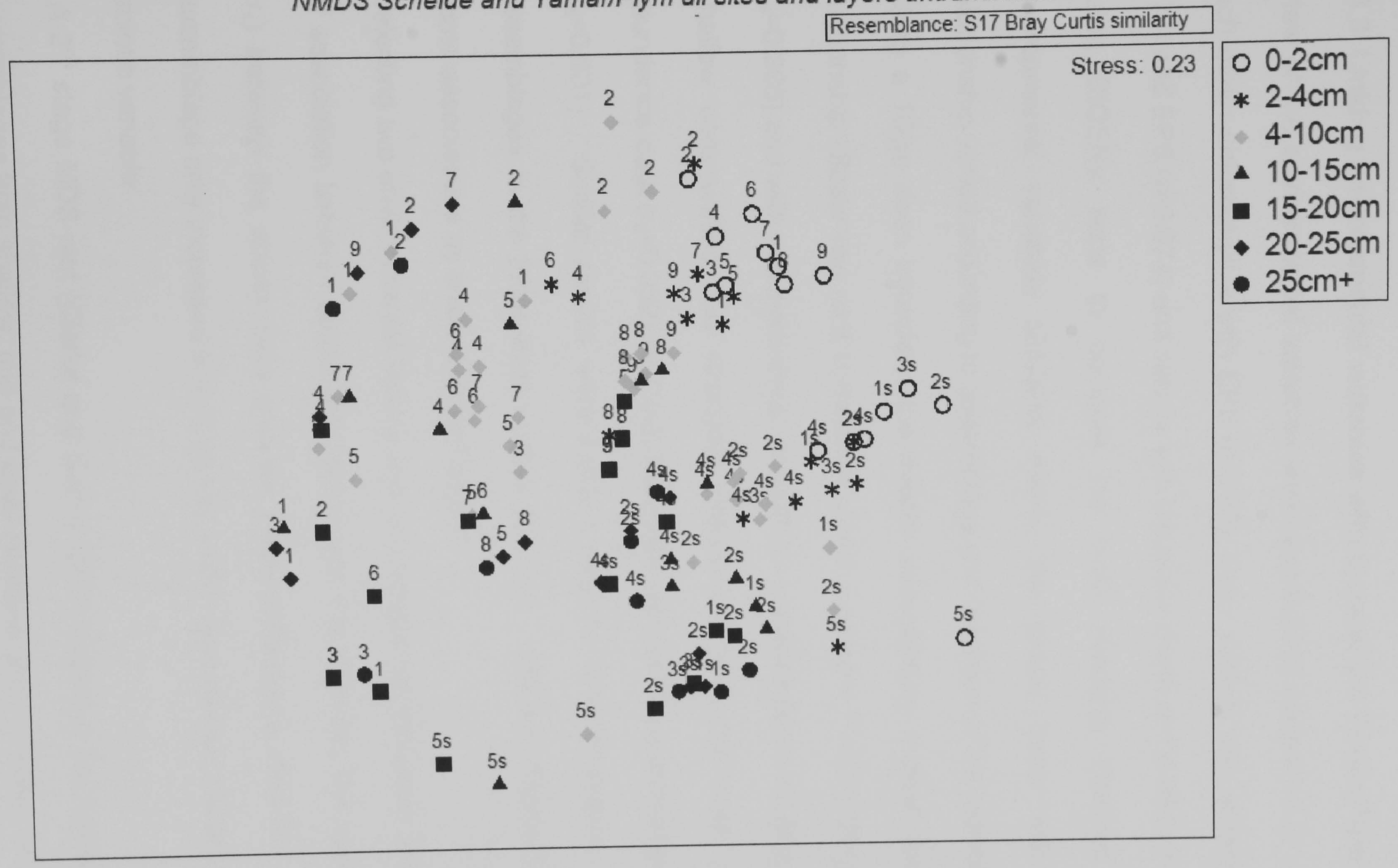


Figure 3.9. NMDS based on abundance data for all sites and depths sampled in both the Schelde and Tamar/Plym. Sites in the Schelde are indicated by site number and suffix "s". Tamar and Plym sites are indicated by the site code from Table 3.2. Sediment depth is indicted by the symbols.

each other, whilst both follow the same pattern of decreasing sediment depth from top right to bottom left across the plot.

3.3.3 Linking environmental variables with biota in the Tamar/Plym

A few of the environmental variables were significantly correlated ($p < 0.05$) with each other: chlorophyll *a* with EPS ($r=0.83$), water content with chlorophyll *a* ($r=0.74$) and EPS ($r=0.074$) and salinity with the mean depth of the RPD ($r=0.93$).

Using BIOENV tests to compare the biotic similarity matrices with the environmental variables similarity matrix, the abiotic factor with strongest relationship varied according to assemblage and precision of the biological data.

Using a 10cm deep boundary, the deeper assemblages showed the strongest relationship (Spearman rank correlation r_s) with sediment TOC for raw abundance ($r_s=0.386$) and with sediment shear strength for presence/absence data ($r_s=0.341$).

Shallow communities had strongest associations with the water content for abundance data ($r_s=0.392$) and with interstitial salinity for presence/absence data ($r_s=0.531$). Similar results were found using the 8cm boundary. Mid layer assemblages in the three-layer models (Groups 1 and 3 in Figure 3.7) had the same associations as shallow assemblages.

Selecting two environmental factors only produced small increases in the strength of association between abiotic and biotic data. For example, the rank correlation (r_s) between the abiotic data and the presence/absence data for the shallow assemblage only increased from 0.531 to 0.586 upon inclusion of another second abiotic variable.

A 2nd stage MDS plot (Clarke and Gorley 2001) depicting the similarity between assemblages from shallow. mid and deep horizons and the matrix of all combined abiotic variables is shown in Figure 3.10. The 2nd stage MDS was produced from

a triangular matrix of ρ coefficients between all the pairs of ordinations i.e. the 2nd stage MDS ordination reflects the similarity between each of the different ordinations produced from each individual dataset. The relationship of the biota with environmental variables alters with the depth in the sediment and with including whether species occurrence or abundance is considered. Influences of depth on community structure and relationships with abiotic variables appear to be stronger than does data consideration of abundance or occurrence.

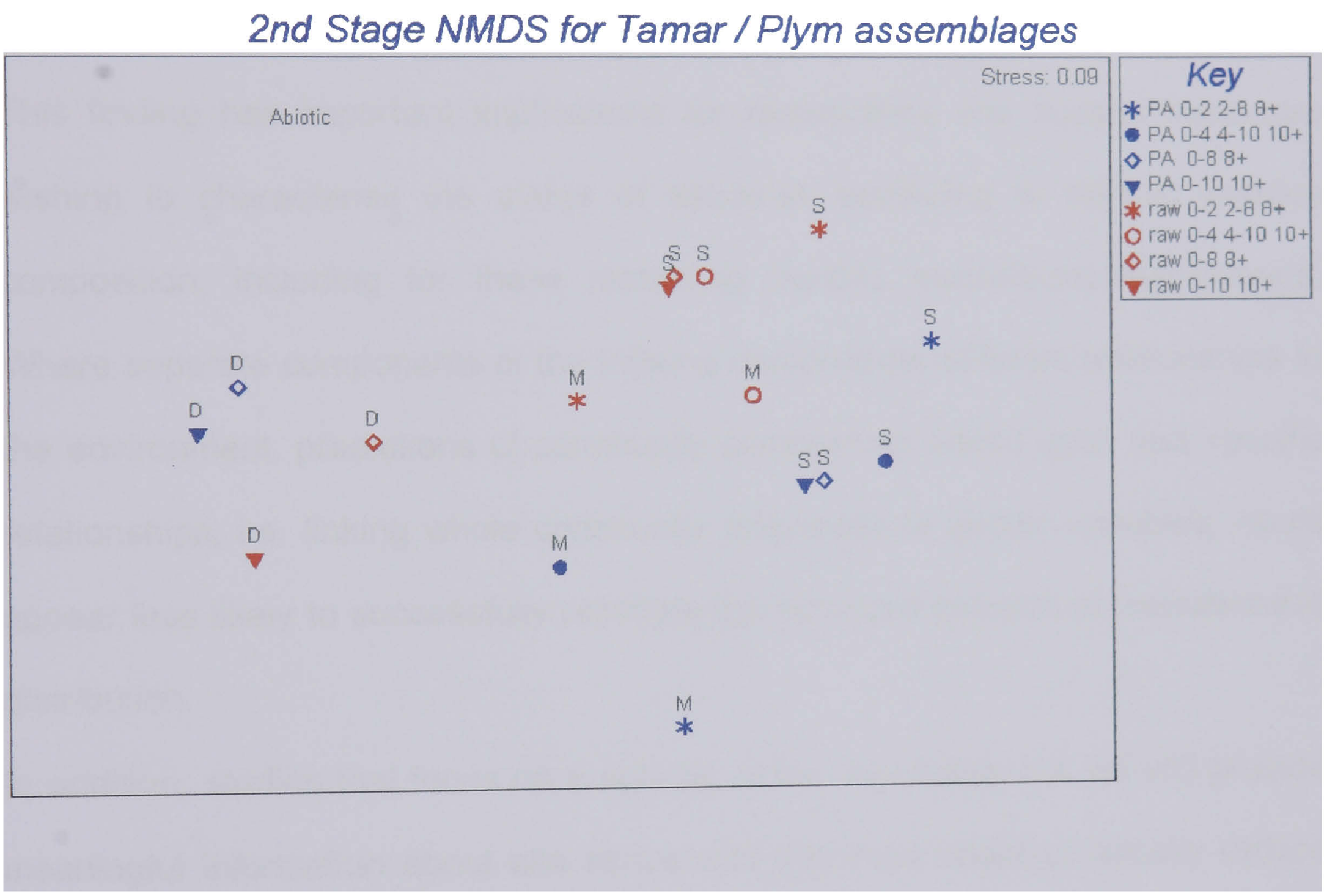


Figure 3.10. 2nd stage MDS plot for Tamar/Plym showing the relationship between the abiotic and biological variables. D="deep" assemblages, "M" = mid layer assemblages", "S" = shallow assemblages. Symbol refers to "depth group classification" and whether abundance or presence/absence data as shown in the key. (For simplicity the 8+ layer is only given by the symbol for the 0-8, 8+ combinations and 10+ layer only by the symbol for the 0-10, 10+ combinations despite both being utilised in more than one combination of depth horizons).

3.4 Discussion

There was clear evidence of vertical stratification of the benthic macrofauna within the sediment of each studied estuary, and some evidence that the benthos could be treated as two separate assemblages, one "shallow" and one "deep". When examined further, the shallow and deep assemblages displayed distinct patterns of inter-site similarity, and were associated with different environmental variables. Consequently, the hypothesis of there being no difference in the nature of the abiotic factors shown to have relationships with the biota. according to the depth range at which the benthic assemblage was found in the sediment, was rejected. This finding has important implications for researchers and coastal managers wishing to characterise the status of estuaries according to benthic species composition, including for those modelling benthic macrofauna distributions. Where separate components of the infauna demonstrate different relationships to the environment, predictions of community composition based upon less specific relationships, i.e. linking whole community responses to abiotic variables. would appear less likely to successfully replicate the surveyed patterns of macrobenthic distribution.

In addition, studies that focus on a sub-set of the community but yet still provide meaningful information about site status and dynamics could potentially reduce costs, given that classification investigations requiring analyses of whole communities across a broad range of separate sites are extremely costly in time and effort. A resulting problem that must be addressed is to identify the most appropriate sub-sets for analysis. This present study advocates a novel approach, which aids identification of those local species within estuarine soft sediment sites that potentially have greater value in differentiating between sites according to biological and environmental status. For some environmental questions it may be

possible to only consider one subset whilst other investigations may benefit by comparing the responses of both shallow and deeper-dwelling assemblages to environmental forcing.

3.4.1 Biotic Patterns across estuaries.

The present study showed a distinction between the structure of the shallow and deep-living biota across geographically-distinct estuarine systems, implying that such differences may be a common feature of many, if not all, estuaries. Although the Schelde and the Tamar/Plym systems are both temperate and physically dynamic (Uncles et al 2002), they are separated by 555 km. Compared to the rural hinterland of the Tamar (EA report 1996), the Schelde system is considerably larger, for the River Schelde alone drains 195,000km^2 (Goosen et al 1997), and its catchment is densely populated with high levels of urban discharge (Muylaert et al 2005). Within the Schelde estuary, only five sites were sampled, all from within a single sandflat. By comparison, the nine sites sampled from the Tamar/Plym system were much muddier. Given such differences, the physiological and physical challenges faced by the infauna considered within this present study varied greatly between estuaries. Despite such differences, similar patterns of vertical macrofauna stratification were observed in both systems.

Within each estuary, the number both of species and individuals decreased with depth in the sediment. Deep assemblages of species were not totally distinct in terms of species identity from the overlying group, but when subjected to multivariate analysis, the assemblages found within the upper 10cm of each estuary showed less spatial differentiation than those from greater depths. This similarity of pattern was evident despite local variations in the depths at which co-occurring species were found.

To help create an operational method for more generalised estuarine modelling. it was necessary to investigate the most appropriate boundary that might be used to separate the shallow and deeper assemblages. To do this. the study described in this chapter assessed setting boundaries at 8cm and 10cm depths, including the possibility of defining a separate "mid-layer" (2-8cm or 4-10cm). The latter approach was rejected as analysis failed to produce consistent patterns of significant differences between macrobenthic depth-related assemblages. Instead, a simple division of shallow and deep-living biota was considered the most parsimonious approach that would minimise sampling effort for any future studies that might be based upon the findings of this present study.

It was therefore necessary to define the depth at which the deep/shallow distinction should be drawn. Shallow and deep assemblages were significantly different from each other whether separated at 8cm or 10cm depth (Table 3.3). Analyses showed that the 8-10 cm horizon included some species that were reaching the limit of their depth range at his horizon e.g. *Nemertea indet., Thyasira sp.*, while the majority of species found deeper than 10cm demonstrated greater exploitation of the deeper layers (Figure 3.5) and hence a pragmatic decision was made to distinguish the shallow and deep assemblages using a 10cm boundary. This decision may have influenced the subsequent results of the study and imposes a theoretical and artificial boundary between the two assemblages that will of course be crossed by many individuals in their daily activities. The assemblage to which each individual is allocated is subject to errors because it is based upon the depth the organism was sampled not its absolute depth exploitation limit. Since the latter was not know. however, it was felt that by choosing 10cm as a cut-off, it was more likely that only species truly exploiting the deeper regions would be included in the deepest assemblage.

The shallow and deep assemblages were significantly different from each other whether using presence/absence or abundance data, leading to the conclusion that differences observed were not driven solely by the higher number of individuals in the surface layers. Although approximately half the species found in the Schelde were common to both estuaries e.g. *Nereis diversicolor*, *Macoma balthica* and *Heteromastus filiformis,* there were several species that exploited deeper sediment horizons in the Schelde that were absent from the Tamar/Plym system e.g. *Arenicola marina*, *Eteone*, *Spiophanes bombyx* and *Scolelepis squamata.* Since the patterns of depth distribution persisted between the estuaries examined here (Figure 3.9), the results of the present study suggest that shallow and deep assemblages might be identified in estuaries with different physical characteristics and dissimilar species pools. It would now be beneficial, however, to extend the study to include other systems and include sub-tidal and high elevation sites, which were not represented in this study.

3.4.2 Biological differences between shallow and deep assemblages.

A group of species could not be identified that characterised deeper assemblages across *all* of the sites surveyed in the Tamar/Plym system. Within any one site, not all the species found at depth were always present in the overlying layers (see Figure 3.5 for depth ranges of individual species). Further, few species were unique to the deeper sediments across all sites surveyed in the Tamar/Plym system. Thus, reasons were sought to explain why only a few individuals from within a species population migrated deeper into the sediment and only at particular sites. A number of studies have reported increased body size of deeper individuals compared to conspecifics living in shallower layers (Zwarts and Wanink 1993, Esselink and Zwarts 1989, Zwarts and Wanink 1989, Davey and Partridge

1998). A simple inspection of the macrobenthic samples from the present study indicated that many animals did indeed tend to be smaller in the shallow surface layers of sediments in the Tamar/Plym: *Scrobicularia plana* found in the surface sediment layer never exceeded 6mm in length but in deeper layers this species reached lengths of 33mm, *Nephtys* indet were all greater than 30mm in length in deep sediments but the majority of individuals in the surface layers were less than 12mm long. The bigger an animal is the more sediment it occupies and if they are to live within the sediment fabric rather than on top of it bigger animals must burrow deeper than small ones. However there is also evidence that there are benefits in actively exploiting deeper regions:

- it might confer a degree of protection from predation (Holland 1980, Zwarts and Wanink 1989);
- it might minimise exposure to environmental fluctuations in inter-tidal areas where sediment water content, salinity and temperature are often more variable close to the sediment surface (Brotas et al 1990, Johnson 1965, Reid 1930,Zwarts and Wanink 1989);
- biological interactions can be minimised (Rhoads 1974, Whitlach 1980, Josefson 1989);
- many deposit feeding species actively feed at depths below the sediment-water interface (Rhoads 1974), for example *Heteromastus filiformis* (Neira and Höpner 1993; and
- it might confer limited protection from low-level physical disturbances to the sediment such as fish feeding (Myers 1977, Thistle 1981, Grant 1981).

Burrowing to depth, maintaining and irrigating a burrow, maintaining complex feeding structures and moving to and from the surface to feed and defecate all have an energetic cost. Hence the benefits of occupying deeper sediment

horizons must outweigh any cost incurred and are only available for those species whose morphology permits such exploitation, for example only bivalve species with extendable siphons. The trade-off between benefits and costs. however. is probably most beneficial for larger-bodied individuals (Myers 1977).

It is probable that within any one site the larger individuals of a species are the oldest. The older a sessile species is, the better its survival reflects environmental conditions integrated over time. Species such as *Nereis diversicolor* may live for up to 3 years (Olive and Garwood 1981), and large bivalves such as *S. plana* or *Mya* even longer (Strasser 1999, Commito 1982), so that their presence and size reflect conditions over a number of years. On the other hand, small polychaetes such as *Pygospio* or *Streblospio* may have a number of cohorts settling out and dying each year. Opportunistic life history strategies are best fitted to short-lived dynamic conditions (Grassle and Grassle 1974, Gray 1974, Pearson and Rosenberg 1978). Where estuarine conditions are dynamic, small-bodied opportunistic species exploit temporarily favourable environments, reproduce and then die; their presence does not necessarily reflect environmental conditions that have been sustained for more than a few months. Older assemblages. then. represent the most useful biological tool with which we can assess the *long-term* integration of the biological and physical environment within an estuary. Within soft sediments, those animals occupying the deeper sediment regions best represent older infaunal assemblages. Conversely, the structure of shallow assemblages provides a useful snapshot of *short-term* variability and may provide a valuable '"early warning" of environmental changes.

3.4.3 Abiotic-biotic relationships in the Tamar and Plym system

The relationship between presence/absence data for shallow assemblages and

salinity was the strongest observed for a single abiotic factor. However, there was no clear evidence from this investigation that shallow assemblages had stronger associations with the abiotic data than did deeper ones. Present findings suggest that abiotic-biotic relationships are variable according to the bias and scale of the investigation. Four different factors were selected by the BIOENV procedure according to which type of biotic data (abundance or presence/absence) and which depth assemblage was under analysis.

3.4.3.1 Interstitial salinity.

In the present study, the number of species in the upper layers reflected the well-accepted estuarine salinity gradient with diversity increasing as salinity approached "marine" values (see Section 3.3.3) (Kinne 1971, Remane 1934). Temporal variation in interstitial salinity is reported in the Tamar, where salinity of the surface sediment layers varies over the timescale of days and that of deeper sediment regions over seasons (Bryan and Uysal 1978, Morris et al 1982). The findings of the present study detected no significant relationship between the deeper-dwelling infaunal assemblages and the salinity of the upper 2cm of sediment. This observation suggests that as a driver of species distribution patterns in deeper assemblages, salinity is either overridden by other measures, or that the interstitial water samples analysed were not indicative of longer-term trends at each site.

3.4.3.2 Water content.

For the shallow assemblages, species abundance data had the strongest relationship with the water content of the sediment surface layer (see Section 3.3.3). The two sites with the highest water content also experienced the

strongest currents and potentially the longest periods of exposure to tidal re-suspension of the sediment surface. However, when considering all sites, there was no consistent association between tidal flows, length of time of exposure to erosive flows and sediment surface water content. Thus, the relationship between sediment water content and dominance patterns in shallow macrobenthic assemblages does not simply reflect levels of tidal resuspension. This should not be surprising, for water content can influence and be influenced by a range of abiotic and biotic factors (Rhoads 1974, Rhoads and Boyer 1982, Rowden et al 1998, Tolhurst et al 2000).

3.4.3.3 Sediment shear strength.

Transformed data for the deeper assemblages had a strong relationship with the sediment shear strength (see Section 3.3.3). Sediment shear strength can be seen as a measure of the ease with which animals might move through sediment and the ability of biogenic structures to persist (Rhoads and Boyer 1982, Brenchley 1982). Sediments with high shear strength are relatively resistant to movement, which can make burrowing and migration difficult or eventually impossible. Although sediments with low shear strengths will be easy to move through, burrow collapse and sinking become problems at very low shear strength values (Rhoads 1974).

3.4.3.4 Organic matter

Analyses undertaken on abundance data for deep-dwelling assemblages showed a strong link to the concentration of TOC in the surface sediment, with a continued but weaker association with occurrence data (see Section 3.3.3). From these findings it could be suggested that patterns of dominance were strongly related to the organic matter supply.

3.4.3.5 Other abiotic factors.

Of the abiotic factors investigated in the present study, many have previously been shown to have strong relationships with the structure of soft sediment communities (Perkins 1974, Herman et al 1999, Rhoads and Young 1970), yet were not identified as significant here. It is possible that increasing the number of sites and estuaries surveyed here may have strengthened some of the weaker abiotic-biotic relationships found in this study. However, it is also possible that increasing the spatial scale of the study may also have introduced greater variability into observed relationships (Chapman and Tolhurst 2007).

It was also not clear from the analyses whether infaunal associations with abiotic factors other than salinity were mainly due to biological responses or biological effects, or a combination of these two. Nevertheless, all of the abiotic factors not selected here had previously been shown to correlate very strongly with sediment water content (Rhoads and Boyer 1982, Hall 1994), sediment shear strength (Thrush et al 2003, Rowden et al 1998) and levels of organic matter in the sediment (Mayer 1994, Snelgrove and Butman 1999, Herman et al 1999), each of which were selected in this study by BIOENV. Thus, apparent biological associations observed with abiotic variables measured in the upper sediment layer here may not have been direct, instead representing an integration of other influences. In particular, strong associations previously reported in the literature for both sediment grain size and water current flows with sediment shear strength and water content (Rhoads and Boyer 1982, Hall 1994, Herman et al 1999, Snelgrove and Butman 1999) may reflect the forces of erosion and stabilisation that are acting upon the sediment and infaunal assemblages.

3.4.3.6 The role of erosion and disturbance

Both the sediment water content and shear strength are linked to the erodibility of the sediment surface: sediments with high water content are relatively fluid and more easily resuspended as are sediments with very low shear strength (Rhoads and Boyer 1982, Hall 1994, Paterson and Black 1999). Although biological activity can increase sediment fluidity with consequent reductions in shear strength and increases in water content, it can also lead to increased sediment shear strength; for example, by the presence of microbial mats, without an accompanying reduction in sediment water content (Tolhurst et al 2000). The present lack of any significant correlation between water content and shear strength in the Tamar/Plym system ($r = 0.49$, $p > 0.1$, $n = 9$) suggested that these parameters cannot simply be considered as representing the "erodibility" or physical "stability" of the sediment surface. It is possible that each represents a different mechanism by which the biota and sediment interact, and that assemblages at different depth horizons experience each mechanism on different spatial and temporal scales.

It is likely that both the compaction of the sediment upper layers and their propensity to erode can impact upon both the shallow and deep infaunal assemblages. More motile species such as *Nephtys*, and burrowing organisms such as *Nereis* and amphipods, may minimise the impact of cyclic erosion-deposition events upon their survival within a particular region (Elliott et al 1998). The distribution of sessile species, on the other hand, or species such as *Mya* that have been found to have reduced success with age in re-establishing themselves following re-suspension (St-Onge et al 2007), are likely to be more influenced by periods of sedimentation or sediment re-suspension. Each assemblage requires a suitable substratum to exploit, and needs to maintain connections to the sediment water interface from within that substratum. Since deeper-living organisms may

be protected to some degree from erosion forces that resuspend the surface layers, factors that moderate infaunal movements and construction within the sediment may be more influential in determining deeper assemblage structure. For shallow assemblages, on the other hand, in those areas subject to frequent and prolonged periods of resuspension, patterns between the infauna and other characteristics of the environment, such as sediment shear strength, may well be obscured by the overriding influence of physical disturbance.

Sediment erosion events vary in spatial and temporal scale and may not necessarily occur evenly across entire flats. Whilst to the observer an intertidal flat may appear as a static, homogenous entity (Amos et al 2000, Winberg et al 2007), erosion measures vary at all scales of measurement from centimetres to hundreds of metres (Black and Peterson 1997, Paterson and Black 1999), being influenced by sediment surface topography and local hydrodynamics (Whitehouse et al 2000, Tolhurst et al 2000, Chrisite et al 2000). Spatial and temporal variability in erosion events will promote heterogeneity both in the sediment fabric and in the topography of intertidal flats. However, with increasing depth in the sediment, the influence of lower intensity erosion events will be less apparent (Thistle 1981, Grant 1981, Rhoads and Boyer 1982). Events that are sufficiently strong to disturb deeper sediments are likely to act more evenly at a broader spatial scale across an entire flat.

Where frequent small-scale disturbances are restricted to the shallow sediment depths, the upper sediment layers are likely to experience more frequent local defaunation and local species removal than deeper sediment regions. Subsequent re-colonisation of defaunated patches on intertidal flats can occur over a matter of weeks at small spatial scales (Zajac 2004), but does not always follow a predictable successional pattern (Bolam et al 2004, Zajac 2004), usually

being driven by changes in ambient macrobenthic populations (Zajac 1982). Thus, such local and low-level disturbances can produce mosaic patterns in assemblage structure and abundance that maintain high diversity across larger scales (Grassle and Morse-Porteous 1987).

Whilst the deeper-dwelling assemblages appear to obtain some degree of protection from low-scale physical disturbance by occupying deeper regions of the substratum, they can also play an important role in recolonisation of disturbed sites. Dernie et al (2003) demonstrated that the entire benthic community recovered far quicker when physical disturbance was restricted to the upper 10cm of sediment than when disturbance extended down to 20cm. Following the disposal of dredged material, upward migration of deeper living species plays a role equal to that of horizontal migration of highly mobile species in the recolonisation of the new sediment surface layers (Richardson et al 1977, Mauer et al 1986). Only under extremely deep layers of overburden, greater than 90cm, does vertical migration seem to be inhibited (Mauer et al 1986).

3.4.4 Implications for estuarine management and classification.

Within estuarine soft sediments the effects of anthropogenic activities, such as disposal of dredged material, do not necessarily impact equally upon all components of the biological community. Deeper-dwelling infaunal assemblages potentially represent a longer time-averaged view of the biological response to human activities and physical forcing than do shallow assemblages. Where deeper assemblages are absent despite suitable physico-chemical conditions, managers can focus their investigations on explaining the absence.

Where they are present, deeper assemblages should tell us more about the time-averaged state of sites and provide better links with general abiotic factors. Being

able to identify species that have successfully matured within a site over relatively long time periods of more than 1 year provides more insight into the dynamics working at that point than examining more ephemeral species.

In contrast the species composition of shallow assemblages is more likely to reflect acute levels of disturbance and as such may act as an "early warning" of adverse human impacts upon the estuarine ecosystem.

Characterisation of the deep and shallow assemblages might also lead to better understanding of ecological resilience (*sensu* Peterson et al 1998) within estuaries. Species that experience their environment on different temporal and spatial scales can reinforce the resilience and hence persistence of an ecosystem where disturbance is limited to a specific scale (Peterson et al 1998). Where disturbances occur across many scales, for example influencing deeper communities as well as shallow ones, estuarine ecosystems may be more vulnerable to ecological reorganisation (Peterson et al1998). Treating the infauna as shallow and deep assemblages, rather than as a single entity, allows investigators the opportunity to glean insight into forces influencing ecological resilience and persistence.

The need to characterise estuarine mud- and sand-flats and assess their status arises for many reasons and at different times. Models that can reduce bias introduced by highly seasonal fluctuations in numbers of species and individuals will be more useful. Shallow assemblages have a greater number of species and thus greater variability in patterns of reproduction and settlement. By contrast, deeper assemblages are relatively longer-lived and hence may better meet the needs of estuarine managers for long-term monitoring. Previously, strong relationships between the benthos and environmental forcing variables have rarely been found to be consistent across large scales, such that scaling up between

studies has appeared of limited use (Thrush et al 2005). The approach presented in this study, however, aims to reduce sources of variability by focusing on species that have lower probability of exposure to the frequent, low-level disturbances and fluctuations that can dominate shallow sediment layer dynamics, thereby elucidating more consistent, and ultimately useful, patterns of abiotic-biotic association.

CHAPTER 4

Detecting the effects of the estuarine macrobenthos upon sediment disturbance using novel functional groups

"What do animals do in ecosystems?"

Lawton 1994

4.1 Introduction

This chapter attempts to develop a tool to group the estuarine macrobenthos according to their ability to promote sediment disturbance and the sediment depths at which their activities are realised. This study then investigates whether the macrobenthic activity produces any detectable signals in the abiotic characteristics of the sediment.

The ability of macrobenthic species to act as "ecosystem engineers" (*sensu* Jones et al 1994) is an influential yet highly variable factor in soft sediment dynamics (Wheatcroft et al 1990, Widdows and Brinsley 2002). This factor is often inadequately parameterised within models of sediment processes (Black et al 2002, Reed et al 2006, Gilbert et al 2007). Although the concept that macrobenthic species can physically influence the substratum is not new (Rhoads 1974, Reise 1979), practical generic algorithms relating biotic activity to substratum dynamics are not easily transferred between studies (Wheatcroft and Martin 1996, Paterson and Black 1999, Black et al 2002, Lundkvist et al 2007).

For many years, studies of aquatic soft sediments have identified co-variation between bulk sediment properties and the species composition of the resident macrobenthic community (Moore 1931, Rhoads 1974, Cadee 1976, Myers 1977, Aller 1982). Subsequent research has shown that biologically mediated modification and mixing of soft sediments impacts upon many important sediment processes (Wheatcroft and Martin 1996, Reed et al 2006, Gilbert 2007), including: the erosion potential of intertidal flats (Yingst and Rhoads 1978, Black and Paterson 1997, Andersen 2001a, Reed et al 2006); solute and particle fluxes between sediments and the overlying water bodies (Aller and Yingst 1985, Mortimer et al 1999, Berg et al 2001, Solan et al 2004); and the degradation of organic matter (Anderson and Kristensen 1991, Rysgaard et al 1998, Solan et al

2004); all having consequent feedback implications for the biological community (Paterson and Black 1999, Herman et al 2001, Chapman and Tolhurst 2007). Despite several investigations into the varied physical and chemical manifestations of biological activity, there is neither consensus on how to incorporate species activity into sediment morphodynamic models (Black et al 2002, Widdows and Brinsley 2002), nor on how to measure bioturbation and quantify the relative contribution of each species within a community to overall levels of bioturbation (Black et al 2002, Solan et al 2004).

The inability of sediment process models to incorporate realistic terms for biotic effects is partly accounted for by difficulties in identifying appropriate abiotic variables to characterise biological activity and partly by conflicting definitions of "biotic activity" itself. To address both of the above difficulties the current study develops a novel classification quantifying the sediment disturbance potential of each of the estuarine macrobenthic species sampled. The proposed classification scheme provides an independent estimate of biotic activity that may be used to investigate patterns in abiotic sediment characteristics.

Traditionally, field investigations have sought correlations between abiotic variables and macrobenthic community structure to derive "functional groups" and infer levels of biotic activity. Such studies are hindered by: complex interactions within the biological assemblage and between the biota and environment; the absence of any proof of causality; and an inability to elucidate mechanisms (Snelgrove and Butman 1994). Consequently, observed associations between environmental factors and the structure of the biological assemblages often represent the "ghost of bioturbation past" with limited predictive capacity of future bioturbatory effects. In contrast, small-scale laboratory investigations are often able to document the activity and hence the impact of a species upon its

immediate environment, yet often fail to accurately characterise dynamics observed in the field (Wheatcroft et al 1998, Gilbert 2007).

Whilst many species can be shown to perturb the sediment under laboratory conditions, as yet an unambiguous way to identify their bioturbatory signals in the field is lacking. Similar abiotic patterns in soft sediment structure could arise from an interaction of many biotic and abiotic processes and hence there are many possible explanations for abiotic patterns.

For some investigators, the taxonomic structure of the community is of little interest compared with its functional capacity (Hooper et al 2002), and there has been much discussion over the existence of key species or of functional redundancy within biotic communities (Pearson 2001, Rosenfeld 2002, Widdows and Brinsley 2002, Loreau 2004). The majority of attempts to classify species according to their bioturbatory capacity produce categories that are purely descriptive (Pearson 2001, Jones et al 1994). Yet those that do attempt to quantify effects are often limited in use to a particular subset of the biotic assemblage. For example, models of gallery-forming benthic species (François et al 2002) can only be applied to species that behave in a very prescribed manner. François et al (2002) proposed five bioturbatory categories that could be related to tracer studies of biologically-mediated particle displacement: biodiffusors, gallery diffusors, regenerators, upward conveyors and downward conveyors. Applying these groupings to field investigations of soft sediment dynamics links species activity to mechanisms of particle displacement but does not, however, quantify overall bioturbatory effects nor provide any means to distinguish between species producing similar bioturbatory effects but on different spatial or temporal scales. Categorising species into very precise bioturbatory effect groups such as those proposed by François et al (2002) requires species to have consistent bioturbatory

behaviour. Some species may not fit easily into any single category, and yet broadening the scope of each bioturbatory category does not necessarily make species allocation any easier. For example, some macrobenthic species are known to promote sediment cohesion (Lee and Swartz 1980, Rhoads and Boyer 1982), and yet separation of assemblages into either sediment "stabiliser" or "de-stabiliser" groups provides only two groups of limited use in differentiating intertidal sites: a major difficulty with such simple classification is that many species can participate in more than one process, albeit on different temporal and spatial scales. In addition, some species effects depend not merely upon their own activity but also upon the presence of other individuals around them. For example, polychaete tubes protruding from the sediment surface can disrupt water flow leading to increased turbulence and localised sediment erosion. The presence of large numbers of such tubes can however protect the sediment surface from such localised erosion and intertwined tubes may even promote sediment cohesion (Lee and Swartz 1980, Rhoads and Boyer 1982, Jumars and Nowell 1984).

For the reasons presented above, the present study developed categories that did not depend upon a precise definition of a *mechanism* by which the sediment was disturbed i.e. no discrimination was made on the basis of the precise physical means by which sediment was disturbed nor whether sediment was actually displaced. The sediment disturbance activity of each species was also determined without any reference to sediment stabilisation since the majority of biological activities that directly disrupt the sediment fabric occur irrespective of any additional role a species may play in sediment stabilising processes. Thus, the present work investigated whether the multi-faceted activity of the biotic community could be categorized according simply to the scale of each species' direct effect on sediment disturbance and disruption. Due to the many factors that

can disrupt and alter bioturbatory signals in the field (Paterson and Black 1999), it was important to develop the biological classifications without reference to the abiotic signal the biota were purported to produce. For this reason, the present classification of estuarine macrobenthic community was derived without reference to any of the abiotic data *collected for the present study*. Rather, the study focussed upon estimation of the overall capacity for biologically-mediated, direct sediment disturbance before investigating whether any signal produced by such disturbance activity could be detected in the abiotic characteristics of the sediment.

The body volume of an individual species has previously been shown to relate to its capacity to influence sedimentary mixing processes (Wheatcroft et al 1990, Swift et al 1996, Gilbert et al 2007). However, estimating the sediment disturbance potential of a species by reference to simple body size could lead to large discrepancies between the predicted disturbance effects and those actually observed. For example, according to its body volume, a large filter-feeding organism could be predicted to have a large disruptive effect upon the sediment fabric, but may in fact be relatively sedentary, with little interaction of any great magnitude with the surrounding sediment. In such cases, estimations of sediment disturbance based upon body volume alone could over-estimate the species' contribution to sediment dynamics.

Swift et al (1996) addressed the problem of calculating sediment disturbance by combining body size and sediment ingestion rates to calculate parameters for Wheatcroft et al's (1990) particle displacement model of diffusive sediment mixing. Swift et al's (1996) results showed a promising link between down-core sediment profiles of DDT and mixing by the biota. However, Swift et al's (1996) "aggregate mixing rate" for each sampled depth horizon of the bulk sediment took little

account of the abundance of those species present. Swift et al (1996) did recognise, however, that sediment-mixing processes were not simply influenced by the overall *amount* of bioturbation but also by the *vertical depths* at which the biological activity occurred within the sediment. Chapter 3 of the present study demonstrated that the biota exploit various depth horizons within the sediment. Therefore, not all biological activity can be regarded as occurring only in the upper 2cm of the sediment surface. However, apportioning the bioturbatory effect of species to the depth horizons where the biological activity has actually occurred is difficult. For example, the study of Swift et al (1996) was based upon a diffusive model of sediment mixing processes but "non-local" mixing that occurred in deeper sediment regions could not be modelled as a diffusive process. Thus, Swift et al (1996) were forced to apply extensive adjustments to the calculations of relative bioturbation coefficients to account for the depth at which biological activity occurred.

Instead of considering individual particle movements, the current study utilises *overall* measures of the sediment *volume* disturbed: the volume of sediment space physically occupied by a species and the sediment volume over which it potentially exerts an effect. In addition, rather than forcing the sediment and species to conform to any particular model of activity or particle displacement, the present study combines the volume of sediment directly influenced by a species together with data on its vertical distribution within the sediment to develop sediment disturbance effect (SDE) groups. There was some evidence in Chapter 3 that, when considering abiotic-biotic associations in estuarine soft sediments, assemblages occupying sediment regions deeper than 10cm from the sediment surface should be considered separately to those assemblages occupying

shallower sediment regions. Thus biological-effect groups are applied to each depth assemblage – "shallow" and "deep" – without reference to each other.

Once the biological SDE groups are defined, the relationships between the biological activity and the abiotic patterns characterising the soft sediments are examined. The abiotic variables investigated in this chapter have all previously been linked to both macrobenthic activity and sediment processes such as sediment erosion and bulk mixing. The present study is able to assess the ability of any one of these abiotic factors to truly act as a proxy for levels of bioturbation since the biological effects are estimated independently from measurements of the abiotic sediment characteristics. The relationships between each of the different SDE groups and the sediment characteristics are also investigated to examine whether some SDE groups have a stronger relationship with abiotic patterns than do others. In summary, the study being presented here:

- develops a classification of the estuarine macrobenthos based upon each species' body size and sediment disturbance activities;
- investigates whether overall levels of bioturbation occurring within the sediment could be predicted by consideration of abiotic factors alone; and
- assesses the relationships between the abundance of individuals within the sediment disturbance categories and the observed patterns in the abiotic characteristics of the sediment.

The specific hypotheses investigated are:

- *There are no relationships between the various abiotic parameters used to characterise the sediment*
- *There is no relationship between the distribution of the different functional groups within the estuary and the abiotic characteristics of the sediment*

- *There is no relationship between measures of total biologically-mediated sediment disturbance and the abiotic characteristics of each site.*

4.2 Methods

4.2.1 Biological data

Biological samples were collected from seven sites in the Tamar estuary and two sites in the Plym estuary, south-west England (see Chapter 3, Figure 3.1). At each study site, ten replicate cores (diameter = 15 cm) were collected and then horizontally sectioned into between 7 and 9 parts, depending upon the depth of core penetration into the sediment. For each layer, the mean number of individuals per m^2 of sediment surface area for each species was estimated.

4.2.1.1 Body size measurements

Body sizes of individuals were estimated either directly under low power magnification or indirectly using image analysis software to obtain measurements from scanned images as outlined below:

- Measurements obtained. For each vermiform individual the overall body length and maximum width were measured. For crustaceans and bivalves, the height of each individual was also measured. For amphipods and thalassinind decapods, lengths were estimated by measuring from the rostrum to telson, and heights measured across the carapace and widths as shown in Figure 4.1. These body dimensions were then used to estimate the maximum cross-sectional surface area presented by an individual as it penetrates the sediment and its overall body volume, according to the

scheme shown in Table 4.1, for later use in section 4.2.1.2. Appendages such as palps and tentacles were ignored in measurements.

- Microscopy. Measurements were made using an eyepiece micrometer with 1mm graduations. Measurements from intact individuals were used to derive linear relationships between maximum width and overall length using ordinary least squares linear regression and the statistical software "R" (R Development Core Team 2007). For incomplete specimens, overall length was then estimated from the measured maximum width using the derived linear relationships (see Data CD).

- Image analysis. For vermiform species that were very abundant, savings in time and effort over microscopic measurement were achieved by employing image analysis. Specimens of the same species from the same sample were scanned using a Hewlett Packard ScanJet 6200C. Images were then viewed using Image-Pro Plus v.5 software, which allowed maximum width to be measured manually, and overall length estimated from the linear relationships derived as described above.

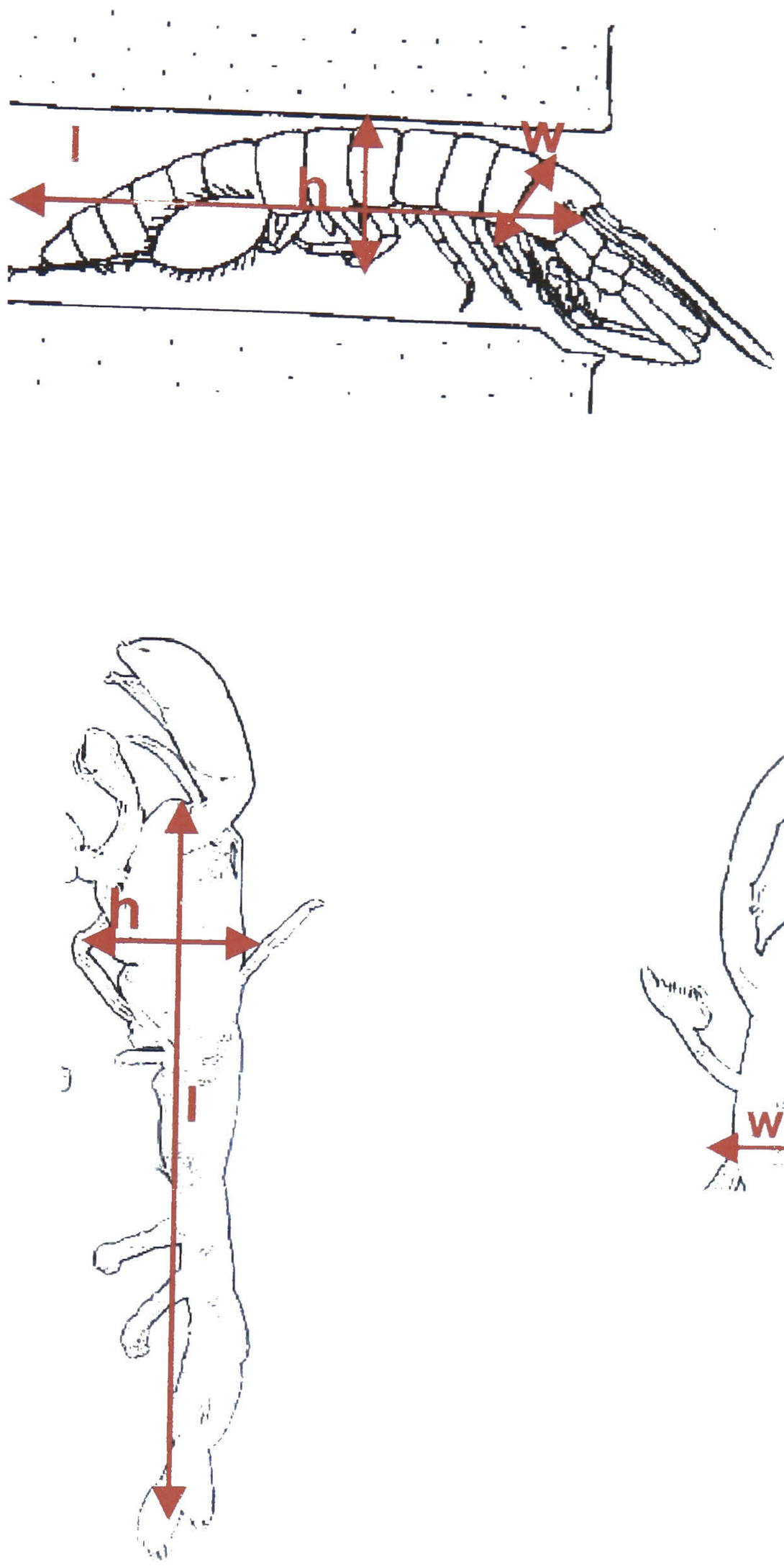


Figure 4.1. Measurements taken from amphipods and thalassinind decapods to allow estimation of cross-sectional surface area and body volumes. l= length, w= width, h= height

Table 4.1. The geometric forms used in approximations of maximum cross-sectional area and body volume for the various taxa for later use in estimating volumes of sediment disturbed.

Taxon	Cross-sectional area estimate	Volume estimate
Polychaeta	Circle	Cylinder
Oligochaeta	Circle	Cylinder
Bivalvia	Ellipse	Ellipsoid
Retusidae	Circle	Cylinder
Hydrobiidae	Circle	Cone
Pyramidellidae	Circle	Cone
Nemertea	Circle	Cylinder
Sipunculidea	Circle	Cylinder
Callianassa	Ellipse	Ellipsoid
Amphipoda	Ellipse	Ellipsoid
Portunidae	Rectangle	Cuboid

4.2.1.2 Species' potential sediment disturbance

A literature search was undertaken to collect data for each species sampled in order to provide a measure of:

- the frequency and distances moved by organisms in routine activities;
- the extent to which feeding behaviour would disturb the surrounding sediment;
- the extent and frequency of any burrowing activity; and
- any studies on sediment reworking and bioturbation potential.

Information derived from the literature search was combined with data from Chapter 3, on species depth ranges within the sediment, to identify likely mode and extent of interaction between an individual of a given species and the surrounding sediment. Associated data were used to estimate the potential:

- volume of sediment space occupied by the species and its burrow / tube systems while at rest; and

- volume of sediment directly disturbed by the species in its routine activities i.e. feeding, irrigation, migration and the relative impact upon both the sediment surface layers and the body of the sediment.

From this information, the total volume of sediment space influenced directly by each species was estimated, and this volume partitioned into an effect upon the sediment surface layers and an effect upon the deeper sediment layers.

It was shown in Chapter 3 that for several longer-lived species such as *Scrobicularia plana* and *Nephtys indet.* there was a tendency for body size to increase with occurrence in deeper sediments. Thus, when calculating the measures of sediment disturbance potential for each species, the influence of changing body size, with deeper sediment exploitation, upon the estimates of sediment disturbed was also examined.

4.2.1.3 Sediment disturbance effect (SDE) groups

Using the sediment disturbance potential of each species as defined above, categories of sediment disturbance effect were derived by evaluating:

- the magnitude of the overall total potential sediment disturbance; and
- the ratio between the magnitudes of disturbance effected upon the upper sediment layer and disturbance effected within deeper sediment horizons.

Boundaries between categories were defined by examining plots of species' disturbance effect upon surface sediment layers against effect upon deeper sediment regions and Figure 4.2 below provides an example of such plots. From

this information, distinctions were made according to whether species clearly had greatest impact on the sediment surface, deeper regions or a similar impact upon both. Species were then allocated into non-overlapping SDE groups under Scheme 1 as shown in Table 4.2.

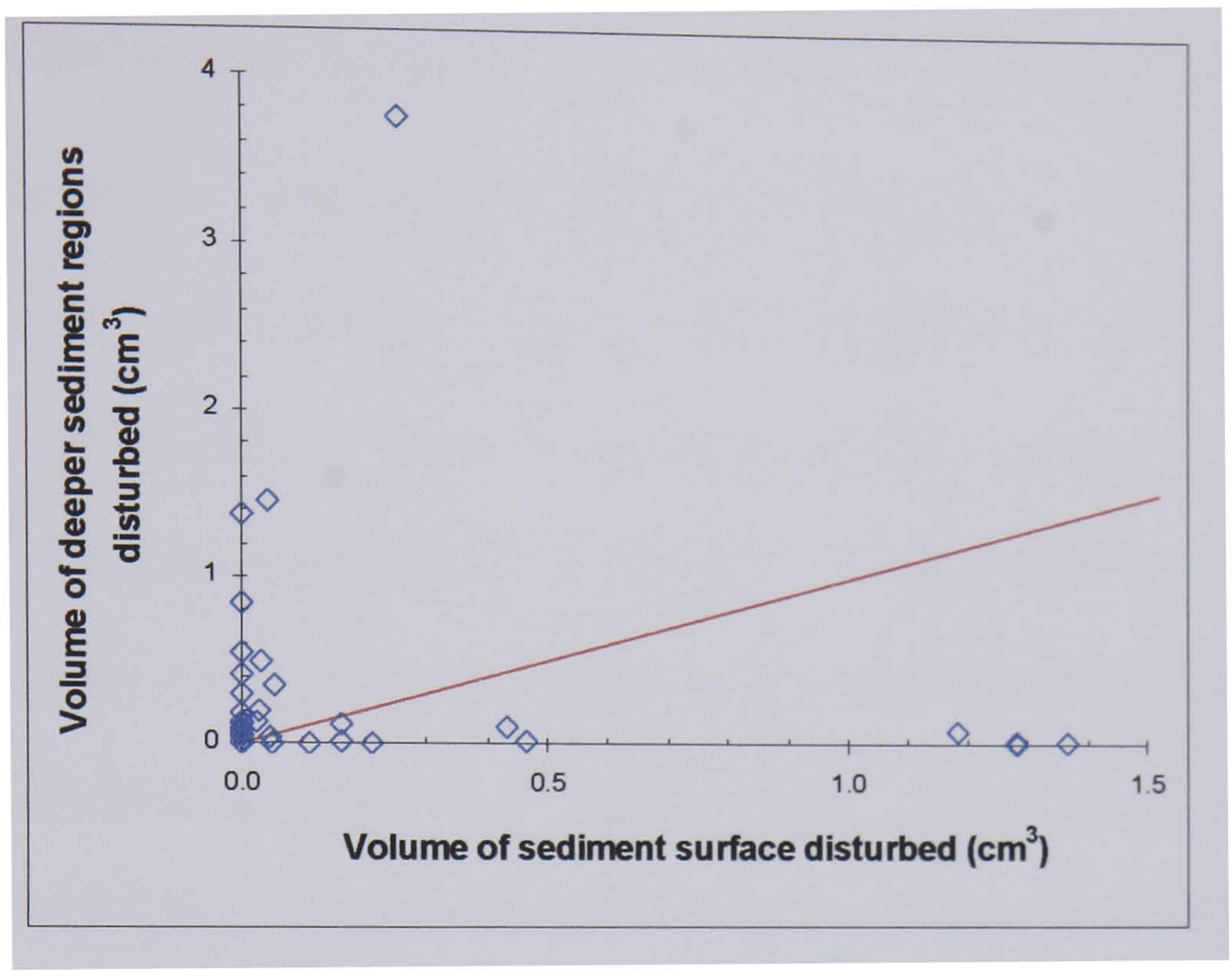


Figure 4.2. An example plot of volume of sediment disturbed (cm^3) by species at the surface against volume disturbed (cm^3) by same species at deeper sediment regions. Plots were considered, together with data on overall sediment effects when developing boundaries for SDE groups

Table 4.2. Scheme 1 of SDE groups applied to both deep and shallow assemblages

Total volume (V) of sediment disturbed across all depths (cm^3)	**Effect greatest on surface sediment**	**Equal effect on surface and deeper regions**	**Effect greatest on sediment regions below the surface**
V ≤ 0.5	A1	B1	C1
>0.5 V ≤ 1.5	A2	B2	C2
> 1.5 V ≤ 5	A3	B3	C3
> 5 V ≤ 20	A4	B4	C4
V >20	A5	B5	C5

It was shown in Chapter 3 that when investigating abiotic-biotic relationships the overall biotic assemblage could be treated as two separate assemblages, one "shallow" occupying the upper 10cm of the sediment and one "deep". Scheme 1 was applied to both shallow and deep assemblage data separately to provide new datasets of SDE group abundance for each depth horizon at each site.

Although Scheme 1 was applied to both shallow and deep assemblages, the position of an individual during sampling determined whether any potential disturbance effect was treated as occurring within shallow horizons or deeper regions. In addition, Scheme 1 did not allow for the fact that some species were restricted to only the upper 4cm whilst others exploited regions deeper than 10cm below the sediment surface (see Figure 3.5). Thus, a second classification scheme was devised, Scheme 2, that incorporated the potential of a species to:

- only exploit sediment regions shallower than 4cm;
- only exploit sediment regions shallower than 10cm; and
- also exploit regions deeper than 10cm from the sediment surface.

Whilst Scheme 1 employed the mean values of the volume of sediment disturbed, for some species there was a trend of increasing body size with depth (discussed in Chapter 3). Thus, Scheme 2 was based upon the maximum potential of a species to disturb or disrupt the sediment. Table 4.3 outlines the SDE groups under Scheme 2.

Table 4.3. The SDE groups into which species were allocated under Scheme 2, allowing for differential exploitation of the sediment depths e.g. distinguishing between two species that both have greatest effect on the sediment body but where only one species also exploits deeper regions.

Total volume (V) of sediment disturbed across all depths (cm^3)	**Effect greatest on upper 4cm**	**Equal effects on surface and sediment body.**	**Effect greatest on sediment body.**	**Equal effects on surface and sediment body.**	**Effect greatest on sediment body.**
	Exploitation limited to upper 4cm	Exploitation limited to upper 10cm	Exploitation limited to upper 10cm	Exploitation extends >10cm	Exploitation extends >10cm
V ≤0.5	1a	2a	3a	4a	5a
0.5 < V ≤1.5	1b	2b	3b	4b	5b
1.5 < V ≤5	1c	2c	3c	4c	5c
5 < V ≤20	1d	2d	3d	4d	5d
V ≤20	1e	2e	3e	4e	5e

4.2.1.4 Overall potential to disturb the sediment

The bioturbation potential of each species was also calculated according to the relationships proposed by the earlier studies of Wheatcroft et al (1990), who estimated bioturbation form theoretical models of the distances and frequency particles were moved by deposit feeding organisms, and Gilbert et al (2007), who studied sediment disturbance in laboratory experiments, as follows:

- bioturbation is proportional to (body length)$^{4.25}$ (Wheatcroft et al 1990); and
- bioturbation effect is approximated by the body volume x 0.35. (Gilbert et al 2007)

Subsequently the overall total sediment disturbance potential of the entire benthic assemblage at each sample site was then estimated by:

- summation of all individuals' sediment disturbance potential based upon Wheatcroft et al's (1990) estimate;
- summation of all individuals' sediment disturbance potential based upon Gilbert's estimate (Gilbert et al 2007); and
- summation of all individuals' sediment disturbance potential based upon the values used to assign each species to an SDE group.

4.2.2 Abiotic characterisation of the sediment

At each site, samples were obtained for the abiotic characterisation of sediments. The precise methodology is given in section 3.2.2.2. In summary:

- a portable annular flume was employed to obtain measurements of the sediment critical erosion threshold and sediment erodibility rates;
- the undrained shear strength of the sediment at various depths below the sediment surface was measured using a 19mm hand held shear vane;
- the depth of the Redox Potential Discontinuity (RPD) and extent of burrowing into the sediment were recorded; and
- three cores were retrieved from each site for investigation into down-core sediment profiles of the following parameters:

  - sediment water content;
  - percentage of sediment particles <63μm in diameter (% fines);
  - concentration of extracellular polymeric substances (EPS);
  - percentage total organic carbon (TOC); and

- concentration of chlorophyll *a* (Chl *a*).

To identify common patterns in the distribution of the above variables within the bulk sediment, the data from the down-core profiles of each pair of variables were compared using Pearson's correlation coefficient.

The down-core profiles of sediment particle size were also used to approximate the depth of a well-mixed upper sediment layer where extensive sediment reworking can promote homogeneity of the sediment fabric (Rhoads 1974). For this purpose, the maximum extent of this layer was assessed as the depth horizon at which the percentage of coarse sediment particles had the greatest rate of increase.

In addition, the down-core profiles of Chl *a* concentration were used to estimate parameters that describe sediment-mixing processes as outlined in the section below.

4.2.2.1 Sediment mixing coefficients determined from Chl *a* down-core profiles

The rate of sediment mixing over the entire depths sampled was approximated using diagenic equations from Rice and Rhoads (1989). Assuming that at intertidal sites lateral mixing of sediment occurs at all sites, Rice and Rhoads (1989) suggested that particulate organic matter in the sediment surface layer can be treated as having a homogenous distribution that is relatively insensitive to sedimentation rates and hence, the sediment surface levels of particulate organic matter can be treated as being in steady state. This allows a simplification of diagenic models by permitting sedimentation rates to be ignored and the resultant

equation was employed in the current study to model the vertical sediment mixing process for Chl *a*, as a proxy for fresh organic matter, at each site.

The volume, G_x, of Chl *a* (cm^3) at a depth x (cm) below the sediment surface is given by

$$G_x = G^* + G_0 e^{-ax} \qquad \text{Equation 4.1.}$$

Where G* is a non negative asymptotic minimum value of Chl *a*, G_0 is the volume of Chl *a* at the sediment surface and a is the decay constant given by:

$$a = \sqrt{\frac{k}{D_b}} \qquad \text{Equation 4.2.}$$

k is the degradation rate of Chl *a* in intertidal muds (yr^{-1}), and Db is the diffusive mixing rate ($cm^2\ sec^{-1}$).

A value of k=0.06 yr^{-1} was used to calculate Db for each site (Rhoads and Rice 1989).

Non-linear least squares regression was then used to fit the equation to the data for Chl *a* for each site, with G* set to the minimum value of Chl *a* at that site and employing "R" statistical software (R Development Core Team 2007). From the equation of the fitted line, k/Db was obtained and the value used for inter-site comparison of diffusive mixing.

Whilst there are many alternative models of sediment mixing that could have been fitted to the data (Boudreau and Marinelli 1994, Boon and Duinveld 1998, Reed et

al 2006), for the reasons described in section 4.1, the present study required a means to compare the observed patterns of Chl *a* concentration in the sediment rather than seeking to elucidate the *mechanisms* producing the observed patterns. The current study sought links between the *overall end effect* of biota upon observed abiotic patterns in sediment characteristics, i.e. a mathematical description of the pattern, not an accurate description of the sediment mixing processes that led to the observed pattern. Hence a simple model was employed rather than a more complex one.

In addition to estimating k/Db from the down-core profiles of organic matter, Rice and Rhoads (1989) proposed an equation to estimate the amount of particulate organic matter that is available at depth (INP, equation 3 below). This same equation was used to estimate the Chl *a* (as a proxy for organic matter) at depths below 10cm (INP) as follows:

$$INP = \left(G_d - G^*\right) \times \sqrt{\left(k \times D_b\right)} \qquad \text{Equation 4.3}$$

Where G_d is the Chl *a* at the 10cm depth in the sediment

4.2.3 Statistical analyses

4.2.3.1 Abiotic variables

All abiotic variables were checked for univariate normality by examining skew and quantile-comparison plots (Crawley 2005). Where necessary, data were transformed to approximate normality. The appropriate transformation was selected by using maximum likelihood to estimate the power transformation using the "box.cox.powers" routine in R (R Development Core Team 2007), as

recommended by Fox (2002). Subsequently, covariance in the abiotic dataset was examined using Pearson's coefficient.

Flemming and Delafontaine (2000) have suggested that many bulk sediment abiotic parameters have strong relationships with the water content of the sediment. Where such strong associations with the sediment water content were found, they were investigated further using Ordinary Least Squares linear regression.

4.2.3.2 Abiotic – biotic associations

The datasets were interrogated for relationships between bioturbatory abilities of species assemblages and abiotic characteristics of the sediments.

4.2.3.2.1 Relationships between the macrobenthic assemblage structure and the abiotic variables

Five different methods (see below) of using the biological data to estimate overall sediment disturbance levels were investigated. The relationship between the abiotic dataset and the biotic assemblage structure using each of the five methods in turn was assessed using the RELATE routine from PRIMER software (Clarke and Gorley 2001). Thus, for both shallow and deep assemblages the RELATE test was employed to consider the strength of relationships between each of the following:

- species abundance;
- species abundance summed for SDE groups under Scheme 1;
- species abundance summed for SDE groups under Scheme 2;
- species abundance x (0.35 x mean body volume);

- species abundance x (mean body length $^{4.25}$);

and an abiotic dataset containing the parameters:

- sediment mixing depth;
- Chl *a* mixing parameter k/Db;
- Chl *a* available at sediment depths below 10cm (INP);
- shear strength of the sediment surface;
- mean shear strength over the whole sediment depth sampled;
- water content of the sediment surface layer;
- sediment erosion rate;
- maximum depth of the Redox Potential Discontinuity (RPD); and
- mean depth to which burrowing extended.

The value of 0.35 times mean body volume was used to compare with the findings of Gilbert et al (2007), whilst mean body length to the power 4.25 was suggested by Wheatcroft et al (1990) to be proportional to the organism's potential to promote biodiffusion.

4.2.3.2.2 Relationship between the various measures of the overall biotic sediment disturbance effect and the abiotic variables

The relationship between the abiotic variables and the overall total sediment disturbance potential of the entire benthic assemblage was investigated using Spearman rank correlations between the biotic effect estimated by:

- summation of all individuals' sediment disturbance potential based upon Wheatcroft's estimate (Wheatcroft et al 1990);
- summation of all individuals' sediment disturbance potential based upon Gilbert's estimate (Gilbert et al 2007); and
- summation of all individuals' sediment disturbance potential based upon the values used to assign each species to an SDE group;

and the same abiotic variables used in the RELATE tests, mentioned above.

4.2.3.2.3 Individual SDE groups and the abiotic characteristics of the sediment.

The relationship between changes in the abundance of individuals in each SDE group with changes in the abiotic characteristics of the sediment was investigated using Spearman Rank Correlation. This method was selected since the biological data did not approximate to univariate normality.

4.2.3.2.4 Individual species abundance and the abiotic characteristics of the sediment

To assess whether any single species had a dominant effect upon the bioturbatory signal, or upon the apparent relationships between SDE groups and the abiotic variables, Spearman Rank correlations were also performed on species abundance against each individual abiotic variable. The correlations could not be performed for many of the individual species due to the low number of sites at which they were found. A pragmatic decision was taken that where species occurred at fewer than seven sites no correlation tests would be performed due to the limitations of making any meaningful deductions from such a small dataset. In such cases, species were aggregated to family level, and where the family occurred at seven or more sites, correlations with abiotic data were investigated. Although correlations performed on data from only seven sites would have little statistical power it was felt to be useful in exploration of relationships.

4.3 Results

4.3.1 Categorisation of the biological disruption of the sediment

4.3.1.1 Species body size

Mean and maximum body lengths for each species together with derived values for body volume, estimated volumes of surface sediment disturbed and the estimated volume of the sediment matrix disturbed are presented in Table 4.4 (see Appendix 2 for full details of calculations). Some species showed trends of increasing body size with sediment depth (e.g. *Nephtys* indet., *Nereis* indet *and S. plana*). For these species, the sediment disturbance volumes were re-calculated for "deep" and "shallow" assemblages separately. No subsequent alteration in the species composition of each individual effect category was observed for shallow assemblages. For deep assemblages three species did change category

- *Nereis* indet changed from being the sole member of category "B3" to the sole member of category "B4" under Scheme 1.
- *Nephtys* and *Scrobicularia* changed from being the only two species in category "C3" to the only two in category "C4" under Scheme 1.

4.3.1.2 Overall sediment disturbed by assemblages

The estimations of overall sediment disturbance effects according to body volume (Gilbert et al 2007), body length (Wheatcroft et al 1990) or total volumes of sediment disturbed by each species are summarised in Table 4.5 (see Data CD

Species	mean length	biovolume	Db = 0.35*biov	Db = L4.25	Depth range of species occurrence	Volume disturbed	Volume disturbed at sediment surface	Volume disturbed in deeper areas	Max length	Max volume disturbed overall	Scheme 1	Scheme 2
	cm	cm^3	cm^3	cm^3	cm	cm^3	cm^3	cm^3	**cm**	cm^3	Category	Category
Nemertea	0.31	0.0005	0.00018	0.0069	0-10	**0.0271**	0.0013	0.0258	**0.41**	0.04	c1	5a
Sipunculidae indet	0.98	0.0021	0.00074	0.9177	4-20	**0.1769**	0.1607	0.0162	**1.74**	0.29	a1	5a
Polyc indet	0.69	0.0008	0.00029	0.2041	0-8	**0.0843**	0.0000	0.0843	**1.48**	0.29	c1	4a
Phyllodoce indet.	1.19	0.0030	0.00106	2.1020	0-4	**0.3020**	0.0000	0.3020	**2.60**	2.38	c1	1c
Syllidae indet	0.36	0.0001	0.00005	0.0130	2-4	**0.0150**	0.0000	0.0150	**0.36**	0.01	c1	1a
Exogone indet.	0.36	0.0001	0.00005	0.0130	2-5	**0.0150**	0.0000	0.0150	**0.36**	0.01	c1	1a
Nereis diversicolor	3.88	0.3100	0.10850	318.0789	0-20	**3.5977**	1.8859	1.7118	**14.34**	320.03	b2	3e
Nephtys hombergii	1.81	0.0289	0.01012	12.3615	0-20	**2.9796**	0.0000	2.9796	**10.47**	178.04	c3	5e
Spionidae indet	0.82	0.0007	0.00026	0.4302	0-8	**0.2171**	0.2112	0.0059	**2.03**	1.39	a1	2b
Polydora indet	1.22	0.0043	0.00151	2.3121	0-8	**0.4802**	0.4661	0.0142	**2.38**	1.88	a1	2c
Tharyx indet	0.82	0.0041	0.00145	0.4214	0-6	**0.1338**	0.0669	0.0669	**0.00**	0.32	b1	2a
Pseudopolydora indet	1.22	0.0043	0.00151	2.3121	0-4	**0.4802**	0.4661	0.0142	**2.38**	1.88	a1	2b
Pygospio elegans	0.59	0.0004	0.00015	0.1085	0-15	**0.1125**	0.1103	0.0022	**1.87**	1.16	a1	2b
Streblospio shrubsolii	0.82	0.0007	0.00026	0.4302	0-15	**0.2171**	0.2112	0.0059	**2.03**	1.39	a1	3b
Magelona indet.	1.13	0.0006	0.00020	1.7001	0-2	**0.2171**	0.2112	0.0059	**2.03**	1.39	a1	2b
Cirratulidae	0.67	0.0013	0.00044	0.1870	0-25	**0.1105**	0.0553	0.0553	**1.97**	0.32	b1	3a
Caulleriella zetlandica	**head only treat as Cirratulidae**					**0.1105**	0.0553	0.0553	**0.00**	0.32	b1	3a
Chaetozone indet.	0.81	0.0025	0.00088	0.4084	0-25	**0.1328**	0.0664	0.0664	**1.90**	0.31	b1	3a
Aphelochaeta indet.	0.82	0.0041	0.00145	0.4214	0-6	**0.1338**	0.0669	0.0669	**1.95**	0.32	b1	3a
Cossura indet.	0.30	0.0001	0.00004	0.0059	0-8	**0.0519**	0.0000	0.0519	**0.79**	0.17	c1	2a
Capitellidae	0.42	0.0013	0.00044	0.0241	0-6	**0.0864**	0.0000	0.0864	**0.73**	0.14	c1	4a
Heteromastus filiformis	2.37	0.0075	0.00264	39.2156	0-15	**0.4110**	0.0000	0.4110	**5.12**	0.00	c1	5b
Mediomastus indet.	1.83	0.0027	0.00095	12.8934	0-2	**0.3023**	0.0000	0.3023	**1.83**	0.30	c1	4a
Galathowenia indet.	0.40	0.0001	0.00003	0.0206	0-2	**0.0509**	0.0505	0.0004	**0.52**	1.26	a1	1b
Melinna palmata	1.86	0.0306	0.01072	13.9775	0-25	**0.2794**	0.1630	0.1163	**3.95**	2.04	b1	3b
Ampharete indet.	0.99	0.0078	0.00272	0.9541	0-20	**0.8489**	0.0461	0.0388	**1.84**	0.39	b1	3a

Table 4.4. The body lengths, volumes and estimated sediment disturbance for all species. Db=0.35*biovolume is estimated volume disturbed based upon Gilbert et al (2007), $Db = L^{4.25}$ based upon estimates of sediment distubed according to Wheatcroft et al (1990), other volumes as derived in this chapter (see Appendix 2 for methodology)..

Species	mean length	biovolume	Db = 0.35*biov	Db = L4.25	Depth range of species occurrence	Volume disturbed	Volume disturbed at sediment surface	Volume disturbed in deeper areas	Max length	Max volume disturbed overall	Scheme 1	Scheme 2
	cm	cm^3	cm^3	cm^3	cm	cm^3	cm^3	cm^3	cm	cm^3	Category	Category
Lanice conchilega	3.20	0.3379	0.11826	140.2450	6-8	**0.8447**	0.0000	0.8447	**3.20**	0.84	c2	2b
Manayunkia aestuarina	0.20	0.0001	0.00002	0.0010	0-10	**0.0026**	0.0000	0.0026	**0.30**	0.01	c1	2a
Oligochaeta indet	**head only treat as Tubificoides**					**0.1138**	0.0000	0.1138	**0.00**	0.59	c1	4b
Paranais littoralis	**head only treat as Tubificoides**					**0.1138**	0.0000	0.1138	**0.00**	0.59	c1	4b
Tubificoides indet	0.69	0.0009	0.00032	0.2117	0-25	**0.1231**	0.0000	0.1231	**1.94**	0.59	c1	5b
Copepoda	0.22	0.0009	0.00031	0.0015	4-20	**0.0087**	0.0000	0.0087	**0.66**	0.20	c1	5a
Portunidae juvenile	0.37	0.0138	0.00481	0.0114	0-20	**0.3968**	0.3226	0.0743	**1.30**	7.59	a1	5d
Portunidae megalopa	0.37	0.0197	0.00688	0.0148	0-20	**0.3968**	0.3226	0.0743	**1.30**	0.00	a1	5d
Ampelisca indet.	0.75	0.0452	0.01581	0.2928	0-20	**0.1852**	0.0000	0.1852	**1.10**	0.52	c1	3b
Corophium indet	0.55	0.0073	0.00257	0.0776	0-6	**0.0883**	0.0531	0.3530	**1.20**	0.68	b1	2b
Cumacea indet	0.35	0.0011	0.00037	0.0120	0-2	**0.0105**	0.0000	0.0105	**0.91**	0.05	c1	1a
Crangon crangon	0.72	0.0147	0.00516	0.2476	0-2	**0.0410**	0.0000	0.0410	**0.92**	0.11	c1	1a
Calianassa	3.70	7.7854	2.72489	259.9306	10-15	**31.5308**	0.0000	31.5308	**3.80**	31.53	c5	5e
Hydrobia ulvae	0.27	0.0016	0.00056	0.0037	0.25	**1.2842**	1.2800	0.0042	**0.00**	1.28	a2	3b
Pyramellid gastropod	0.40	0.0015	0.00052	0.0212	2-8	**1.2826**	1.2800	0.0026	**0.43**	1.28	a2	2b
Tragula fenestrata	0.30	0.0012	0.00043	0.0057	0-6	**1.2884**	1.2800	0.0084	**0.00**	1.29	a2	2b
Retusa indet	0.12	0.0008	0.00028	0.0001	0-20	**1.2846**	1.2800	0.0046	**0.00**	1.28	a2	3b
Bivalve indet	0.40	0.0200	0.00700	0.0193	0-15	**0.2286**	0.0294	0.1992	**0.88**	2.24	c1	3c
Nucula nitidosa	0.18	0.0020	0.00071	0.0007	0-2	**1.3744**	0.0000	1.3744	**0.22**	1.37	c2	1b
Thyasira indet.	0.66	0.1403	0.04910	0.1688	2-10	**1.3744**	0.0000	1.3744	**0.93**	1.37	c2	1b
Mysella bidentata	0.30	0.0091	0.00318	0.0063	15-25	**1.3744**	0.0000	1.3744	**0.32**	1.37	c2	1b
Parvicardium exiguum	0.25	0.0070	0.00245	0.0028	2-10	**0.5195**	0.0314	0.4880	**0.25**	0.52	c1	2a
Cerastoderma edule	0.53	0.1002	0.03507	0.0668	0-15	**1.4962**	0.0440	1.4522	**3.50**	6.70	c2	3d
Phaxus pellucidus	3.66	0.6493	0.22724	249.3508	0-2	**0.6493**	0.0000	0.5459	**3.66**	0.65	c2	1b
Macoma balthica	0.33	0.0129	0.00452	0.0092	0-4	**1.2573**	1.1827	0.0745	**0.51**	1.51	a2	1c
Scrobicularia plana	1.21	0.4359	0.15255	2.2246	0-15	**4.0096**	0.2537	3.7559	**3.34**	43.60	c3	3e
Abra alba	0.23	0.0095	0.00333	0.0019	8-10	**1.3744**	1.3649	0.0095	**0.25**	1.37	a2	3b
Mya indet.	0.33	0.0102	0.00357	0.0085	0-4	**0.1589**	0.0243	0.1343	**0.62**	0.41	c1	1a

Table 4.4 contd. The body lengths, volumes and estimated sediment disturbance for all species. Db=0.35*biovolume is estimated volume disturbed based upon Gilbert et al (200 Db = $L^{4.25}$ based upon estimates of sediment distubed according to Wheatcroft et al (1990), other volumes as derived in this chapter (see Appendix 2 for methodology)..

for full dataset). Whilst the two measures of bioturbation based upon simple body size were highly correlated with each other ($r=0.95$, $p<0.001$), relationships with estimates derived from the volumes of sediment directly disturbed by a species were weaker($r=0.42$ with (biovolume x 0.35, $p=0.27$), $r=0.35$ with $(\text{body length})^{4.25}$, $p=0.35$).

Table 4.5. Comparison of estimated volume of sediment disturbed by entire community based upon the mean abundance of each species multiplied by either (i) species biovolume x 0.35 (Gilbert et al 2007), (ii) species body length (L) to power 4.25 (Wheatcroft et al 1990) or (iii) the volume of sediment directly disturbed by species routine activities, as assessed here.

Site	biovolume x 0.35 (cm^3)	$L^{4.25}$ ($cm^{4.25}$)	Volume of sediment disturbed (cm^3)
1	18	14156	5880
2	205	587109	8368
3	12	11641	2971
4	94	77845	7535
5	23	25948	8688
6	65	63540	9758
7	109	229616	16297
8	115	305352	9828
9	95	233275	14419

4.3.2 Abiotic characterisation of the sediment

The values recorded for sediment critical erosion threshold, erosion rate, shear strength and depth of the RPD are given in Table 4.6. The relationships between these variables and the other abiotic parameters are addressed in section 4.3.2.2.

Bale et al (2006) demonstrated that for the sites sampled in this study, the critical erosion thresholds of the sediments were directly proportional to the sediment bulk density and water content. As a result, only the sediment water content was included in further analyses here, rather than including the sediment critical erosion threshold.

Site	Critical Erosion Threshold ($m\ s^{-1}$)	Erosion rate ($kg\ m^{-2}\ s^{-1}$)	Water Content of Surface 2cm layer (%)	Shear Strength of Surface 2cm layer (measured as torque)	Mean shear strength over whole core depth (measured as torque)	Mean depth of RPD (cm)
1	0.1301	0.00036	46.8	0.45	2.109	4
2	0.0652	0.00021	62.0	0.45	2.036	6.8
3	0.202	0.00056	34.2	1.4	8.727	2.7
4	0.186	0.00186	36.7	0.50	17.571	2.5
5	0.0963	0.00255	54.2	0.27	1.070	4
6	0.1813	0.00173	37.4	0.45	1.636	2
7	0.146	0.00018	43.7	0.00	6.117	3
8	0.1011	0.00027	53.0	0.09	6.701	3
9	0.1229	0.00017	48.3	0.00	8.727	2

Table 4.6. Critical erosion thresholds, erosion rates, water content, shear strengths and mean RPD depth for sediments at each sample location.

4.3.2.1 Down-core profiles of abiotic parameters.

Initial examination of data for each of the sediment abiotic variables revealed that distributions of Chlorophyll a (Chl *a)*, extracellular polymeric substances (EPS), shear of the sediment, and TOC did not approximate univariate normality. Thus these variables were $\log_{10}$ transformed, with the exception of TOC for which the presence of zero values necessitated a $\log_{10}$ (x+0.09) transformation.

All down-core profiles of abiotic variables were highly variable between sites. For most variables intra-site variability was also evident. The between core variability was most evident for measurements of TOC as shown in Figure 4.3.

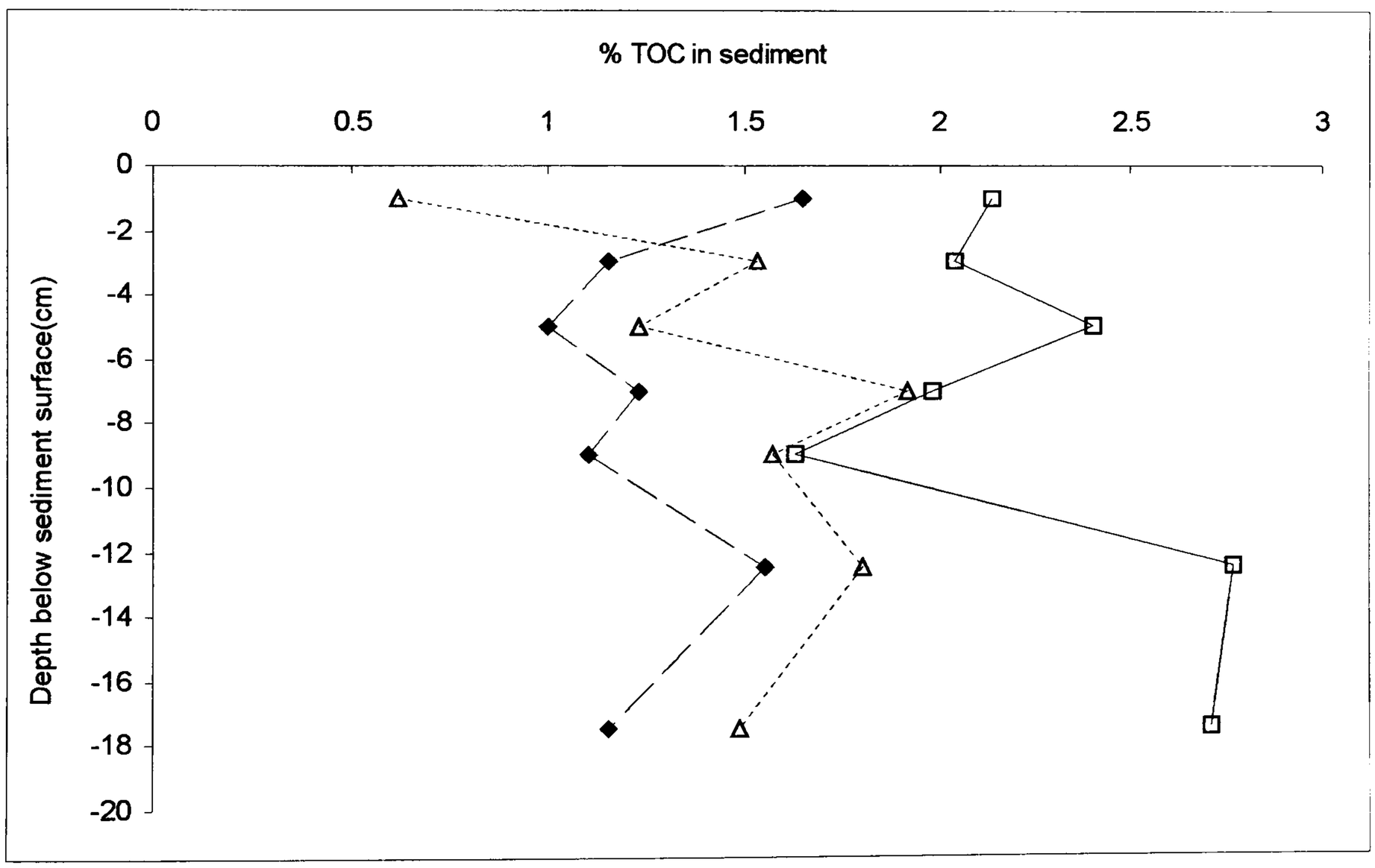


Figure 4.3. Plots of the % TOC at depths below the sediment surface for 3 cores from site 6 (Looking Glass Point). Each core is represented by a different symbol.

TOC, Chl *a*, EPS and sediment shear strength were found to have significant relationships with the corresponding value for sediment water content at that depth

and hence apparent relationships were further investigated using Ordinary Least Squares Linear Regression:

- Sediment water content and TOC: R^2=0.47, p<0.001, n=53

  [*TOC = (0.038 x water) – 0.37*];

- Sediment water content and Chl a: R^2=0.42, p<0.001, n=73

  [*Chl a = (2.2198 x water) - 1.8357*];

- Sediment water content and EPS: R^2=0.49, p<0.001, n=73

  [*EPS = (2.2198 x water) - 1.8357*];

- Sediment water content and sediment shear strength: R^2 = 0.44, p<0.001, n=53

  [*Shear = (-0.54 x water) + 28.9*].

Only Chl *a* and EPS revealed a consistent pattern of decrease in concentration with increasing sediment depth. Chl *a* and EPS were highly correlated with each other (r=0.73, p<0.05, n=73) and each also had a strong correlation (p<0.05) with sediment shear strength (r=-0.72, -0.64, n=53).

4.3.2.1.1 Chl *a* down-core profiles and sediment mixing

The strong trend of decreasing Chl *a* concentration with sediment depth allowed lines to be fitted well by the equation proposed by Rice and Rhoads (1989) (Figure 4.4). The derived values for k/Db and the available Chl *a* at depths over 10cm (INP) are shown in Table 4.7.

Table 4.7. The values of k/Db (mixing of Chl *a*) and INP (Chl *a* available at depths below 10cm) for each site derived from the lines fitted to the values of Chl *a* for various depths within the sediment, together with the approximate extent of the "well mixed" layer into the sediment.

Site	1	2	3	4	5	6	7	8	9
k/Db	0.1	0.06	0.18	0.07	0.19	0.08	0.07	0.10	0.03
INP	4.50	8.42	1.45	7.06	1.25	5.69	6.81	4.43	16.14
Depth of well mixed layer (cm)	6	8	6	4	6	6	4	4	6

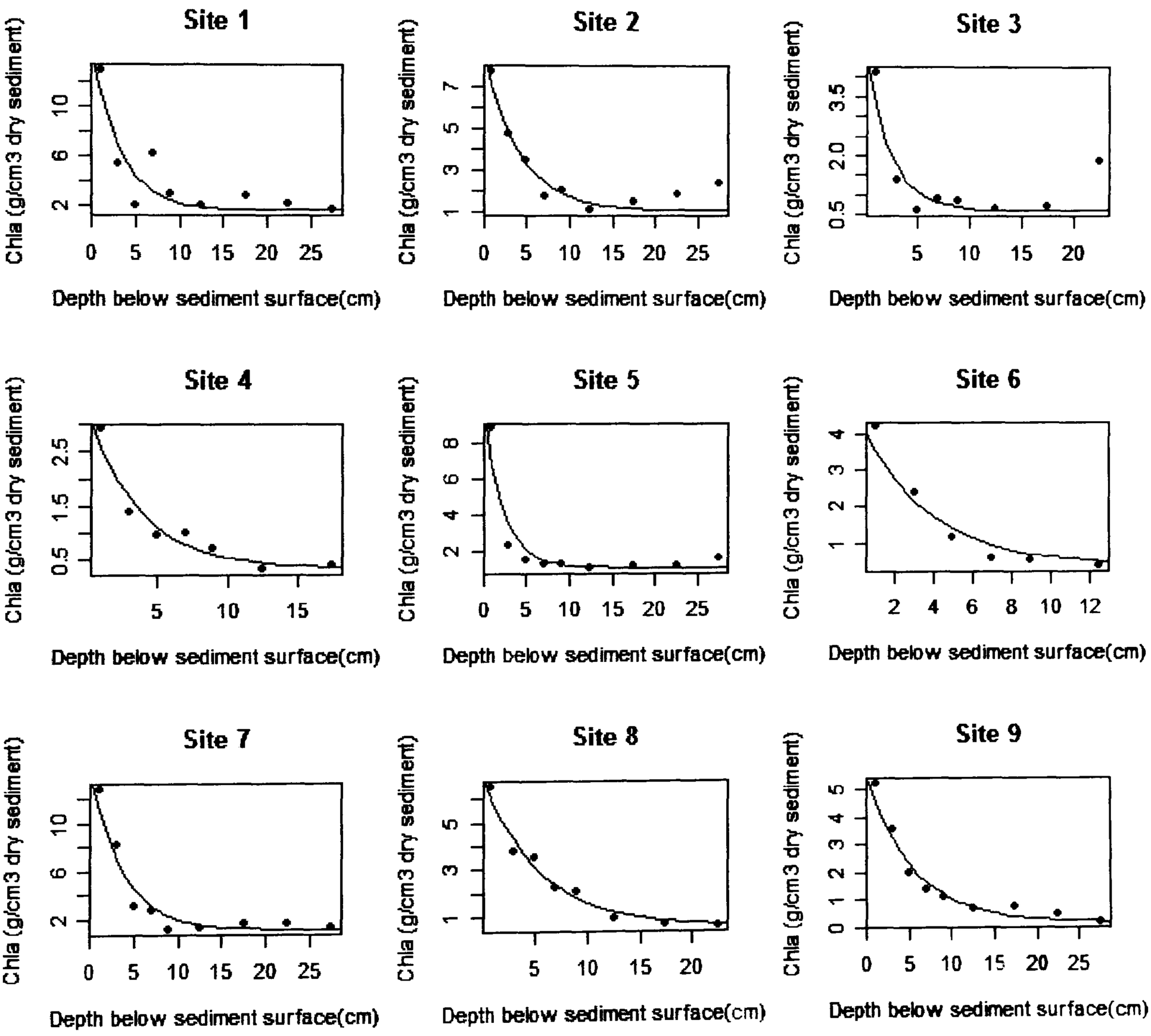


Figure 4.4 Plots of volume of Chl *a* (g/cm^3 dry sediment) against depth (cm) within the sediment for each sample site. The solid line is fitted using Equation 4.1 and all were significant at $p<0.01$ (see data cd for regression equations and significance values)

The profiles of the percentage of fine particles (<63 μm) within the sediment had poor correlations with the other parameters ($r<0.4$, $p>0.05$ see Data CD). However, the depth to which mixing appeared to produce homogeneity of the sediment fabric ("depth of well mixed layer") is given in Table 4.7, being estimated as the base of the depth range showing greatest rate of increase in percentage of coarse sediment. Figure 4.5 below is an illustrative example.

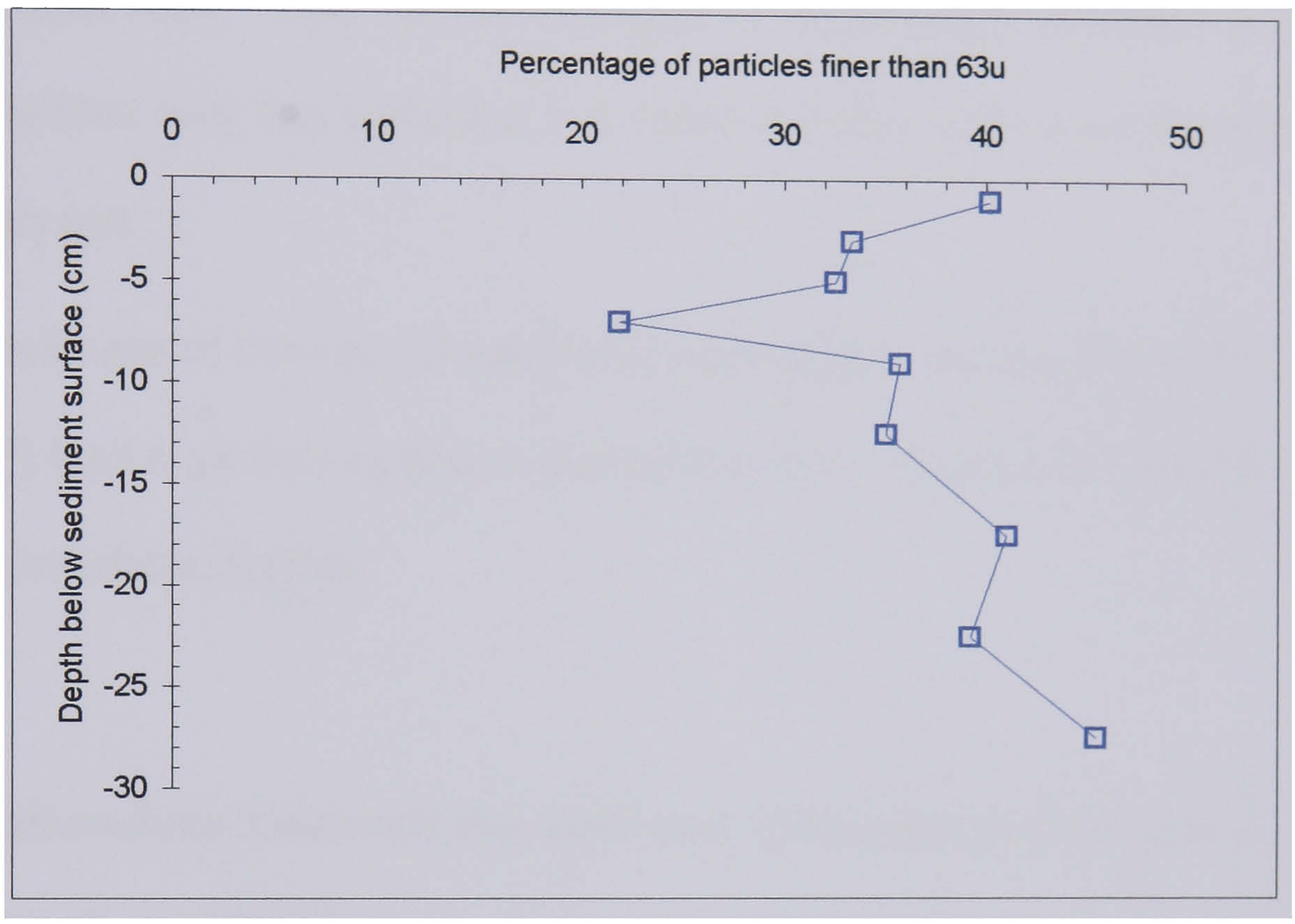


Figure 4.5 Plot showing the percentage of sediment particles finer than 63μm occurring at depths below the sediment surface for Site 1. The maximum depth of the well-mixed layer was interpreted as being the 8cm sample depth, since this depth (6-8cm) had the greatest rate of increase of coarse particles.

4.3.2.2 Relationships between the different abiotic measures of sediment properties.

The abiotic data from the flume, shear vanes and cores were examined for similar patterns across the sample sites. Most of the variables had distributions that did approximate normality with the exception of the following:

- k/Db was transformed using $\log_{10}(k/Db)$;

- the available Chl *a* at 10cm depth (INP) was transformed using $\log_{10}$(INP); and

- shear strength of the upper 2cm of sediment was transformed using $\log_{10}$(shear+0.02).

Correlation of the abiotic variables revealed that several abiotic factors had strong correlations with other variables and in particular with the sediment surface water content (Table 4.8). Due to the strength of covariance between some of the abiotic variables only the variables 1-9 listed in Table 4.8 below were included in further analyses.

k/Db (an estimate of the rate of sediment mixing) and the available Chl *a* at 10cm depth (INP) had a perfect negative correlation (-1). Therefore only the results for k/Db are considered further.

4.3.3 Relationships between the sediment disturbance potential of the biota and the abiotic variables

4.3.3.1 Relationships between overall sediment disturbance by the whole assemblage and abiotic variables

Comparing the different methods to calculate *total* overall volumes of sediment disturbed at each site (see Section 4.2.1.4) revealed variable relationships with the abiotic variables.

Abiotic factor		1	2	3	4	5	6	7	8	9	10	11	12
1	depth of well mixed region												
2	k/Db	-0.02											
3	INP	0.02	-1.00										
4	Surface sediment shear strength	0.37	0.59	-0.59									
5	Mean bulk sediment shear strength	-0.57	-0.25	0.25	-0.05								
6	Surface sediment water content	0.43	-0.16	0.16	-0.24	-0.51							
7	Sediment erosion rate	-0.07	0.45	-0.45	0.39	0.02	-0.21						
8	Mean depth of RPD	0.63	0.07	-0.07	0.26	-0.46	0.76	-0.18					
9	Mean depth to which oxic burrows extend	-0.15	0.32	-0.32	-0.23	-0.02	0.52	0.00	0.44				
10	Mean sediment water content over whole sample depth	0.74	0.26	-0.26	0.21	-0.88	0.74	-0.07	0.78	0.24			
11	Mean shear strength of upper 10cm	-0.47	-0.28	0.28	0.05	0.80	-0.77	0.02	-0.74	-0.55	-0.90		
12	Mean shear strength deeper than 10cm	-0.47	-0.27	0.27	0.08	0.71	-0.75	0.26	-0.69	-0.56	-0.86	0.93	

Table 4.8. Pearson's coefficient correlations between the abiotic characteristics of the sediment (n=9, r>0.56 significant at p≤0.05)

The first two measures of total bioturbation were based solely on body size (Gilbert et al 2007, Wheatcroft et al 1990) and both correlated with the water content of the sediment surface (r=0.55 n=9 p=0.06, 0.71 n=9 p=0.02 respectively) and levels of Chl *a* flux to deeper sediment horizons (r=0.66 n=9 p=0.03, r=0.53 n=9 p=0.07 respectively). The third method of estimating overall sediment disturbed was based upon the mean sediment disturbance effect of each species (SDE group approach) and this method had much weaker associations with sediment water content (r=0.21 n=9 p=0.29) but similar correlations with Chl *a* flux (r=0.57 n=9 p=0.05). The SDE group approach did, however, have a very strong negative association with shear strength of the sediment surface (r=-0.84 n=9 p=0.0002).

4.3.3.2 Relationships between shallow or deep assemblages and abiotic variables

Results from data exploration employing the RELATE routine from PRIMER-E to compare patterns of inter-site similarity in the abiotic dataset with inter-site similarity in the biological data are summarised in Table 4.9 for each of the approaches used to group the species according to sediment disturbance. In summary the RELATE Tests revealed that:

- shallow assemblages had strongest associations with the abiotic data if species were aggregated into the categories defined as Scheme 1;
- for shallow assemblages, when the biotic structure was based upon species abundance, relationships with the abiotic dataset were only slightly weaker than when species were grouped under Scheme 1; and

- deep assemblages had no relationship with the combined abiotic dataset irrespective of how the species were grouped.

Table 4.9 Results of RELATE tests between the biological assemblages and the combined abiotic parameters 1-9 from Table 4.8. The values given are for the spearman rank correlation between the biotic variables and the abiotic ones with 1 being a perfect correlation and 0 no correlation.

	Shallow assemblage	**Deep assemblage**
Abundance	0.35	0.05
Abundance x Scheme 1	0.39	0.02
Abundance x Scheme 2	0.36	0.05
Biovolume x 0.35	0.28	0.04
(Body length) $^{4.25}$	0.29	0.08

4.3.3.3 Correlations between the abundance of individuals in an SDE group and abiotic variables

Correlations between the abundance of individuals in an SDE group and each separate abiotic factor are summarised below in Table 4.10 for shallow assemblages summed into Scheme 1 categories (categories not represented by species for the Tamar and Plym are not included in the Table). Although correlations with ρ values exceeding 0.5 have been highlighted the results should be viewed as an exploration of relationships and highlighting as an aid to viewing stronger (not necessarily significant) relationships. As a general guide, correlations could be considered as significant if:

- $\rho > 0.56$ for nine sites, or
- $\rho > 0.62$ for eight sites, or
- $\rho > 0.66$ for seven sites,

although caution should be exercised in placing confidence on the significance of any results due to the low number of sites available in total (nine) and the large number of tests performed. Despite the low number of sites included in the current study, some strong ($\rho>0.6$) and significant ($p<0.05$) associations were found. Thus the null hypothesis that there is no relationship between the distribution of the different functional groups within the estuary and the abiotic characteristics of the sediment was rejected. Results are included in Table 4.10 below for groups that were present at fewer than seven sites for completeness.

Table 4.10 Spearman rank correlations between the abundance of individuals in each SDE group found in the Tamar/Plym from shallow assemblages under Scheme 1 and each individual abiotic variable. k/DB is a mixing parameter for Chl *a*. Correlations with $r>0.5$ are highlighted in bold and underlined (a guideline to significance is given in text above). The number of sites at which the SDE group was present and the numbers of species in each SDE group are also given.

SDE group	**A1**	**A2**	**B1**	**B2**	**C1**	**C2**	**C3**
No. of sites group recorded	*9*	*9*	*9*	*7*	*9*	*6*	*9*
No. of species in SDE group	*10*	*6*	*10*	*1*	*22*	*5*	*2*
Abiotic variables							
Mixing depth	0.07	-0.45	-0.37	0.08	0.02	**-0.63**	-0.22
k/DB	0.15	0.07	0.15	**-0.59**	**-0.52**	0.12	0.36
Surface sediment shear strength	-0.24	**-0.79**	0.2	-0.34	**-0.63**	0.3	0.11
Whole core shear strength	0.07	0.1	0.02	-0.34	0.03	0.29	-0.32
Sediment water content	-0.1	0.07	**-0.75**	0.43	0.48	**-0.71**	-0.35
Sediment erosion rate	0.02	**-0.53**	0.42	**-0.75**	**-0.75**	0.46	**0.72**
Mean depth of RPD	-0.19	-0.12	**-0.51**	0.21	0.01	**-0.52**	-0.23
Mean depth of deepest burrows	-0.05	0.23	-0.20	0.23	-0.22	-0.03	-0.02

For the same abiotic factors, correlations with the abundance of individuals in deep assemblage SDE groups, categorised under Scheme 1, are summarised in Table 4.11.

Table 4.11. Spearman rank correlations between the abundance of individuals in each SDE group from deep assemblages under Scheme 1 and each individual abiotic variable. k/DB is a mixing parameter for Chl *a*. Correlations with r>0.5 are highlighted in bold and underlined to aid comparisons (a guideline to significance is given in text above). The number of sites at which the SDE group was present and the numbers of species in each SDE group are also given.

SDE group	**A1**	**A2**	**B1**	**B2**	**C1**	**C3**
No of sites SDE group recorded	*6*	*6*	*4*	*4*	*8*	*6*
No of species in SDE group	*5*	*2*	*4*	*1*	*5*	*3*
Abiotic variables						
Mixing depth	0.32	-0.40	**-0.53**	0.18	0.45	0.19
k/DB	0.41	0.19	-0.02	-0.13	-0.12	0.43
Surface sediment shear strength	0.32	**-0.66**	-0.01	-0.45	-0.38	-0.24
Whole core shear strength	-0.09	-0.19	-0.02	-0.15	-0.38	**-0.94**
Sediment water content	0.3	0.34	-0.31	**0.82**	**0.68**	0.47
Sediment erosion rate	-0.40	0.03	0.46	-0.37	-0.37	0.34
Mean depth of RPD	-0.23	-0.27	-0.18	0.31	**0.69**	0.41
Mean depth of deepest burrows	0.18	0.32	0.24	0.39	**0.58**	0.26

Most SDE groups under Scheme 1 were found to correlate with at least one abiotic variable with the exception of group "A1" for both shallow and deep assemblages. No consistent pattern emerged across all SDE groups under Scheme 1.

Applying Scheme 2 to the biological assemblages also produced some strong correlations (but see caution above re significance) between individual biological effect categories and individual abiotic factors as outlined for shallow assemblages in Table 4.13 and for deep assemblages in Table 4.12.

Most SDE groups were found to have moderate (ρ in range 0.4 – 0.6) to strong (ρ >0.6) correlations with at least one abiotic variable. Some SDE groups were represented at only a few sites but the results are presented in the respective tables for completeness. As with Scheme 1, no consistent patterns emerged across all SDE groups for abiotic-biotic relationships.

Table 4.12 Spearman rank correlations between the abundance of individuals in each SDE group from deep assemblages under Scheme 2 and each individual abiotic variable. k/DB is a mixing parameter for Chl *a*. Correlations with r>0.5 are highlighted in bold and underlined to aid comparisons (a guideline to significance is given in text above). The number of sites at which the SDE group was present and the numbers of species in each SDE group are also given

SDE Group	**3b**	**3e**	**5a**	**5b**	**5e**
Number of sites SDE recorded	*6*	*7*	*5*	*5*	*4*
No of species in SDE category	*5*	*3*	*2*	*2*	*2*
Abiotic variables					
Mixing depth	**-0.55**	0.13	**0.51**	0.30	-0.20
K/Db	0.12	-0.13	-0.17	-0.17	0.40
Surface sediment shear strength	**-0.59**	**-0.62**	**0.50**	**-0.60**	0.09
Whole core shear strength	0.05	0.08	0.31	-0.49	-0.37
Sediment water content	0.31	**0.89**	-0.14	**0.86**	0.04
Sediment erosion rate	0.07	0.34	-0.17	-0.41	**0.79**
Mean depth of RPD	-0.21	0.47	0.20	**0.65**	-0.16
Mean depth of deepest burrows	0.42	0.44	-0.43	**0.64**	0.11

SDE group	1a	1b	1c	2a	2b	2c	3a	3b	3c	3d	3e	4a	4b	5a	5b	5d	5e
No of sites SDE group recorded	*7*	*6*	*6*	*8*	*9*	*4*	*9*	*9*	*2*	*4*	*7*	*4*	*5*	*7*	*9*	*8*	*8*
Number of species in SDE group	*6*	*5*	*3*	*4*	*8*	*1*	*7*	*7*	*1*	*1*	*2*	*3*	*3*	*3*	*2*	*2*	*2*
Abiotic variable																	
Mixing depth	**-0.64**	-0.47	**-0.55**	**-0.55**	-0.15	-0.37	-0.37	-0.30	0.23	-0.08	0.00	-0.12	0.19	-0.19	0.06	**-0.64**	-0.22
k/DB	-0.13	-0.19	0.08	0.00	0.00	-0.13	0.1	-0.22	0.43	0.42	**-0.55**	-0.35	**-0.76**	0.05	**-0.50**	-0.24	0.37
Surface sediment shear strength	0.23	0.32	-0.08	**-0.72**	**-0.73**	0.34	0.23	**-0.52**	**0.56**	0.07	-0.40	0.31	0.10	**0.64**	**-0.55**	-0.17	0.11
Whole core shear strength	0.42	**0.56**	0.22	-0.47	-0.25	**0.91**	0.07	-0.07	0.25	0.14	0.23	**0.71**	0.17	-0.13	-0.02	-0.29	-0.32
Sediment water content	**-0.79**	**-0.85**	**-0.51**	0.12	0.18	**-0.51**	**-0.80**	-0.27	-0.46	-0.49	**0.51**	-0.46	0.21	0.03	0.47	**-0.54**	-0.35
Sediment erosion rate	0.15	0.2	-0.03	-0.10	-0.17	0.07	0.35	-0.12	0.11	0.17	**-0.80**	0.02	-0.17	**0.61**	**-0.67**	-0.13	**0.72**
Mean depth of RPD	-0.46	**0.82**	**-0.62**	-0.23	-0.21	**-0.55**	**-0.51**	**-0.52**	0.12	-0.17	0.31	-0.42	-0.21	0.36	-0.06	-0.38	-0.23
Mean depth of deepest burrows	-0.36	-0.36	-0.14	0.13	0.05	-0.15	-0.32	-0.08	-0.27	0.23	0.17	**-0.51**	-0.30	-0.23	-0.33	-0.33	-0.12

Table 4.13. The Spearman rank correlations between the abundance of individuals in each SDE group from shallow assemblages under Scheme 2 and each individual abiotic variable. Correlations with r > 0.5 are highlighted in bold and underlined, see Section 4.3.3.3 for significance value guidance.

4.3.3.4 Dominance of individual species

Within both the shallow and deep assemblages, there were few species that occurred at all sites (see Appendix 3 and Figure 3.5). For deep assemblages, the low numbers of species occurrences prevented determination of any relationship between individual species and abiotic variables. For shallow assemblages, species occurrences were also low for several species:

- fifteen species only occurred at one of the nine sites;
- a further nine were found only at two sample locations; and
- less than half of the species occurred at 5 or more sites.

Table 4.14 below summarises the correlations between the abiotic variables 1, 3-9 listed in Table 4.8 and those species occurring at seven or more sites within shallow assemblages:

For shallow assemblages under SDE Group Scheme 1, there were some similarities between each species' relationship with abiotic variables and its allied SDE group's relationships with the same environmental datasets for example *M.palmata* had consistent associations with the depth of the RPD and the water content of the sediment surface. In SDE group "A1", however, species appeared to have associations as individuals e.g. *P.elegans* with sediment shear strength and *S.shrubsoli* with sediment erosion rates and Chl *a* derived measures, which were not evident for the SDE group.

For shallow assemblages under SDE Group Scheme 2, *Portunidae* indet., *Spioindae* indet. and *S. shrubsolii* did not have the same associations with the abiotic data as did the SDE groups to which they belonged. The other eight species demonstrated very similar relationships with the abiotic data when compared to the SDE groups with which they were associated, suggesting that the

Species	Melinna palmata	Nereis diversicolor	Portunidae indet	Cirratulid III	Nephtys hombergii	Chaetozone indet	Hydrobia indet	Pygospio elegans	Spionidae indet	Streblospio shrubsolii	Tubificoides indet
SDE group Scheme 1	B1	B2	A1	B1	C3	B1	A2	A1	A1	A1	C1
SDE group Scheme 2	3b	3e	5b	3a	5e	3a	3b	2b	2b	3b	5b
No of sites species recorded	7	8	8	8	7	9	9	7	9	9	9
Abiotic variables											
Mixing depth	**-0.57**	-0.07	-0.45	**-0.52**	-0.22	-0.37	-0.45	-0.22	-0.19	**0.61**	0.06
k/Db	0.12	-0.49	0.05	0.27	0.37	-0.07	0.12	-0.10	**0.57**	0.38	**-0.50**
Surface sediment shear strength	0.15	-0.48	0.11	0.17	0.11	0.08	**-0.83**	**-0.77**	0.26	0.07	**-0.55**
Whole core shear strength	0.14	0.17	0.38	0.03	-0.32	0.17	0.05	-0.22	0.02	-0.40	-0.02
Sediment water content	**-0.59**	**0.64**	**-0.75**	**-0.70**	-0.35	**-0.77**	0.12	0.08	-0.05	0.25	0.47
Sediment erosion rate	**0.54**	**-0.61**	-0.08	0.45	**0.72**	0.22	-0.47	-0.25	**0.53**	0.27	**-0.67**
Mean depth of RPD	**-0.53**	0.32	-0.26	-0.48	-0.23	**-0.72**	-0.12	-0.35	0.48	0.14	-0.06
Mean depth of deepest burrows	0.05	0.48	-0.27	-0.05	-0.02	-0.28	0.35	0.02	0.38	-0.18	-0.33

Table 4.14. Spearman rank correlations between the individual species from shallow assemblages and each individual abiotic variables. Correlations where $\rho > 0.5$ are highlighted in bold and underlined, see Section 4.3.3.3 re significance value guidance. The sediment disturbance effect (SDE) groups under Schemes 1 and 2 are given for each species, together with the number of sites at which the species was present.

group responses may be dominated by those species with greatest representation across all sites. This was more evident for *Nereis diversicolor, Nephyts hombergii and Tubificoides* indet since each was classified in an SDE groups that only contained 2 species in total.

Whilst relationships could have been investigated for other species, the remaining species were each present at fewer than 7 sites. Thus, there would have been little evidence that any perceived relationships between species and abiotic variables were in fact reflecting true abiotic-biotic associations. By combining species at the family level however, more species were included and Table 4.15 details Spearman Rank correlations between the abiotic variables and those families that were represented at a minimum of 7 sites.

Table 4.15. Spearman Rank correlations between families of species from shallow assemblages and each individual abiotic parameter. k/DB is a mixing parameter for Chl *a*. Correlations r>0.5 are highlighted in bold and underlined (a guideline to significance is given in text above in Section 4.3.3.3). The number of sites at which the family was present is also given.

Family	**Spioniidae**	**Cirratulidae**	**Ampharetidae**	**Scrobicularidae**
No. of sites family present	*9*	*9*	*7*	*7*
Abiotic variables				
Mixing depth	0.15	-0.37	**-0.57**	0.13
k/Db	0.18	0.10	0.10	-0.22
Surface sediment shear strength	-0.27	0.23	0.24	-0.45
Whole core shear strength	-0.05	0.07	0.26	-0.07
Sediment water content	-0.08	**-0.80**	**-0.70**	**0.64**
Sediment erosion rate	0.00	0.35	0.49	-0.45
Mean depth of RPD	-0.21	**-0.51**	**-0.59**	0.38
Mean depth of deepest burrow	0.10	-0.32	-0.02	-0.03

Aggregating the species to family level changed the associations of the spionids, which subsequently had no strong associations with the abiotic datasets when treated as a single entity. For Cirratulidae there was little change in the abiotic variables that correlated most highly with the biota although the strength of some of the relationships varied.

Relationships between Ampharetidae and the abiotic variables revealed weaker associations with those abiotic factors previously shown to be associated with SDE group "B1", which contained both species of Ampharetidae.

4.4 Discussion

4.4.1 Developing functional groups

The current study developed a novel methodology to estimate and categorise the effect of the macrofauna upon an important estuarine process: sediment mixing. In so-doing, this study considered the motility, feeding, construction and other relevant routine activities of all the species sampled, to quantify each one's direct contribution to sediment disturbance, according to its own peculiar activities. Subsequently, rather than considering each species' contribution to particular mechanisms of sediment mixing (such as biodiffusion, advective or non-local mixing) or simply using body size alone, the current study attempted to address limitations of earlier studies by considering the *overall* effects of species' activities and also took into account the abundance and depth stratification of each species within the sediment.

This chapter built upon the earlier studies of Wheatcroft et al (1990) and Gilbert et al (2007), which suggested that the bioturbatory ability of a species could be inferred simply from its body size. However, in this study, species' body size was used as a weighting in the assessment of each species' overall effect upon

sediment disturbance in concert with other information upon activity type and rates from the literature. Thus, in determining the potential of any one species to disturb the sediment, the role of body size varied according to whether *the magnitude* of the effect of a given activity was *related* to body size.

Whilst species body size has been shown to influence many biological activities (Peters 1987, Brown et al 1993, Cohen et al 2003, Basset and Angelis 2007), the overall impact of any species on the dynamics of intertidal soft sediments will also be influenced by the type and frequency of biological activity (Swift et al 1996, Pearson 2001). For some activities such as burrowing through sediment, the magnitude of the effect is greatly dependent upon body volume. For other activities, such as using palps to scrape the sediment surface, total body *volume* does not take account of sediment disturbance that arise due to feeding activity. Hence, the present study included factors such as ratios of palp length to body length to estimate feeding radii, or the proportion of the animal's body that is extended from burrows onto the sediment surface to estimate sediment disturbance effects.

The frequency with which an activity is performed will also determine a species' potential to promote sediment mixing. Thus, the effect of highly abundant and active small-bodied species could appear to be negligible in schemes dependent upon body size alone.

Body size could be defined in many ways, and whilst Gilbert et al (2007) employed a fraction of each species' body volume, Wheatcroft et al (1990) utilised body length to the power of 4.25. Gilbert et al (2007) derived relationships from observed levels of activity and measured body size during laboratory experiments. Wheatcroft et al (1990), however, applied a theoretical approach to decompose a bioturbatory coefficient (Db), which represents one-dimensional particle diffusion

(down-core), into "step lengths" and "rest periods" in order to relate the movement of individual sediment particles to macrofaunal ingestion rates. The implication that the bioturbatory effect of an organism scales to the power of 4.25, however, appears unrealistic, since a relatively small increase in body length will have a profound effect upon sediment disturbance. The relationships observed by Gilbert et al (2007) merit further investigation to assess whether such a simple algorithm holds for the majority of the benthic macrofauna.

Estimates of total bioturbation occurring at any one site based upon the findings of either Gilbert et al (2007) or Wheatcroft et al (1900) will be subject to over and under-estimates according to variable levels of biotic activity. Whilst both methods are likely to produce a similar ranking of sites according to bioturbation levels (hence promoting high values for correlations between the two approaches), the absolute values will be substantially different. For practical management purposes or extrapolation to models of sediment dynamics, there is little evidence to suggest which estimate provides the most realistic term of overall sediment disturbance levels occurring in the field, although, as mentioned above, the method of Wheatcroft et al (1990) should be viewed with extreme caution. Equally, the method utilised by Swift et al (1996) was partially based upon Wheatcroft et al's (1990) parameters for "step length" and "rest periods" and also did not include allowances for the abundance of each species.

In contrast, the classification scheme developed in the current study was derived from estimates of volumes of sediment directly disturbed by a range of species activities, including burrowing, migrating and feeding and was not based simply upon body size alone. Schemes that estimate *overall* volumes of sediment disturbed and which are based upon a range of species' activities should provide more realistic indications of actual effects in the field. By considering many

species traits such as burrow construction, feeding behaviour and commensalism it is possible to assess each species independently, to determine its unique potential to disrupt the sediment, provided sufficient information about each species exists.

Within the estuarine macrobenthic community, there are many different ways in which species can disturb soft sediments. The majority of schemes that attempt to group species according to functions they perform focus on a particular mechanism e.g. the direction in which sediment is displaced, the mechanics of food capture or various descriptors of mobility (Fauchald and Jumars 1979, Wheatcroft et al 1990, Pearson 2001). A major difficulty in assigning species to groups under such schemes is that many species can perform several functions and do not fit neatly into one category (Pearson 2001). In addition those schemes that are developed to describe particle transfer processes do not necessarily reflect other sediment disturbance effects, for example sediment irrigation (Pearson 2001).

Given this complexity, schemes developed in the current study do not describe particle transfer processes. Rather they attempt to quantify the biotic "activity levels", and no account is made of whether any sediment is displaced. Indeed, it is likely that much of the same sediment is being disturbed by more than one individual or species. The current study treated the overall sediment disturbance occurring at any site as an additive process. Whilst such an approach may not be appropriate for some processes (e.g. particle displacement), for other factors such as sediment irrigation an additive approach may approximate the overall degree to which the factor is influenced. Extensive reworking of the same sediment can have conflicting effects upon the sediment particle size distribution, and yet promote increased sediment fluidity. For example "conveyor belt" species may

transport sediment to shallower sediment regions whilst "reverse conveyor belt" species many move sediment down from the sediment-water interface, yet the combined activities of both groups will increase sediment irrigation.

Thus, this chapter developed novel categories of biotic sediment disturbance effects that have potential to be applied to any estuarine macrobenthic species, and group the species according to size of effect regardless of the biological mechanism by which the effect was produced.

In estimating biological sediment disturbance effects, many assumptions were made about species' feeding ranges, mobility, frequency of activity and the morphology of biogenic structures such as burrow systems. Every effort was made to base assumptions upon evidence from the literature for the species under investigation. However, some species were under-represented in the literature. Indeed even when such information can be obtained for the relevant species, it is well-recorded in the literature that most biological activities vary with factors such as an individual's age or reproductive state, the ambient temperature, predation and food supply (Cammen 1989, Wheatcroft and Martin 1996). Since, however, each of sediment disturbance effect (SDE) groups spanned a range of size effects the influence of variable species' activity levels on the species classification was minimised.

The current study used actual body measurements to calculate bio-volumes and combined this information with data on each species' activities and sediment depth distribution to calculate sediment disturbance effects. Measuring all individuals for all future investigations would be impractical. However, depending upon whether, when calculating overall body volume (and any subsequent values such a burrow volume), the mean or maximum body dimensions were considered, in the present study, only a few species could potentially have been classified into more than one

biological effect group. In most instances where such changes in classification would have occurred, species moved to the next size of effect category, but since few individuals reached the maximum size, the use of the mean body size was more appropriate. For a minority, however, which were relatively larger and/or longer-lived species, there were large differences in the estimated sediment disturbance effect. For example, *Nereis* indet. had an estimated mean sediment disturbance effect of 3.6 cm^3 but a maximum estimated effect of 320 cm^3 of sediment disturbed, according to its routine activities.

Further studies that allow sediment disturbance effects to be estimated for different size ranges for the most cosmopolitan and abundant estuarine macrofaunal species would greatly aid the development of this new classification scheme for use in estuarine systems as a tool for assessing in-field bioturbation levels. For those species with multiple biological effect category membership, a simple estimation of the body size frequency could be ascertained, for example by using nested sieves of different mesh size, and hence bioturbatory levels approximated.

4.4.2 Sediment bulk properties and erosion potential

This chapter revealed that strong correlations existed between several of the abiotic parameters used to characterise the sediment and also evidence that sediment water content could be used as a proxy for other sediment characteristics. The null hypothesis that there are no relationships between the various abiotic parameters used to characterise the sediment was therefore rejected. Performing multiple comparisons does increase the risk of identifying a significant relationship when one does not in fact exist (Type I error). A statistical correction for this increased likelihood of incorrectly identifying a relationship was

not made since the low number of sample sites had already precluded too much emphasis being placed on the statistical significance of the results. The correlations were instead viewed as an exploration of the data and relationships. Despite strong evidence of co-linearity in the abiotic sediment characteristics, however, no strong pattern emerged to support the use of any of the tested abiotic measures as a proxy for biologically mediated sediment disturbance effects.

Investigations of sediment dynamics frequently quantify "bioturbation" at different scales, employing different methodologies (Paterson and Black 1999, Paterson et al 2000, Tolhurst et al 2000, Widdows et al 2007). Hence, meaningful comparisons between studies are difficult. Thus, for practical field-investigations and modelling studies, much time and effort could be saved if a reduced number of abiotic proxies for bioturbatory activity could be identified. Unfortunately, this study was unable to identify any such proxies and the null hypothesis that there is no relationship between estimates of total biologically-mediated sediment disturbance and the abiotic characteristics of each site was retained. This inability to elucidate direct links could have arisen for many reasons. Firstly, there was no evidence to suggest that the estimates of biotic activity did in fact approximate reality. In addition, the abiotic parameters considered in this study are influenced by a range of other abiotic factors as well as the activity of the macrobenthos. The relationships found between overall sediment disturbance levels and the abiotic characteristics are discussed further in Section 4.4.3.1 below. The study did, however, provide support for using the sediment water content of the surface as a master variable (Flemming and Delafontaine 2000) to act as a proxy for a range of other abiotic variables and some evidence that the RPD could also be a useful proxy for some sediment characteristics.

The two main foci of studies into estuarine sediment dynamics are the erosion potential of the sediment and mixing processes within the sediment body. The potential of the sediment to erode is influenced by both stabilising and destabilising biotic factors. For example, microphytobenthos have been shown to promote sediment stability without significantly influencing mixing processes within the sediment body (Paterson et al 2000, Herman et al 2001). Thus, those abiotic factors influenced by processes occurring at the sediment surface might be expected to exhibit strong co-linearity but to have weaker associations with other abiotic factors that characterise processes occurring within deeper sediment regions.

The current study did reveal co-linearity between many of the abiotic parameters in broad agreement with other studies (Christie et al 2000, Paterson et al 2000). In addition, there appeared to be a dichotomy between those abiotic factors that correlated well with the water content of the sediment surface, and hence with sediment critical erosion thresholds, and those parameters derived from down-core sediment profiles that correlated with sediment erosion rates. Such a dichotomy was in broad agreement with Paterson et al (2002), who suggested that where the depth resolution for abiotic measurements exceeded the top few mm of the sediment, variables would correlate best with sediment erosion rates rather than with the sediment critical erosion thresholds. In the current study, abiotic parameters were measured over 2cm sediment depth intervals for the upper 10cm of sediment and over 5cm depth intervals for deeper regions. In agreement with the results of Paterson et al (2000), the present field investigation found that sediment erosion rates related more to processes occurring within the whole sediment body but that conversely, critical sediment erosion thresholds maintained

strong associations with sediment surface dynamics despite the relatively coarse scale of measurement.

Despite the apparent lack of association between parameters derived from Chl *a* profiles and the sediment surface water content, the mean Chl *a* values for each sediment depth sampled had a significant correlation with water content in the same depth layer sample. Similar results were found for the Skeffling mudflats in the Humber estuary (Christie et al 2000). Strong associations were also found between most abiotic variables and the sediment water content, suggesting that down-core profiles of the sediment water content provided sufficient information to approximate the other sediment mixing coefficients. Flemming and Delafontaine (2000) proposed that absolute water content could act as a "universal master variable" from which "any other sediment parameter" could be estimated. Hence, the present findings, imply that profiles of the water content from sediment cores may provide a relatively cheap and robust proxy for many other environmental parameters, characterising the nature of both the sediment surface and the sediment body. Whilst sediment water content may vary in the upper few cm of a core due to dewatering processes, the water content of deeper layers is likely to be less variable, so that profiles of sediment water content are likely to provide robust relationships with several other abiotic parameters.

4.4.3 Linking environmental factors to overall sediment disturbance

By developing biological effect classification without reference to the abiotic data collected during the same fieldwork, it was possible to question whether sediment disturbance levels could be predicted from abiotic characterisation of the sediments. Results presented in this chapter highlight the difficulties of identifying abiotic patterns in sediment characteristics that are produced by the varied

bioturbatory activities of estuarine macrobenthic fauna. Analyses of the abiotic data suggested that sediment water content could be used as a proxy for many other abiotic characteristics of estuarine soft sediment but consistent relationships were not found between measures of the overall level of bioturbatory activity at a site and surface sediment water content.

4.4.3.1 Total sediment disturbance by the biota

The three measures of estimating overall levels of sediment disturbance by the biotic assemblages all had strong correlations ($\rho>0.6$ $p<0.05$, $n=9$) with at least one abiotic factor that related to properties of the sediment surface. The relationships were not consistent across all methods used to estimate total volumes of sediment disturbed. This inconsistency, combined with the lack of any means to validate the estimations of disturbance level, meant that little confidence could be applied to interpreting the perceived abiotic-biotic relationships. The relationships are, however, discussed further in this thesis, as an exploration of the patterns and to inform any future decisions in studies on sediment-dynamics. With the exception of the mixing of Chl *a*, the biological data had only weak associations with abiotic factors characterising the bulk sediment such as depth of the RPD and the mean depth-averaged water content and sediment shear strength.

The mixing of Chl *a* was determined with reference to profiles of Chl *a* concentration down sediment cores. Chl *a* mixing rates in the sediment were obtained by fitting a model of exponential decrease with depth. Chl *a* degradation occurs rapidly in oxic layers. However, both Chl *a* and its degradation products have been shown to be relatively stable coloured compounds under anoxic conditions (Sun et al 1993). Thus, it was possible that most Chl *a* degradation

occurred above the RPD and that the derived mixing rates were more heavily influenced by degradation in the upper few cm than by biological mixing processes within the whole of the bulk sediment. A comparison of Chl *a* profiles (Figure 4,4) and RPD depths (Table 4.6) does lend some support to this suggestion. The calculations of availability of Chl *a* (INP) in deeper regions assumed a constant degradation rate over the whole sediment sample region, which is unlikely to have been a realistic representation of Chl *a* degradation processes within soft sediments (Sun et al 1993). Thus, the strong associations between sediment mixing parameters derived from Chl *a* profiles and biotic estimates of sediment disturbance may rather reflect links between bioturbatory activity and abiotic characteristics of the sediment surface, than indicate links between processes occurring in the bulk sediment.

The nature of relationships between biological measures and abiotic characteristics of the sediment surface suggested that any bioturbatory signal was most easily detected in abiotic parameters measured at the sediment surface. Since the species are active over much of the sediment depth ranges sampled, it was expected that abiotic-biotic relationships would be stronger with parameters characterising the sediment body rather than just the sediment surface, where confounding factors of sediment stabilising processes, conflicting biotic activity and external abiotic forcing were more evident. Nevertheless, it was not clear whether the observed patterns in the environmental variables were the product of bioturbatory activity or whether biological activity was responding to and constrained by changes in measured environmental variables.

4.4.3.2 Linking the biotic assemblages structure and abiotic factors

This study demonstrated that shallow and deep macrobenthic assemblages had different, or no, patterns of association with environmental data. For shallow

assemblages, relationships between assemblage structure and sediment characteristics were strongest if species were classified using the sediment disturbance Scheme 1. For complete deeper assemblages, however, none of the species classification methods had relationships with environmental variables.

The abiotic characteristics of the sediment structure mostly reflected patterns occurring in the upper region of sediment cores. The shallow assemblages are by definition more intimately associated with the upper sediment layers than are deep-living organisms so that a stronger association with the abiotic factors might be expected. Nevertheless, many of the deeper living organisms have been shown to have the potential to produce strong, dominant bioturbatory signals, such as *Nereis diversicolor* (Mermillod-Blondin et al 2005) and thalassinid arthropods (Swift et al 1996). The lack of any association between the overall pattern of abiotic factors and the structure of deeper assemblages suggested that either the deeper-living species are not producing dominant signals or that the magnitude or longevity of any such signal is undetectable under the sampling regime employed in the present study. However, whilst no abiotic-biotic association was evident for the combined deep assemblage, patterns were evident at the level of individual SDE group from deep assemblages.

For those SDE groups with sufficient across-site representation, correlations with individual abiotic variables indicated that, with the exception of group "A1", all groups in both Scheme 1 and Scheme 2 had at least one moderate ($\rho > 0.4$), though not necessarily significant, association with an individual abiotic variable. However, the relationships were not consistent across assemblages or SDE groups and some groups were poorly represented, hence limiting any ability to draw conclusions about the true significance of some of the suggested relationships. The smallest effect group under Scheme 1 (A1) comprised species

associated mainly with the surface of sediment, e.g. Spionidae and *Galathowenia*, and revealed no strong associations with any single abiotic factor. Although this could imply that signals from small bioturbators were lost due to the activities of other species, other "small effect" groups did demonstrate strong associations ($\rho>0.6$) with at least one abiotic measure.

There was, however, little consistent evidence that the relationships between individual biotic groups and abiotic factors reflected an effect exerted on the sediment matrix by bioturbating organisms, e.g. the relationships found for SDE group "B1" (including Cirratulidae, *Melinna palmata* and *Corophium volutator*) implied a negative relationship between the abundance of component species and the sediment water content and the depth of the RPD. Since increased bioturbatory activity is expected to increase sediment water content and deepen the RPD, the results for category 'B1' suggest either that other unmeasured interactions are dominating "B1"s dynamics or alternatively that the associations observed may represent responses of the species to increased sediment fluidity. Examination of relationships for the other groups revealed several similar associations that are better explained as biological responses to environmental forces rather than as a biological effect. However, some exceptions were evident within groups with increased abundance levels associated with increased sediment water content and reduced sediment mean-core shear strength.

The exact species composition of groups that had strong positive associations with sediment water content varied according to the sediment depth range of the assemblage and the biological effect scheme under investigation. However, *Nereis* indet., *Tubificoides* indet. and *Heteromastus filiformis* were consistently represented in such categories for both shallow and deep assemblages. For deeper assemblages, however, categories containing *Nephtys* indet. and *S. plana*

also had similar positive associations with the sediment water content and negative relationships with the whole-core mean shear strength. Examining the individual species' associations with sediment abiotic characteristics revealed that some of the species displayed consistent patterns with the abiotic parameters, whether categorised according to a bioturbatory effect or left as an individual species e.g. *N.diversicolor* had a consistent association with the water content of the sediment surface, *H.ulvae* with the shear strength of the sediment surface and *M.palmata* with the depth of the RPD and the water content of the sediment surface. However, very few species' responses to abiotic variables could be investigated and larger species such as *N. diversicolor* and *N. hombergii* were placed in SDE groups that had very few members. Thus it was not possible to determine whether a few individual species were dominating the apparent abiotic-biotic relationships between SDE groups and environmental variables, or if the bioturbatory signals of the majority of species sampled in the current study were hidden by the combined activity of the group or overall assemblage.

Evident variations in the strength and form of the abiotic-biotic relationships show that a simple model relating all functional groups to the same single bioturbation proxy was unlikely to succeed. Whilst sediment water content had good relationships with some other abiotic measures, it did not have strong correlations with all SDE groups. The SDE groups seemed to follow the same dichotomy in their relationship with abiotic factors as was seen in relationships between individual abiotic variables themselves: SDE groups generally demonstrated either relationships with abiotic factors that correlated well with sediment surface water content or, relationships with factors that were themselves correlated with sediment mixing parameters and erosion rates.

Some smaller species, more usually associated with the sediment surface layers were also found in deeper assemblages. It may be that deeper layers were contaminated during sampling procedures. Alternatively, for example in the case of *Hydrobia ulvae*, some species may have been displaced by the activities of other bioturbating species, e.g. by entering burrows. Thus, although *H.ulvae* showed a strong association with the mixing of Chl *a*, it is unlikely it had actively promoted downward displacement of Chl *a* to deeper regions. As mentioned above, Chl *a* is relatively resistant to further degradation within those regions below the RPD in soft sediments. Thus, the mixing rates obtained in this study may reflect Chl *a removal* from the surface layers rather than *transport* to deeper regions. This highlights the dangers of developing categories of bioturbatory effects simply from correlations between species abundance and abiotic parameters without reference to information about species activities.

The ability of any abiotic proxy to accurately characterize bioturbatory activity depends upon the spatial and temporal scales of investigation and the true ability of a species to mobilise sediment. Where small-scale spatial effects are produced by sufficiently large numbers of individuals an overall signal may still be detected if effects are at least additive. On the other hand, the roles of rare species acting on low spatial and/or temporal scales are likely to remain "invisible" to the researcher. Any forces acting at the broad scale of intertidal flats or greater, however, may remove smaller scale signals and promote homogeneity of the sediment. Where such homogenisation of the bioturbatory signal occurs, any consistent patterns of similarity found between the biota and environment would be more likely to be indicative of biological responses to environmental forcing rather than of a biological effect upon the environment.

Whilst many species have previously been shown to influence sediment characteristics (Hall 1994, Paterson and Black 1999), there are many other species for which relatively little is known of their true contribution to sediment disturbance. Even for species shown to promote a discernible abiotic pattern under laboratory conditions, the field situation may be very different (Wheatcroft et al 1998). The biota is not the only element to influence soft sediment characteristics. For example wave action and tidal stress may also play a role in sediment erodibility or water content (Paterson and Black 1999). Furthermore abiotic effects may not be additive in nature and indeed many may act in conflict, so that any resultant "signal" conveys little information about the nature and magnitude of component processes.

The findings of the present study show that not all abiotic measurements can be related to the patterns in overall macrobenthic community activity. Not all components of the macrobenthic community contribute equally to the abiotic manifestations of bioturbatory activity that we can measure. For some abiotic parameters such as down-core profiles of percentage TOC, it appears that the scale at which we can characterise a tidal flat in the field is too coarse to establish biologically-induced patterns of sediment mixing. It has been suggested that non-local mixing by macrobenthic invertebrates, for example subduction of surface material into burrows, can be identified in laboratory studies over a short time span. However, over greater temporal and spatial scales extensive biological reworking of the sediment and abiotic forcing parameters will promote sediment homogeneity. Under these conditions, whilst "diffusive sediment mixing" models often provide good matches to observed field patterns (Reed et al 2006, Gilbert et al 2007), this imparts little information about the mechanisms of mixing (Reed et al 2006).

Models estimating the overall sediment disturbance usually impart little direct information about mechanisms. However, the overall disturbance that infauna inflict upon the sediment affects many ecosystem processes such as sediment oxygenation and nutrient and resource availability. Hence, functional groupings that link species to overall bioturbation may still help elucidate and predict levels of other important processes occurring within the sediment. By focusing on a greater understanding of species activity rates and ranges, estimations of sediment modification and mixing can be produced independently from abiotic values, disentangling some of the processes at work in estuarine soft sediment dynamics. Combining a clear, independent classification of bioturbatory effect with data derived from sediment down-core water profiles may provide a means to explore and model the relative importance of abiotic and biotic variables acting at any one site. From such studies a better understanding of the multiple interactions and feedback loops operating in soft sediment system dynamics may start to emerge.

The SDE groups developed and described in this chapter provide an important foundation upon which to base future studies linking macrobenthic species activity and estuarine sediment dynamics. If relationships can now be found that link the distribution of SDE groups to environmental gradients within estuaries, the way will be open to model biological contribution to sediment mixing processes at the ecosystem level and hence facilitate comparisons between systems. Such ability would allow the effects of anthropogenic disturbance upon ecosystem functioning to be investigated for both academic and management purposes.

Chapter 5

Prediction of sediment disturbance effect group abundance from abiotic-biotic relationships

"Prediction is a tricky business – perhaps the only thing worse than a prediction is no prediction at all" (Faraway 2002)

5.1 Introduction

Following the development of new functional groups, the SDE groups from chapter 4, this chapter examines whether generic predictive models can be produced that would describe the distribution of the SDE groups within an estuary.

Chapters 2, 3 and 4 of this thesis have shown that our perception of relationships between environmental factors and the structure of macrobenthic communities can be influenced by:

- employing measures of biological function instead of species abundance to characterise the biota;
- utilising bioturbatory functional groups to characterise the macrobenthos,;
- weighting the contribution of a species to a biological function with some measure of species' body size; and
- treating the overall biological assemblages as two separate components – shallow and deep assemblages.

Following on from these findings, biological functional-effect groupings were derived in Chapter 4 of this thesis by assessing the ability of species to disturb and disrupt the sediment. Derived groups were then used to characterise the biota in further analyses to assess how biological assemblage structure compared to abiotic sediment characteristics, revealing some evidence that functional effect groups might be used as biological "response" groups, showing some strong associations with environmental forcing factors.

The present Chapter explores relationships between the biological sediment disturbance effect (SDE) groups developed in Chapter 4 and a suite of commonly measured environmental variables. The primary objective of the chapter is to

identify general, practical methods that predict the abundance of SDE groups, and hence levels of sediment disturbance, for implementation in any estuary, with low costs in time and equipment.

Infauna perform many important roles in the functioning of estuarine ecosystems (Biles et al 2002): they facilitate nutrient fluxes between the sediment and water (Solan et al 2004); they promote the degradation of organic matter (Anderson and Kristensen 1991); they can both stabilise and destabilise soft sediments (Yingst and Rhoads 1978, Black and Paterson 1997); and they provide food resources for many migratory birds and commercially important fisheries. Ability to predict the distribution and abundance of either the infaunal community or the functions that they perform would aid researchers and managers to predict the effects of environmental changes on estuarine ecosystem functioning. Managers are frequently concerned with how the distribution of species impacts upon a particular function rather than simply predicting the distribution of species *per se* (Fairweather 1999 and the references therein, Mouillot et al 2006 and the references therein). Thus, any model that can predict the levels of function occurring at estuarine sites could potentially meet the needs of many investigators without necessarily needing to predict species identity.

Techniques such as Linear Modelling and Generalised Linear Modelling (GLM) have been used to simulate the occurrence of some macrobenthic species in response to environmental factors (Ysebaert et al 2002, Ellis et al 2006). Anderson et al (2004) employed a combination of GLM and non-parametric regression to demonstrate the influence of sediment characteristics upon the distribution of estuarine macrobenthic species. The study presented here also undertakes a combined approach, using non-parametric means to determine the environmental variables that have strongest associations with functional groups,

followed by GLM methods to develop predictive models for the abundance of each biological effect group.

The aims of the work presented in this chapter were to:

- identify the environmental variable, or combination of variables, that best explained variability in the biological data for each SDE group;
- develop simple, cost-effective models that fitted the selected environmental variables to the SDE group abundance data; and
- validate predictions from the models developed by predicting the abundance of each SDE group at a new site.

The specific hypothesis addressed in this chapter was:

- *There is no significant association between the total abundance of individuals in any SDE group and one, or a combination, of the abiotic factors.*

5.2 Methods

The data used in this chapter to derive predictive models of biologically-mediated sediment disturbance were first introduced in Chapter 3. The biological data were subsequently used to develop the sediment disturbance effect (SDE) groups of Chapter 4, where some of the abiotic sediment characteristics examined in the current chapter were also discussed.

To validate the predictive ability of models developed in this chapter, further samples were collected from a new site at St. John's Ford in the Tamar Estuary (SX447696). This additional sampling at St. John's Ford provided independent abiotic and biological datasets. The abiotic data was used as independent variables in the existing models of SDE group distribution, and hence to predict the abundance of individuals occurring in each SDE group at St John's Ford. The

predicted numbers of individuals within each SDE group were subsequently compared to the observed biological data from the site.

St. John's Ford (see Figure 5.1) was visited in March 2005, when 5 cores were retrieved for faunal analysis and processed as set out in Chapter 3. Shallow and deep assemblages were separated and the species categorised into SDE groups according to the schemes outlined in Chapter 4, providing the estimated mean abundance of individuals for each SDE group in shallow and deep assemblages.

Abiotic samples were obtained and processed as outlined in Bale et al (2006) and Chapter 3 of this thesis to provide:

- surface sediment water content;
- interstitial salinity;
- concentration of chlorophyll *a* (Chl *a*) of the sediment surface layer;
- concentration of extracellular polymeric substances (EPS) of the sediment surface layer;
- percentage of particles <63μm in diameter in the sediment surface layer;
- mean depth of the Redox Potential Discontinuity (RPD);
- surface sediment shear strength; and
- the current flow at 10cm above the sediment surface as predicted by the BELLPLUME model (Robinson and Riddle 2004, see Chapter 3).

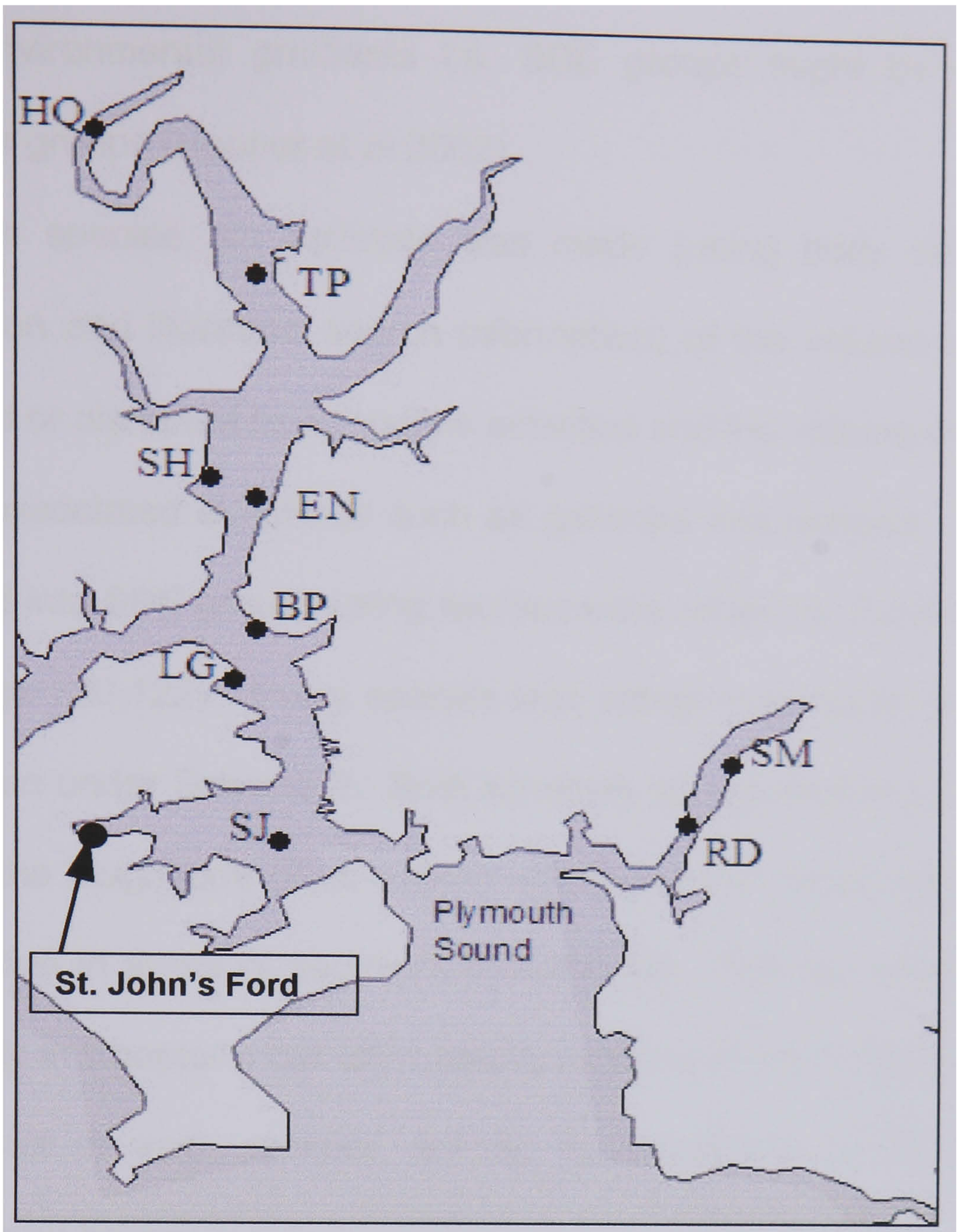


Figure 5.1 Location of the additional site (St. John's Ford) in relation to the original 9 sample sites in the Tamar and Plym estuaries utilised in model development: HQ is Halton Quay, TP is Thorn Point, SH is Saltash, EN is Ernesettle, BP is Bull Point, LG is Looking Glass Point, SJ is St. John's, SM is Saltram and RD is The Ride. Reproduced from Ordnance Survey data by permission of the Ordnance Survey © Crown copyright 2001.

5.2.1 Biological data used in model development

The SDE groups derived and discussed in Chapter 4 were developed to quantify the impact of species activities upon sediment disturbance. The findings of Chapter 4 suggested that some SDE groups may have strong relationships (ρ>0.6, p<0.05) with many environmental parameters (see Section 4.3.3.3), and that such relationships might be used to model the distribution of SDE groups

along environmental gradients i.e. SDE groups might be used as *functional response* groups (Hooper et al 2002).

For each species, an estimate was made (using body size, sediment depth distribution and literature search information) of the volume of sediment directly disturbed or disrupted by its routine activities and the volume of sediment occupied by any associated structures such as galleries and burrows. Species were then allocated into SDE groups using two separate schemes: Scheme 1 and Scheme 2 (see page 120-122). Every species was categorised firstly under Scheme 1 and then again under Scheme 2. Both schemes categorised every species according to both the magnitude of its overall effect and the depth regions in which it was most active in terms of sediment disturbance. The two schemes are discussed more fully in Chapter 4 but differ mainly in terms of the sediment horizons at which the impact of each species' activity is considered to be most influential as summarised below:

- **SCHEME 1**. Species were grouped according to the magnitude of any effect upon sediment disturbance and whether the effect occurred:
  - only on the sediment surface layer (0-2cm) ; or
  - with equal impact upon the sediment surface and deeper layers; or
  - mainly within the deeper sediment layers with only a minor proportion of that species effect impacting upon the sediment surface.

- **SCHEME 2.** Species were grouped according to the magnitude of the effect upon sediment disturbance and whether the effect occurred:
  - only in upper 4cm; or

- with equal impact upon the sediment surface and upon the deeper sediment regions to depths shallower than 10 cm below the sediment surface; or
- mainly below the sediment surface region extending to depths no greater than 10cm below the sediment surface, with only a minor proportion of that species effect impacting upon the sediment surface; or
- with effect split equally between that upon the sediment surface and that upon deeper regions extending to depths greater than 10 cm below the sediment surface; or
- mainly below the sediment surface region extending to depths greater than 10cm below the sediment surface, with only a minor proportion of that species effect impacting upon the sediment surface.

Within each scheme, the magnitude of any biological effect upon sediment disturbance was also considered giving rise to the SDE groups listed in Table 5.1 for Scheme 1 categorisation and Table 5.2 for SDE groups under Scheme 2

Table 5.1 Scheme 1 of SDE groups applied to both deep and shallow assemblages

Total volume (V) of sediment disturbed across all depths (cm^3)	**Effect greatest on surface sediment**	**Equal effect on surface and deeper regions**	**Effect greatest on sediment regions below the surface**
V ≤ 0.5	A1	B1	C1
0.5< V ≤ 1.5	A2	B2	C2
1.5 < V ≤ 5	A3	B3	C3
5 < V ≤ 20	A4	B4	C4
V >20	A5	B5	C5

Table 5.2. The SDE groups into which species were allocated under Scheme 2, allowing for differential exploitation of the sediment depths

Total volume of sediment disturbed across all depths (cm^3)	**Effect greatest on upper 4cm**	**Equal effects on surface and sediment body.**	**Effect greatest on sediment body.**	**Equal effects on surface and sediment body.**	**Effect greatest on sediment body.**
	Exploitation limited to upper 4cm	Exploitation limited to upper 10cm	Exploitation limited to upper 10cm	Exploitation extends >10cm	Exploitation extends >10cm
V ≤ 0.5	1a	2a	3a	4a	5a
0.5 < V ≤ 1.5	1b	2b	3b	4b	5b
1.5 < V ≤ 5	1c	2c	3c	4c	5c
5 < V ≤ 20	1d	2d	3d	4d	5d
V >20	1e	2e	3e	4e	5e

The mean abundance of individuals in each SDE group per m^2 of sediment surface area was modelled in response to abiotic variables, for both shallow and deep assemblages.

5.2.2 Abiotic variables

The abiotic variables included in this study, in analyses to explain the distribution of SDE groups, were selected from parameters that have been shown in previous studies to explain a significant proportion of the variability in the distribution of the estuarine macrobenthos (Pearson and Rosenberg 1978, Warwick and Uncles 1991, Snelgrove and Butman 1994,Ysebaert et al 2002, Freeman and Rogers 2003, Anderson et al 2004, Ellis et al 2006). The variables used in the analyses were selected with a view to ultimately producing a set of practical, generic tools for prediction. Therefore, emphasis was placed on variables that are commonly collected by the routine studies of statutory bodies or are available from routine environmental monitoring.

Model development in this chapter utilised the abiotic data from Chapter 3 that had been employed to characterise each of the nine original sample sites, providing an abiotic dataset containing:

- sediment critical erosion threshold;
- sediment erodibility rates;
- undrained shear strength of the sediment surface;
- mean depth of the Redox Potential Discontinuity (RPD);
- surface sediment water content;

- percentage of sediment particles < 63µm in diameter (% fines) in the sediment surface layer;
- concentration of extracellular polymeric substances (EPS) of the sediment surface layer;
- percentage total organic carbon (TOC) of the sediment surface layer;
- concentration of chlorophyll *a* (Chl *a*) of the sediment surface layer;
- mean depth to which oxic burrows extended; and
- predicted current flow at 10cm above the sediment bed, obtained from the BELLPLUME model (Chapter 3).

Prior to analysis, all abiotic variables were examined for univariate normality and only interstitial salinity, the percentage of TOC and surface sediment shear strength needed transformation prior to modelling. Appropriate transformations to normality were selected by using maximum likelihood to estimate the power transformation (Fox 2002), implemented in "R" (R Development Core Team 2007), so that:

- interstitial salinity was transformed using $(\text{salinity})^3$;
- TOC was transformed using $(\text{TOC})^3$; and
- surface sediment shear strength was transformed using $\log(x+0.02)$.

Subsequently, covariance within the abiotic dataset was examined using Pearson's coefficient.

5.2.3 Biological responses to environmental factors

Before modelling responses of SDE groups to variation in environmental parameters, comparisons were made between the strength of abiotic-biotic

relationships for both shallow and deep horizons when species were characterised by

- abundance
- abundance in SDE groups under Scheme 1; and
- abundance in SDE groups under Scheme 2.

To this end, the relationships between the abiotic characteristics of the sites and the structure of both the shallow and deep macrobenthic assemblage were examined using the RELATE procedure of PRIMER-E (Clarke and Gorley 2001). RELATE, which calculates the Spearman rank correlation between matrices, was applied to both the species abundance data and the functional groups defined above.

From these preliminary investigations using RELATE, the effects upon perceived abiotic-biotic associations of characterising biological assemblages by the abundance of individuals in SDE groups rather than employing individual species abundance, were examined for both shallow and deep assemblages. Subsequently, the SDE group schemes that provided the strongest abiotic-biotic relationships were selected for both shallow and deep horizons and used in further investigations to:

- determine the combination of abiotic variables that had the strongest relationships with the shallow and deep assemblages when each was characterised by the abundance of individuals in the SDE groups, across the nine original sites; and
- model the abundance of individuals in each separate SDE group as a response to the environmental variables for shallow and deep horizons across the nine original sample sites.

Thus, for all further analyses, assemblages from shallow and deep horizons were treated separately. Within each depth-related assemblage, animals were allocated to an SDE group and the total number of individuals within each group calculated. The aim of the modelling was to predict the total abundance of individuals within each SDE group.

To determine which abiotic factors had the strongest relationships with the abundance of the biota the DISTLM routine of the PERMANOVA software (Anderson 2001, McArdle and Anderson 2001) was implemented in PRIMER-E version 6 (Clarke and Warwick 2001) for the multivariate case, i.e., a dataset which contained the abundance of individuals within several SDE groups across the nine original sample sites (Chapter 3) was compared to the abiotic data. DISTLM is described in detail below.

5.2.3.1 DISTLM

DISTLM performs a non-parametric multivariate multiple regression analysis using any symmetric distance matrix (Anderson 2004) to test the hypothesis that no relationship exists between the biota (abundances) and one, or a range of, abiotic predictor value(s). Where relationships are found, the DISTLM routine provides a means to partition variance between the predictor variables and employs a permutation test to calculate the significance (p) of the multivariate test statistic (psuedo-F) (Anderson 2001, McArdle and Anderson 2001).

McArdle and Anderson (2001) have shown that for any term in a multivariate regression the sums of squares can be obtained from the original distance matrix itself. McArdle and Anderson (2001) and Anderson (2001) have also shown that a "pseudo-F" statistic can be derived to test whether the model accounts for a large proportion of the variability in the response (dependent variable) and that the

variability can be partitioned according to the contribution of each of the predictors (independent variables). Thus for any model, the significance of including each parameter in the model, given that the other terms are already accounted for, is also calculated. Some of the advantages of using DISTLM are:

- DISTLM makes no assumptions about the distribution of the data;
- DISTLM is based upon distance-based matrices and, unlike many other non-parametric tests, any distance measure of choice may be employed, including semimetrics such as the Bray-Curtis distance (McArdle and Anderson 2001);
- In DISTLM the number of abiotic variables included is not limited by the number of biological samples or observations obtained; and
- In DISTLM the procedure may be run for the univariate (e.g a single species or group) or multivariate (e.g. a community response) case.

The statistical theory underlying the DISTLM routine is given in more detail in McArdle and Anderson (2001) and Legendre and Anderson (1999) whilst examples of its application to ecological investigations are given in Anderson (2001).

5.2.3.2 Univariate modelling of the relationship between the individual SDE groups and the environmental variables

5.2.3.2.1 The models

Three modelling techniques were employed to develop a predictive model of the abundance of individuals within each SDE group based upon their response to environmental variables:

1) DISTLM. DISTLM can be employed for univariate analysis, i.e. it was used to examine the responses of a single SDE group (the dependent variable) to environmental factors (independent variables). This non-parametric test makes no assumptions about the distribution of the response (biological) data and allows many predictors to be considered in the search for those predictors that have the strongest associations with the biota. It does not, however, provide regression coefficients that can be used in a predictive capacity.

2) Least Squares Linear Regression (hereafter referred to as lm model). The lm model is suitable for continuous data with normally distributed errors and can be used to make predictions.

3) Generalized Linear Model (GLM) (Nelder and Wedderburn 1972). When errors are not normally distributed and/or the error variance is not constant, GLM with a gamma distribution can provide an alternative means to fit linear models to continuous and even skewed data. It can be used in a predictive capacity.

5.2.3.2.2 Implementing the modelling procedures

Many SDE groups were not represented at all stations and hence the data matrices frequently contained zero values. The presence of many zero abundances in biological datasets precludes modelling with DISTLM and certain GLM procedures such as those based upon the Gamma distribution. Where a small number of zero abundance did occur for an SDE group, abundance data were transformed as follows:

- shallow SDE group "B2": log (x+40);
- shallow SDE group "C2": log (x+3); and

- all deep SDE groups: log(x+3).

The value of the constant included in the log_{10} (x + constant) transformation was estimated using maximum likelihood (Fox 2002) as explained above.

As discussed in Chapter 4, where SDE groups were absent at many sites little confidence could be attached to any models or derived results. Thus, abiotic-biotic relationships and models were not investigated for SDE groups that were absent at 4 or more of the nine original sites (Chapter 3).

Faraway (2006) recommended that GLM be applied to untransformed data where possible, therefore transformations were not applied to those SDE groups that were present at all sites.

The data were modelled first using the DISTLM procedure, and the results used to select the best combination of abiotic variables upon which to base predictions of the abundance of each SDE group occurring at a new site. Thus, the abiotic variables selected by DISTLM were then used in both lm model and GLM methods.

Although data were available for several abiotic factors, there was a danger of overfitting models when using lm and GLM methods i.e. fitting the abiotic data to the biological responses so well that the model had no predictive power. With a low number of sample sites (9) and large number of potential predictors (11), the observed data in the current study could easily be overfitted, and this was partially addressed by using DISTLM; hence, removing the variable selection procedure from the lm and GLM modelling process. Crawley (2005) suggested that the number of parameters to be fitted with a model should be limited to a number equivalent to one-third the number of sampling units. Therefore, in this study, the maximum number of abiotic parameters fitted to any model was three. Although there was no intention to fit more than three variables to the observed data,

parsimony dictated that the simplest model be selected. Thus the DISTLM routine was also run to provide the AIC (Akiake Information Criterion) to assess whether a model with fewer than three parameters might be more parsimonious. Comparison of the "AIC" value for each nested model (i.e. comparing 3-variable models with smaller models, in which parameters have been dropped from the original model) indicated how the maximum likelihood of the model parameters fitting well changed by the deletion of an abiotic parameter from the model. The AIC is defined as:

$$AIC = 2v - 2\ln(L) \qquad \text{Equation 5.1}$$

where v is the number of parameters fitted and L the maximised value of the likelihood function

A small value of AIC indicates a better fit than a large AIC value.

Although model selection was based upon the AIC, the adjusted R^2 was recorded to aid interpretation of model results. The adjusted R^2 value represents the proportion of variance explained by the regression but also takes into consideration the effect of including extra parameters in the model. Thus, the "adjusted R^2" was calculated as follows:

$$ {}_{adj}R^2 = \left[\frac{\left(\frac{RSS}{(n-v-1)} \right)}{\left(\frac{SST}{(n-1)} \right)} \right] \qquad \text{Equation 5.2} $$

where RSS is the regression sum of squares, SST is the total sum of squares, n is the number of response observations and v is the number of predictive parameters included in the model.

5.2.3.2.3 Modelling with DISTLM

The DISTLM procedure, as described above, was run for each of the single sediment disturbance groups. Variable selection was carried out under the "BEST" option in the DISTLM and the following results were recorded:

- the single variable with the strongest association with the biota and its associated significance, AIC and adjusted R^2 values;
- the two-variable combination with the strongest association with the biota and the associated significance, AIC and adjusted R^2 values; and
- the three-variable combination with the strongest association with the biota and the associated significance, AIC and adjusted R^2 values.

Whilst stepwise multiple regressions could have been run, there were far more independent variables (abiotic factors) than sites. Unlike standard stepwise multiple regression, the DISTLM procedure can be run with all variables included and hence, it was possible to avoid making *a priori* decisions as to which independent variables (abiotic factors) should be included for the other modelling approaches. Instead, the independent variables to be included in later modelling attempts were dictated by the DISTLM results.

5.2.3.2.4 Modelling with Least Squares Multiple Linear regression (lm)

The lm models were used to obtain regression coefficients and develop a predictive model of SDE abundance based upon the independent variables indicated by the DISTLM procedure. Although data exploration revealed that some of the biotic data did not approximate univariate normality (see Chapter 4), the data were mean abundances not count data. Where mean values are obtained from several sampling events, the central limit theorem shows that there is a tendency for the means to approximate a normal distribution (Crawley 2005). Thus, lm modelling was used to fit the abiotic data to each SDE group dataset, and diagnostic plots were examined for evidence of any strong violation of the assumptions of normality in the models. In addition, the *p*-value associated with each abiotic variable selected by the DISTLM procedure was compared to the *p*-value associated with the same variables in the lm models. Whereas lm assumed a normal error distribution structure to calculate the significance of the model and each variable, DISTLM employed a permutation test with no assumption of normality. A comparison was then made between significance of the each variable chosen by DISTLM and the significance of the same variable under the lm model to assess how any deviation from normality had influenced the results.

All lm models were run using R statistical software (R Development Core Team 2007) and the following results were recorded:

- the F-statistic, its significance and associated degrees of freedom; and
- for each selected abiotic parameter, the statistical significance of the model with a limit at p=0.05 and its associated degrees of freedom.

The null hypothesis that the model was not a significantly better fit than the null model, in which each abiotic parameter=0 (i.e. there is no relationship between the SDE abundance and any of the abiotic factors being included), was tested

according to Faraway (2002) by comparing the "F-statistic" to a critical value of F. If the calculated F statistic was greater than the critical value of F, then at least one of the abiotic variables was linearly associated with the response and the null hypothesis was rejected. When the calculated F statistic was less than or equal to the observed critical value, then there was no evidence that any predictor was associated with the response and the null hypothesis failed to be rejected.

When a model was not shown to be significantly different from the null model at the 95% confidence level, the model was retained for prediction since it still had some explanatory power. Although the confidence level for the model was lower than desired, predictions remained possible, whereas the null model had very little predictive power, since it estimated a common mean for all responses regardless of changes in the environmental variables (Faraway 2002). Whilst the probability of any model being a better fit than the null model was assessed, the true predictive ability of all the models was determined by applying the models to provide predictions for abundances of individuals in SDE groups at St. John's Ford.

Diagnostic plots were examined for a lack of "goodness of fit" of each model and violation of any of the model assumptions (see Appendix 2). Plots of residuals against fitted values were examined for any patterns that would indicate a lack of normality or deviation from constant variance, which would indicate that lm was not an appropriate model. In addition, plots of Cook's distance statistics were examined to investigate how the model fit would change if a particular observation were excluded, and the existence of highly influential points was assessed using plots of residuals against "leverage" (Fox 2002). With a small number of sample sites, removal of any observations from the models was not practical, however,

examination of the diagnostic plots allowed the suitability of each modelling approach to be compared.

5.2.3.2.5 Modelling with GLM

An initial examination of the data revealed that treating abundance of individuals in each SDE groups as count data and modelling with GLM using the Poisson error distribution or the quasi-Poisson was inappropriate (pers comm. KR Clarke). Therefore, the data were treated as continuous, skewed data with an unknown distribution and modelled using GLM with a Gamma distribution (Faraway 2006). A GLM model has three components:

- a *Linear Predictor (η)*. This is "a linear sum of the effects of one or more explanatory variables" (Crawley 2005);
- the *error structure*, or distribution, of the response variable. For the purposes of the current study a Gamma distribution was selected since the data were continuous and skewed; and
- a *link function* that describes how the linear predictor and the *mean* of the response are related (Faraway 2006). The value (*η*) that is calculated by the *linear predictor* is transformed to a *predicted value* via the *link function*. Whilst there are different link functions that could be employed for each different type of error structure, in the current study the predicted abundances were required to be equal or greater than zero and the "log link" was the preferred option (Crawley 2005). Employing a "log link" and, hence the use of antilogs in the prediction stage, avoided any negative values.

The GLM Models were run using R software (R Development Core Team 2007) to fit the variables selected by the DISTLM procedure to the biotic data. The following statistics were recorded for each GLM model:

- for each selected abiotic variable, the statistical significance at p=0.05 and the associated degrees of freedom; and
- the Null deviance (i.e. deviance from fitting the null model) and the residual deviance of the GLM model.

Maximum likelihood estimates were used to fit GLMs to the data i.e. to select the set of parameters that provided the maximum likelihood of predicting the observed data (Faraway 2005). The improvement of the model fit over that of the Null model was assessed by comparing the residual deviance to the null deviance.

As with the lm models, diagnostic plots (see Appendix 3) were examined for evidence of violation of model assumptions and the presence of unusual data points such as outliers and highly influential (high leverage) points. For GLM models, however, the *deviance* residuals were plotted against fitted values in preference to the *response* residuals. Deviance residuals have already scaled out the variance function and hence any patterns in the plots could indicate possible violations of the model assumptions (Faraway 2006).

5.2.3.2.6 Minimum adequate model selection

It was not possible or recommended to make direct and objective comparisons between the initial results of the lm and GLM models since they are not nested and have different error distributions (Faraway 2006). Although the AIC (Akaike Information Criterion) has sometimes been used to compare models, this approach is not recommended unless comparing nested models (Faraway 2006).

Thus, subjective comparisons were made between the lm and GLM models on the basis of whether:

- the fit of either model was more significant than the comparable Null model; and
- all the abiotic variables selected by the DISTLM procedure explained a significant proportion of the variability.

5.2.4 Prediction from the lm and GLM models: Abundance of SDE groups at St John's Ford

To make a more objective comparison of the models and test their ability to generalise relationships between SDE groups and the environment, the models were used to predict the abundance of individuals in each SDE groups at St. John's Ford.

Sediment erosion rate data was not available for St. John's Ford, nor was the mean depth of deepest burrows known. Thus, predictions could not be made for 3-variable models that included sediment erosion rates and the mean depth of the deepest burrow as predictor parameters. For some SDE groups, however, although the 3-variable models included either sediment erosion rates or burrow depths as predictors, the 2-variable models did not. In such cases, the 2-variable model was employed for prediction.

5.3 Results

5.3.1 Biological Data

Biological data are summarised in Table 4.4 (chapter 4). Two shallow assemblage groups and seven of the deep assemblage groups were not modelled, since they occurred at too few sites.

5.3.2 Abiotic data

Environmental data are summarised in Table 5.3 for all nine original sites and the new site at St. John's Ford. Examination of the data for co-linearity revealed some strong correlations ($\rho>0.6$, $p<0.05$) between several abiotic factors as shown in Table 5.4, although none were perfect ($\rho=1$), or near perfect ($\rho>0.9$) relationships. Co-linearity can influence the sign of regression coefficients and cause difficulty in evaluating the true value of each independent variable in the model. The results for each independent variable in each model presented below should, therefore, be viewed with some caution, although co-linearity is not considered to be a major problem if the model is to be used for prediction, as was the intention in this thesis, provided predictions are based within the range of the independent variables used in model development.

5.3.3 Abiotic and biotic relationships

5.3.3.1 Inter-site similarity according to abiotic and overall biotic data

The RELATE tests revealed that relationships between the abiotic variables and overall structure of macrobenthic assemblages were strongest (Table 5.5) if the species were grouped according to sediment disturbance activity under Scheme 1 for shallow assemblages. For deep assemblages, all relationships were weaker than for shallow assemblages, whilst characterising the biota by SDE groups under Scheme 2 slightly increased the strength of abiotic-biotic associations. This would suggest that the only real gain by using SDE groups rather than species abundance when searching for relationships between the abiotic factors and the structure of deep assemblages as a whole, is the potential to model function directly and develop generic models.

Environmental variable	SITE									
	TP	HQ	EN	SJ	SH	LG	BP	RD	SM	St john's Ford
	1	2	3	4	5	6	7	8	9	
Chl a	16.91	16.38	3.78	2.88	14.45	4.18	15.43	10.36	7.18	34
s.e.	n=1	2.54	2.24	0.32	3.96	0.03	n=1	2.29	2.02	n/a
EPS	228.64	159.14	64.32	80.74	248.12	62.39	130.55	153.06	119.26	434
s.e	n=1	8.62	38.30	19.16	36.34	n=1	n=1	35.03	28.2	n/a
% < 63um	40.18	44.78	20.51	51.58	48.99	28.98	31.70	44.75	44.19	80.0
(pooled samples)	n=1	n=1	n=1	n=1	n=1	n=1	n=1	n=1	n=1	n=1
Salinity	24	9	28	35	30	33	33	31	32	31.5
s.e	0.33	0.33	2.03	0	0.17	0	0	0.33	0.33	0
Torque	0.45	0.45	1.40	0.50	0.27	0.45	0.00	0.09	0.00	0.00
se (n=11)	0.16	0.21	0.24	0.16	0.14	0.16	0	0.09	0	n/a
TOC	1.82	1.54	1.31	0.74	1.56	1.47	1.43	1.62	1.52	n/a
s.e	0.23	0.17	0.14	0.15	0.27	0.48	0.16	0.14	0.25	n/a
% water content	46.79	61.96	34.22	36.71	54.15	37.44	43.74	53.00	48.33	63.8
s.e	n=1	2.35	2.31	1.63	1.71	1.17	1.54	0.30	1.93	n/a
maximum erosion rate	0.00036	0.00021	0.00056	0.00186	0.00255	0.00173	0.00018	0.00027	0.00017	n/a
	n=1	n=1	n=1	n=1	n=1	n=1	n=1	n=1	n=1	n=1
Maximum water current - 10cm above bed	0.277	0.102	0.321	0.188	0.378	0.023	0.113	0.107	0.014	0.004
	n=1	n=1	n=1	n=1	n=1	n=1	n=1	n=1	n=1	n=1
mean extent of oxic burrows into sediment	110	158	132	130	205	40	180	160	112	n/a
s.e	34.8	18.1	0	n=1	5	n=1	20	n=1	14.6	n/a
mean RPD depth (cm)	4	6.8	2.7	2.5	4	2	3	3	2	2.8
s.e	0	3.5	1	0	0	0	0	0	0	n=1

Table 5.3 Summary of the mean values and s.e. for all environmental data for all of the sites considered in this chapter. n=3 unless otherwise stated. For St.John's Ford, data was taken from Bale et al (2006) and s.e. was not available. Site codes given in Figure 5.1

Abiotic factor code	Abiotic Factor	1	2	3	4	5	6	7	8	9	10
1	Chl a										
2	EPS	0.83									
3	% fines	0.25	0.50								
4	Transformed salinity	-0.60	-0.45	0.02							
5	Transformed sediment shear strength	-0.25	-0.10	-0.18	-0.36						
6	Transformed TOC	0.69	0.71	0.03	-0.55	-0.13					
7	sediment water content	0.74	0.70	0.57	-0.61	-0.24	0.54				
8	erosion rate	-0.29	0.07	0.26	0.39	0.39	-0.35	-0.21			
9	mean depth of RPD	0.71	0.53	0.29	-0.86	0.26	0.34	0.76	-0.18		
10	mean depth oxic burrow	0.55	0.55	0.36	-0.17	-0.23	0.01	0.52	0.00	0.44	
11	current at 10cm	0.19	0.47	0.00	-0.22	0.53	0.07	-0.07	0.39	0.20	0.47

Table 5.4 Correlations between the enviromental variables used in model development using Pearson's coeffiecient, n=3, r>0.56 is significant at p≤0.05

Table 5.5 The results of RELATE tests to examine similarity between abiotic and biotic datasets. ρ is the Spearman rank coefficient and indicates the degree of agreement between the abiotic and biotic matrices, where ρ=0 represents absence of any match, ρ=+1 represents complete agreement and ρ=-1 represents complete opposition (Clarke and Warwick 2001).

SDE Group Scheme	Shallow assemblages	Deep assemblages
	ρ	ρ
Scheme 1 SDE Group Abundances	0.48	0.16
Scheme 2 SDE Group Abundances	0.37	0.26
species abundance	0.38	0.23

Further analyses only considered Scheme 1 for shallow assemblages and Scheme 2 for deep assemblages.

5.3.3.2 Multivariate analysis of abiotic-biotic relationships using DISTLM

DISTLM was run for the multivariate shallow and deep assemblage datasets, where the biota was grouped into abundance of individuals in each SDE group under Scheme 1 for shallow assemblages and Scheme 2 for deep assemblages. The DISTLM procedure was run using the BEST routine to show the combinations of variables (from 1 variable to the full dataset) that explained greatest variance in the dependent (biotic) dataset. Results revealed that for shallow assemblages the strongest relationships were between:

- for the 1-variable model: surface sediment water content (R^2_{adj}=0.25);
- for the 2-variable model: surface sediment water content and the current at 10cm above the sediment bed (R^2_{adj} =0.47); and
- for the 3-variable model: surface sediment water content, the current speed at 10cm above the sediment surface and the mean depth of the RPD (Redox Potential Discontinuity) (R^2_{adj} =0.55).

For deep assemblages the strongest relationships were between:

- for the 1-variable model: interstitial salinity (R^2_{adj} =0.15);
- for the 2-variable model: interstitial salinity and surface sediment water content (R^2_{adj} =0.43); and
- for the 3-varaible model: interstitial salinity, surface sediment water content and the mean depth of the RPD (R^2_{adj} =0.44).

5.3.3.3 Univariate modelling of the relationship between the individual sediment disturbance effect groups and the environmental variables

5.3.3.3.1. Variable selection for lm and GLM using DISTLM

Tables 5.6a and 5.6b summarise the variables selected by DISTLM as showing the strongest associations with shallow assemblage (Table 5.6a) and deep assemblage (Table 5.6b) for:

- a single abiotic variable;
- two abiotic variables combined; and
- three abiotic variables combined.

The value of AIC, used to select the best variable or combination of variables is given, along with the adjusted R^2 to aid interpretation of the results. In addition, the significance of including each individual parameter in the DISTLM model, as calculated by permutation testing, is included in the tables.

SDE Group	Best single variable	R_{adj}^2	AIC	Best 2 variables	R_{adj}^2	AIC	Best 3 variables	p	R_{adj}^2	AIC
a1	Mean depth of RPD	0.31	56.4	EPS concentration Mean depth of RPD	0.59	53	Sediment Shear strength Mean burrow depth Current 10cm above bed	0.62 0.86 0.55	0.6	52.51
a2	Sediment Shear strength	0.39	66.3	Sediment Shear strength Mean depth of RPD	0.58	64	EPS concentration Sediment Shear strength Mean depth of RPD	0.35 0.001 0.206	0.86	54
b1	Sediment water content	0.21	72	Sediment water content Current 10cm above bed	0.3	71.5	Sediment water content Mean depth of RPD Current 10cm above bed	0.042 0.178 0.24	0.5	68.79
b2	Sediment erosion rate	0.42	45.7	Mean burrow depth Current 10cm above bed	0.78	37.4	Sediment erosion rate Mean burrow depth Current 10cm above bed	0.06 0.44 0.096	0.94	25.59
c1	Current 10cm above bed	0.22	65.3	EPS Current 10cm above bed	0.5	61.9	EPS Sediment erosion rate Current 10cm above bed	0.64 0.095 0.03	0.66	58.73
c2	Sediment water content	0.37	57.4	Salinity Sediment Shear strength	0.49	56.1	% particles <63 diameter Salinity Mean depth of RPD	0.31 0.05 0.14	0.63	53.49
c3	Sediment erosion rate	0.25	69.1	Sediment erosion rate Mean depth of RPD	0.45	66.9	Chl a concentration Sediment water content Sediment erosion rate	0.81 0.09 0.03	0.56	65.16

Table 5.6a. The DISTLM results for shallow assemblage sediment disturbance effect groups.

SDE Group	Best single variable	R_{adj}^2	AIC	Best 2 variables	R_{adj}^2	AIC	Best 3 variables	p	R_{adj}^2	AIC
3e	% particles <63 diameter	0.57	56	% particles <63µm diameter Sediment erosion rate	0.76	51.7	% particles <63µm diameter Sediment erosion rate Mean burrow depth	0.004 0.702 0.152	0.77	51.27
5a	Salinity	0.19	56.8	Chl a Salinity	0.31	55.9	% particles <63um diameter Salinity Sediment water content	0.92 0.139 0.962	0.47	53.87
5b	Sediment water content	0.64	53.1	Sediment water content Sediment shear strength	0.78	49.2	Salinity Sediment shear strength Sediment erosion rate	0.352 0.108 0.494	0.83	47.14
5d	Current 10cm above bed	0.76	46.8	% particles <63µm diameter Current 10cm above bed	0.84	43.5	Salinity Mean depth of RPD Current 10cm above bed	0.464 0.881 0.002	0.92	37.3

Table 5.6b. The DISTLM results for shallow assemblage sediment disturbance effect groups.

For the shallow assemblage, the adjusted R^2 for the 3-variable model varied from only 0.5 for the sediment disturbance effect group "B1" to 0.94 for group "B2". The current speed at 10cm over the sediment surface was selected by DISTLM for all three of the smallest SDE groups, i.e. SDE groups containing species that disturbed less than $0.5cm^3$ of sediment overall. In the 3-variable models for shallow assemblages, surface sediment water content and shear strength were included by DISTLM for four of the SDE groups, and sediment erosion rate for three SDE groups, whilst the percentages of fine sediment was only included for one SDE group. Several SDE groups also showed associations with either interstitial salinity or the mean depth of the RPD.

For the deep assemblages, the R^2 for the 3-variable model varied from 0.47 for group "5a" to 0.92 for group "5d". For 3-variable models, salinity was included by DISTLM for three of the four SDE groups modelled, as well as the percentage of fine sediment and the sediment erosion rate for two SDE groups. EPS, TOC and Chl *a* were not selected by DISTLM in any of the optimal three-variable combinations for the deep groups, although Chl *a* was included in the optimal two-variable combination for group "5a".

For each abiotic variable included in the 3-variable models, given that the other two variables were already included in the model, there was little statistical evidence that the addition of the third abiotic variable significantly increased the fit of the model, as indicated by the probability value "*p*" given in Tables 5.6a and 5.6b. However, for both shallow and deep models, both the AIC and R^2 suggested that a three-variable model always accounted for more variability in the data than a model with fewer parameters. Hence no parameters were removed.

5.3.3.3.2. Least Squares Linear Regression (lm model) and Generalised Linear Model (GLM)

The results for each model fitted to each biotic sediment disturbance group are summarised for shallow and deep assemblages, respectively, in Table 5.7a and 5.7b which detail:

- the three abiotic variables selected by the DISTLM routine as having the strongest combined relationship with the biotic data;
- for each selected abiotic variable, the statistical significance of including that variable in the model and the associated degrees of freedom ;
- for lm models, the F-statistic, significance and degrees of freedom for the models; and
- for GLM the null deviance (i.e. deviance from fitting the Null model) and the residual deviance of the GLM model.

GLM models all explained more variability in the data than their related null models. However, four of the lm models (a1, b1, c1, 5a) were not statistically significant improvements over the null models at p=0.05. In addition, for each SDE group, more of the individual abiotic variables explained a significant proportion of the variance (see significance of including that variable in Table 5.7a and 5.7b) when using GLM methods than when applying lm models.

From examination of diagnostic plots for each model (see Appendices 4 and 5), it appeared that the assumptions of the lm model were often violated with the majority of models displaying signs of heteroscedasticity (i.e. non-constant

Assemblage **Shallow**

Disturbance Effect Scheme **Scheme 1**

Sediment Disturbance effect group	Variables selected by DISTLM	Multiple Least Squares Linear Regression (lm model)				Generalised Linear Model (GLM)			
		Pr(>|t|)	F	p	df	Pr(>|t|)	Null deviance	Residual deviance	df
a1			4.71	0.064	3 & 5		2.21	0.33	8 & 5
untransformed	(Intercept)	0.05810				$6.09x10^{-7}$			
	Shear x	0.01840				0.00221			
	Burrow depth	0.44000				0.00205			
	10cm current	0.01970				0.00469			
a2			10.27	0.014	3 & 5		12.99	1.59	8 & 5
untransformed	(Intercept)	0.85046				$8.22x10^{-5}$			
	EPS	0.94556				0.0402			
	Shear x	0.00412				0.01920			
	RPD(xsal)	0.70949				0.00900			
b1			2.00	0.233	3 & 5		29.74	10.56	8 & 5
	(Intercept)	0.05660				0.00246			
untransformed	%water	0.17260				0.09877			
	RPD(xsal)	0.64140				0.41003			
	10cm current	0.17030				0.90717			

Table 5.7a The results of lm models and GLM models applied to shallow assemblages sediment disturbance effect groups
For each variable the probability is given for that variable being significant given that the other two variables are already included in the model

Sediment Disturbance effect group	Variables selected by DISTLM	Multiple Least Squares Linear Regression (lm model)				Generalised Linear Model (GLM)			
		Pr(>|t|)	F	p	df	Pr(>|t|)	Null deviance	Residual deviance	df
b2			32.11	0.001	3 & 5		0.78	0.03	8 & 5
transformed log(x+40)	(Intercept)	0.00043				0.00080			
	erosion rate	0.01623				0.00680			
	burrow depth	0.00198				0.00076			
	10cm current	0.00173				0.00066			
c1			3.79	0.094	3 & 5		6.97	0.52	8 & 5
untransformed	(Intercept)	0.05010				$5.14x10^{-7}$			
	Eps	0.16280				0.00119			
	erosion rate	0.35010				0.71065			
	10cm current	0.05500				0.00043			
c2			8.47	0.021	3 & 5		2.70	0.58	8 & 5
transformed log(x+3)	(Intercept)	0.63440				0.14330			
	fines	0.01880				0.02550			
	salinty x	0.01370				0.01510			
	RPD	0.06330				0.07400			
c3			23.40	0.002	3 & 5		14.56	2.96	8 & 5
	(Intercept)	0.06441				0.00048			
untransformed	Chl	0.07944				0.04123			
	% water	0.05340				0.00610			
	erosion rate	0.00056				0.00585			

Table 5.7a contd. The results of lm models and GLM models applied to shallow assemblages sediment disturbance effect groups For each variable the probability is given for that variable being significant given that the other two variables are already included in the model

Assemblage **Deep**
Disturbance Effect Scheme **Scheme 2**

Sediment Disturbance effect group	Variables selected by DISTLM	Multiple Least Squares Linear Regression (lm model)				Generalised Linear Model (GLM)			
		Pr(>|t|)	F	p	df	Pr(>|t|)	Null deviance	Residual deviance	df
	Intercept	0.187	7.345	0.0279	3&5	0.0002	3.602	0.1662	8 & 5
3e	fines	0.014				0.0003			
transformed	erosion rate	0.043				0.0028			
log(x+2)	burrow depth	0.495				0.0669			
	Intercept	0.013	3.976	0.0858	3&5	0.0127	1.415	0.4179	8 & 5
5a	fines	0.175				0.1750			
log(x+3)	salinity x	0.019				0.0186			
	% water	0.060				0.0599			
	Intercept	0.001	14.41	0.0068	3&5	0.0907	3.168	0.2106	8 & 5
5b	salinity x	0.002				0.0007			
log(x+3)	Torque x	0.002				0.0004			
	erosion rate	0.015				0.0079			
	Intercept	0.005	29.1	0.0014	3&5	0.0549	2.674	0.0723	8 & 5
5d	salinity x	0.010				0.0033			
log(x+3)	RPD	0.009				0.0033			
	10cm current	0.001				0.0001			

Table 5.7b The results of lm models and GLM models applied to deep assemblages sediment disturbance effect groups
For each variable the probability is given for that variable being significant given that the other two variables are already included in the model

variance) and skew in the data. For GLM models, fewer models (six) displayed heteroscedasticity, indicating that the assumption of a gamma distribution was incorrect for those data. Whilst a change from lm model to GLM improved the fit for some SDE group models, there were more outliers identified in the GLM models than lm models and all high leverage points remained influential regardless of modelling approach. Tables 5.8a and 5.8b summarise findings from examination of the diagnostic plots for each model.

There was little consensus between models as to the significance of the inclusion of individual abiotic parameters in determining the fit of the model. For some abiotic variables, the null hypothesis, which was that the variable did not explain a significant *additional* proportion of variability in the data over that explained by the other variables, could not be rejected. However, dropping the variable from the model affected the significance of the other parameters and hence the overall fit of the model. Since all of the DISTLM AIC and $_{adj}R^2$ results indicated that including three abiotic variables improved the model fit and increased the amount of variability explained by the regression, all three parameters were retained in the lm and GLM models.

Shallow Assemblage							
Model	**Multiple Least Squares Linear Regression (lm)**				**Generalised Linear Model (GLM)**		
Diagnostic Plot	Residuals vs fitted	Q-Q plots of ordered residual vs quartiles of the Normal distribution	Residuals vs Leverage with Cook's distance contours		Deviance Residuals vs fitted	Residuals vs Leverage with Cook's distance contours	
Reason for test	Patterns in plot indicate lackof fit and incorrect assumption about variance of errors	To check that errors are Normally distributred	To detect outliers and high leverage points that can be influential to the plot		Patterns in plot indicate lack of fit and incorrect assumption about variance of errors	To detect outliers and high leverage points that can be influential to the plot	
Looking for signs of?	Any strong patterns?	Linear fit?	Very high leverage points(≥ 0.8)	Potential outliers (Cook's Distance >1)?	Any strong patterns?	Very high leverage points(≥ 0.8)	Potential outliers (Cook's Distance >1)?
Category							
a1	Slight heteroscedasticity	Slight skew	None	None	Slight heteroscedasticity	None	Yes
a2	Slight heteroscedasticity	Approximated linear	Yes	y	None	Yes	Yes
b1	Heteroscedasticity	Skewed	Yes	y	Slight heteroscedasticity	Yes	None
b2	Heteroscedasticity	Skewed	Yes	None	Heteroscedasticity	Yes	Yes
c1	Heteroscedasticity	Skewed	Yes	None	None	Yes	Yes
c2	Slight heteroscedasticity	Skewed	Yes	None	Heteroscedasticity	Yes	Yes
c3	None	Approximated linear	Yes	None	None	Yes	Yes

Table 5.8 a Summary of observations form examination of diagnostic plots for lm and GLM for shallow assemblages.

Deep Assemblage							
Model	**Multiple Least Squares Linear Regression (lm)**				**Generalised Linear Model (GLM)**		
Diagnostic Plot	Residual vs fitted	Q-Q plots of ordered residual vs quantiles of the Normal distribution	Residuals vs Leverage with Cook's distance contours		Deviance Residuals vs fitted	Residuals vs Leverage with Cook's distance contours	
Reason for plot	Patterns in plot indicate lack of fit and incorrect assumption about variance of errors	To check that errors are Normally distributred	To detect outliers and high leverage points that can be influential to the plot		Patterns in plot indicate lack of fit and incorrect assumption about variance of errors	To detect outliers and high leverage points that can be influential to the plot	
	Any strong patterns?	Linear fit?	Very high leverage points(≥ 0.8)	Potential outliers (Cook's Distance >1)?	Any strong patterns?	Very high leverage points(≥ 0.8)	Potential outliers (Cook's Distance >1)?
Category							
3e	Slight heteroscedasticity	Skewed	Yes	Yes	Slight heteroscedasticity	Yes	Yes
5a	None	Skewed	Yes	None	None	Yes	Yes
5b	None	Skewed	Yes	None	None	Yes	Yes
5b 2 variable	Heteroscedasticity	Skewed	None	None	Slight heteroscedasticity	None	Yes
5d	Heteroscedasticity	Approximated linear	Yes	None	None	Yes	Yes

Table 5.8 b Summary of observations form examination of diagnostic plots for lm and GLM for deep assemblages.

5.3.4. Prediction of the abundance of sediment disturbance effect groups at St. John's Ford

Whilst models were developed to describe the response of the abundance of individuals in the SDE groups to environmental factors, it was necessary to assess the ability of the models to generalise beyond the sphere of development i.e. to predict using data not employed in model development. This was done using the independent dataset from St. John's Ford to:

- determine the mean abundance of individuals in each SDE group at St. John's Ford based upon field samples (see Table 5.9); and
- predict the abundance of individuals for each modelled SDE group at St. John's Ford using the new environmental data to provide values for the abiotic predictor variables of the existing models.

Predictions were made using only those models for which abiotic data existed for St John's Ford: data for sediment erosion rates and the mean depth of the deepest burrow were not available. Table 5.10 summarises:

- the SDE groups for which predictions of abundance were made;
- the abiotic variables included in the models; and
- the abundance and standard error for both the actual abundance and predicted abundance for each SDE group at St John's for each model fitted.

For the shallow group "A1" both the lm model and the GLM model predicted a value much higher than the upper 95% confidence limit of the mean abundance from field observations. The 95% confidence interval for the GLM model prediction encompassed zero abundance. Thus, predicted abundance could not be shown to be different from zero. However, the 95% confidence interval for the lm model did encompass some of the upper range from the 95% confidence intervals for the mean from field observations.

Species	Shallow Assemblage		Deep Assemblage	
	Mean Abundance ind m^{-2}	category S1	Mean Abundance ind m^{-2}	category S2
Nephtys hombergii	104	c3	0	5e
Nereis diversicolor	898	b2	23	3e
Streblospio shrubsolii	3482	a1	0	2b
Pygospio elegans	572	a1	0	3b
Polydora sp	260	a1	0	2c
Manayunkia aesturiana	2806	c1	0	2a
Spionidae indet	207	a1	0	2b
Syllidae indet	0	c1	0	1a
Chaetozone sp	0	b1	0	3a
Cirratulidae indet.	14	b1	0	3a
Heteromastus filiformis	0	c1	23	5b
Capitella indet	156	c1	0	4a
Tubificoides indet	13616	c1	102	5b
Phyllodoce sp.	104	c1	0	1c
Hydrobia ulvae	3066	a2	113	3b
Retusa sp	208	a2	0	3b
Abra tenuis	2910	a2	11	3b
Polyc indet	0	c1	34	4a

Table 5.9 The mean numbers of individuals for each species found at St. John's Ford in both the shallow (above 10cm) deep (below 10cm) assemblages. The SDE groups into which each speceis was placed are also given

Sediment Disturbance Effect group		Variables used in models	lm predicted abundance			GLM predicted abundance			Observed Abundance		
Assemblage	**Group**		**Mean**	**s.e.**	**95% C.I.**	**mean**	**s.e.**	**95% C.I.**	**mean**	**s.e.**	**95% C.I.**
Shallow	**A1**	2, 9	11899	3162	5575 – 18223	29698	16110	17479 – 41918	4521	920	2681 – 6361
Shallow	**A2**	2, 5, 9	5546	2145	1256 – 9836	112609	127983	-143357-368575	6184	1551	3082 – 9286
Shallow	**B1**	7, 9, 11	0	0	0	117	196	-275 – 509	14	14	-14 – 42
Shallow	**C1**	2, 11	42242	13502	15238 – 69246	1501148	911424	-321700 – 3323996	16682	5130	6422 – 26942
Shallow	**C2**	3, 4, 9	0	0	0	0	0	0	nil	Nil	nil
Deep	**5a**	3, 4, 7	2.9	2.6	-2.3 – 8.1	2.9	2.6	-2.3 – 8.1	nil	Nil	nil
Deep	**5b**	5, 7	446	2.1	442 - 450	446	2.37	441 – 451	124.5	45.3	34 – 215
Deep	5d	4, 9, 11	1.8	1.2	-0.6 – 4.2	2.4	1.1	0 – 4.6	nil	nil	nil

Table 5.10 The observed and predicted abundance, s.e and 95% confidence intervals for each sediment disturbance group at St. John's Ford in the Tamar estuary. For predicted abundances that were less than 0.5 or negative, the value "nil" is recorded. The abiotic variables included in the models are 2) extracellular ploymeric substances (EPS), 3) percentage of fine sediment, 4) interstitial salinity, 5) sediment shear strength, 7) sediment water content, 9) mean depth of the RPD, 11) the current flow at 10cm above the sediment surface.

For the lm model of shallow SDE group "A2", the predicted value for abundance at St John's Ford lay within the confidence limits of the mean abundance from the field observations. The confidence limits for the predicted value from the lm model both encompassed and were wider than the confidence intervals for field data. By contrast, the predicted value for group "A2" abundance at St John's Ford predicted by the GLM model was larger than the lm model prediction, with larger confidence intervals that included zero abundance. Thus, predicted values from the GLM model could not be shown to differ from zero: on the other hand predicted values from the lm model were always greater than zero for the 95% confidence intervals.

Group "B1" was rare at St. John's Ford and not predicted to occur by the lm model. The GLM model predicted low abundances; but once again, the confidence intervals for the GLM prediction included zero abundance.

The shallow group "C1" was predicted to have far higher abundance by both lm and GLM models than was recorded for St John's Ford, when both predictions exceeded the confidence intervals for the mean from field observations. However, the sample mean did lie within the confidence intervals for the lm model prediction. The GLM model abundance prediction was very high and included zero abundance in the associated confidence interval.

Groups "C2", "5a" and "5d" were all absent from the St John's Ford samples. Both the lm model and GLM models predicted zero abundances for the group "C2". For groups "5a" and "5d", both lm and GLM models predicted very low abundances with confidence intervals that encompassed zero abundances. In addition, the actual abundances and standard errors predicted by the lm and GLM models were identical for group "5a" and very similar for group "5d".

When developing the models of SDE distribution, the SDE groups "5a" and "5d" were not represented at all of the sites sampled and hence the abundance data for

both groups had been transformed before modelling. Transformation of data is often used to improve the approximation of the data to univariate normality. According to Faraway (2006), when the normal distribution is well approximated by the gamma distribution very similar results are produced by both GLM modelling and lm modelling of *log* transformed data. How well a normal distribution is approximated by a gamma distribution can be determined by examining the "shape parameter" of the gamma distribution, as given by 1/dispersion. Where the shape parameter is large then the gamma distribution approximates normality; even at shape parameter values as low as 6, the shape of the distribution becomes more symmetrical and starts to approximate a normal distribution probability function (www.uta.edu/faculty/sawasthi/Statistics/glsof.html, www.brighton-webs.co.uk/distributions/gamma.asp accessed 19/09/2088). The GLM gamma distribution shape parameter was 11 for the model of group "5a", and 71 for "5d" suggesting that when using the GLM gamma model approach, abundances for both of these SDE groups did indeed approximate normality.

For SDE group "5b", abundance was also *log* transformed before modelling. Predicted abundances of group "5b" at St John's Ford by both lm and GLM models were greater than the upper confidence interval for the mean from field observations. The confidence intervals for the predicted values from both lm and GLM models were small in comparison to those for the sampled data, and again the lm model and GLM models converged on a predicted value for SDE abundance. However, the predictive model for group "5b" was based upon only two predictor variables, since erosion rate data were unavailable for St. John's Ford. The shape parameter for the GLM gamma distribution was 7, again suggesting that the distribution of the transformed response approximated normality.

In summary, for those SDE groups for which predictions could be made:

- the groups that were absent at St John's Ford were not predicted to occur by any of the models;
- for all SDE groups from shallow assemblages, except the rare group "B1", the models did correctly predict the occurrence of the sediment disturbance effect groups although the estimated abundances were usually far higher than would be suggested from examination of the sample data; and
- overall it appeared that the lm models provided far better predictions than the GLM models since for most lm models the mean from field observations lay within the 95% confidence interval of the predicted value.
- The GLM models had much larger standard errors associated with the predicted values and hence, far wider confidence intervals that frequently encompassed zero; and
- there was no obvious advantage in using GLM with gamma distributions when the biological abundance data needed to be transformed before modelling.

5.4 Discussion

To assess the status of estuarine ecosystems and the likely impact of anthropogenic activity upon ecosystem processes, many investigators have examined the distribution of macrobenthic species (Bilyard 1987, Borja 2000, 2004, Fano and Rossi 2003, Hirst 2004, Tagliapetra et al 2005, Mouillot et al 2006). The macrobenthos have often been found to have predictable responses to stresses, both natural and anthropogenic (Pearson and Rosenberg 1978, Warwick 1986, Dauer 1993, Fano and Rossi 2003, Reiss and Kröncke 2005). Whilst advances have been made in modelling and predicting the presence or

absence of some species based upon empirical studies, modelling macrobenthic species abundance in response to environmental variables has proved difficult, due to the high levels of both spatial and temporal variability in the taxonomic composition of communities (Barnes and Hughes 1988, McArdle and Blackwell 1989, Dyer et al 2000, Hewitt et al 1996, Thrush et al 2003, Reiss and Kröncke 2005), including complex biotic and abiotic interactions that occur within soft sediments (Snelgrove and Butman 1994, Thrush et al 2003, Ellis et al 2006).

Empirical model development often requires several sampling sites and temporal replication to characterise the macrobenthic fauna (Tagliapietra et al 2005, Reiss and Kroncke 2005). As was demonstrated in Chapter 4, several species within the Tamar/Plym system were represented at very few sites e.g. *Calianassa* sp. *Corophium* sp. and *Mya* sp., resulting in datasets with many zero values for abundances. Where sampling is inadequate, models may often be restricted to the more cosmopolitan and abundant species, even though they may not be the species of interest. This chapter shows that by characterising and grouping species according to their functional contribution, there is some mitigation of these difficulties, since several species can combine within a single SDE group, and effective models can be developed to describe the distribution of biota in an estuary.

Some successful models of species distributions have been developed for particular estuaries (Ysebaert et al 2002, Thrush et al 2003). It has not, however, been possible to produce generic predictions for all individual species responses to abiotic variables that are easily transferred to systems other than the one in which the model was developed. The approach employed in this Chapter shows that by aggregating species according to their sediment disturbance effect and the depth of sediment exploited, generically useful tools might be developed that

predict the distribution of biological effects in estuarine soft sediments in response to commonly measured abiotic variables. The utility of such model tools will of course depend upon the ability of the models to produce accurate predictions and this in itself depends upon the initial categorization of the fauna and model development. The results of this chapter suggest that the SDE approach merits further development and testing.

In addition to predicting the distribution of each SDE group directly from abiotic data alone, there is the potential for the predictions to be used to estimate the overall biological effects of each assemblage, hence providing managers and researchers with an estimate of collective biotic contribution to ecosystem processes. Mouillot et al (2006) stressed the need to make inter-site comparison based upon differences in biological effect, rather than taxonomic variation alone. Several researchers have suggested that it is *functional* rather than *species* diversity that determines the resilience of ecosystem processes (Hooper et al 2002, Naeem and Wright 2003, Petchey et al 2004, Mouillot et al 2006). For researchers interested in linking species' effects to ecosystem processes, modelling SDE groups removes the need to first model species distributions and then to estimate each individual species impact upon processes of interest. Where there is a desire to predict the distribution of particular species, it is possible that this could also be derived from models that predict functional group distribution, using knowledge of each species' traits to allocate it to a functional group. Therefore, the SDE groups developed in this thesis have the potential to fulfil many roles and facilitate investigations into:

- the impact of the macrobenthos upon sediment dynamics;
- the role of functional diversity in ecosystem resilience; and
- the role of species diversity in maintaining functional diversity.

5.4.1 Modelling and predicting the abundance of individuals in SDE groups

Models developed in this Chapter generally accounted for a large amount of the variability in data e.g. the lm model for B2 had an $_{adj}R^2$ of 0.92 and for C2 had an $_{adj}R^2$ of 0.72 (see Appendix 4), and the models were used to predict the occurrence of individuals for eight of the SDE groups at St. John's Ford. Owing to the lack of data for two of the abiotic variables (sediment erosion rate and mean depth of burrowing) at the St. John's Ford site, predictions could only be made for eight SDE groups, and it is these groups that are considered in the discussion below.

For SDE group that were modelled from the Tamar/Plym study but that were absent in field observations at St. John's Ford, both the lm and GLM approaches predicted values that were not statistically different to zero abundances. For SDE groups that were recorded at St. John's Ford, both the lm and GLM predictions generally estimated higher numbers of individuals in each SDE group than were actually observed. The exception was SDE group "B1" from shallow assemblages, which occurred as very low abundances of *Cirratulidae* at St. John's Ford: predicted values were zero for lm models and confidence intervals encompassed zero for GLM models. Thus, both the lm and GLM models for "B1" produced predicted values that were not significantly different from zero.

Most of the model predictions for shallow SDE groups had wide confidence limits, which may partly have been driven by the low number of sites, and by extrapolating the model beyond abiotic values used in model development. Values recorded at St. John's Ford for extracellular polymeric substances (EPS), chlorophyll *a* (chl *a*), the percentage of fine sediment and the surface sediment water content were all greater than values recorded at any site used in model development. In addition, the maximum current flow at 10cm above the sediment

surface was lower at St. John's Ford than at any other sampled site. For any prediction, the confidence intervals increase as the new data get further away from the original values (Faraway 2002) and predictions become less reliable.

The initial model development had suggested that the GLM approach provided models with a better fit than the lm approach: all GLM models explained significantly more variability in the data than the comparable null model, whereas three of the lm models did not.

The lm models of the distribution of SDE groups "A1" (represented by *Spionidae* at St. John's Ford) and "C1" (represented by *Tubificoides* sp, *Capitellidae* and *Phyllodoce* sp. at St.John's Ford) were not statistically significant improvements over the null model. For predictive purposes, only two of the three variables used in model development were available (sediment shear strength and current speed at 10cm above the bed). Using the lm and GLM approach for predictions, both "A1" and "C1" models over-estimated the abundance of individuals at St. Johns. It is possible the predictions could have been closer to the observed values if data had been available for the third abiotic factor. The model for SDE group "B1" also did not produce a significant improvement in fit over the null hypothesis, although the actual abundance from field observations was very low, making comparison between prediction and observation inadequate.

Although both lm and GLM approaches appeared to correctly predict the occurrence of most SDE groups at St. John's Ford, for GLM models the 95% confidence intervals for the estimated abundance of individuals were wider than lm models and frequently encompassed zero abundance. In addition, when the biological data needed to be transformed before modelling, there was little to choose between the lm and GLM approaches since both produced almost identical predictions.

The GLM approach was undertaken in this present work since there was evidence of non-normality in the biotic datasets, such that an alternative error distribution was needed to accommodate skewed data. Although the model diagnostics for lm models did indicate non-constant variance and the existence of influential data-points for several lm models, the lm models generally produced predictions that were closer to field observations than GLM models. The lm models also had smaller standard errors.

The lm models performed very well and appeared to be robust, given that:

- the models of SDE group distribution were developed using data from only nine sample sites;
- co-linearity existed among the abiotic variables;
- there was evidence of non-normality in the models; and
- model evaluation was based upon predictor values outside of the ranges used in model development for most abiotic parameters.

Thus, the lm approach provided the most realistic predictions of the occurrence of SDE groups and of the abundance of individuals within each functional group. Therefore, the lm approach appeared to be most appropriate for modelling SDE group distribution in response to the environmental factors examined here.

The models developed and evaluated in this chapter appeared to be capable of generic prediction beyond the sphere of development. They are, however, limited to the SDE groups that were present at several sites within the Tamar/Plym system. As a result, the models cannot be used to predict the distribution of several SDE groups that were either absent from the Tamar and Plym estuaries or which occurred infrequently. For example, *Mya* indet. can attain lengths of 15 cm (Gibson et al 2001), but in the field-sampling used for model development it was never observed to exceed 1 cm although larger specimens were observed in

preliminary studies. Consequently the larger specimens of *Mya* indet would fall into SDE groups that could not be modelled with the existing data. Further investigations are required to identify and model the distributions of those species with sediment disturbance effects that fall into SDE groups not recorded in the current study. In addition, model development was restricted to predominantly muddy sediment in the Tamar-Plym system in late spring/early summer. Whilst the models appeared to perform well for muddy sediments, their ability to predict biological effects in sandier environments is less apparent. It would be beneficial to now extend the approach to other estuaries, and to evaluate the predictive accuracy of the models in systems experiencing very different hydrodynamic regimes presenting a range of sediment grain sizes. Further testing would allow consideration of whether:

- refinement of the models employed in this chapter would produce stronger, generic and more powerful tools to predict the distribution of functional groups in estuaries; or whether
- a hierarchical approach should be employed with different models of SDE group response to environmental variables being developed for a range of broad scale abiotic factors such as wave exposure and sediment type.

In addition, the influence of seasonal effects (Reiss and Kroncke 2005) should be examined to assess how well the model can generalise functional impacts over different temporal scales.

5.4.2 Abiotic drivers of the distribution of the estuarine SDE groups

The multivariate application of DISTLM revealed abiotic variables that were correlated with both the shallow and deep assemblages when each assemblage was characterised by the abundance of individuals in all the SDE groups.

However, the observed patterns could not be used for prediction of SDE group distribution, and the relative contribution of each SDE group to the overall pattern was not evident from the multivariate results. Comparing the results of the multivariate and univariate DISTLM application revealed that the abiotic parameters selected by the multivariate DISTLM were only selected once as a 3-variable group in the univariate studies: for SDE group "B1" (current speed at 10cm above the sediment bed, water content of the sediment surface and the mean depth of the RPD). However, at least one of the 3 parameters selected by the multivariate DISTLM was also selected for univariate models for each SDE group from shallow assemblages and for two of the deep assemblage models.

Although the multivariate and univariate DISTLM regressions determined the abiotic variables with the strongest associations with the biotic datasets, different techniques were required for predictions to be made. The multivariate and univariate DISTLM comparison suggested that the general pattern of abiotic-biotic associations across whole assemblages masked some of the more subtle associations between individual SDE groups and the abiotic data. Thus, univariate modelling based upon each individual SDE group's response to abiotic factors was preferable to a single model based upon the overall assemblage associations with environmental variables. This suggests that the different components of the community do not have identical responses to environmental forcing nor that a single influencing factor, biotic or abiotic, is likely to be detected.

Although the univariate DISTLM application selected different 3-variable combinations of abiotic factors for each SDE group model, there were some environmental factors that were selected more frequently than others:

- For shallow assemblages, the variables most often included in models were the current speed at 10cm above the sediment surface, the mean depth of the RPD and the sediment erosion rate; and
- For deeper assemblages the most frequently modelled variables were the interstitial salinity, the percentage of fine sediment present, the sediment erosion rate; and the surface sediment shear strength.

Most of the abiotic factors selected for modelling have previously been shown to have strong associations with the estuarine infauna (Forster et al 2006). These factors include current flow (Ysebaert et al 2002, Thrush et al 2005, Ellis et al 2006), salinity (Bonsdorff and Pearson 1999, Ysebaert and Herman 2002) and the percentage of fine sediment particles (Gray 1974, Snelgrove and Butman 1994, Anderson et al 2004). However, not all abiotic factors were selected by DISTLM with equal frequency for both shallow SDE groups and deep assemblage SDE groups. Both the percentage of fine sediment and the interstitial salinity were indicated by the DISTLM results to have been less influential on the distribution of shallow SDE groups than for the deep ones. However, many of the abiotic variables were highly correlated with each other indicating relationships between RPD and salinity, water content and shear strength of the surface sediment, and EPS and Chl *a*. Correlations might lead to the selection of a parameter that is not itself influential on the distribution of SDE groups, but which is highly correlated with other factors. Although co-linearity can influence the precision of regression coefficients, the use of a variable selection method (DISTLM) mitigates potential problems (Faraway 2006). Nevertheless, it may be that parameters selected for modelling the distribution of the SDE groups were not the factors responsible for patterns of biological distribution. As a result, a distinction should be made between the predictive ability of the models and their ability to inform about

processes involved in structuring macrobenthic assemblages. For example water content may actually represent the influence of porosity and permeability upon the benthic community rather than simply acting alone. While the mean depth of the RPD was selected in several shallow assemblage models, it was strongly correlated with interstitial salinity. Although it was the mean depth of the RPD that was selected by DISTLM for prediction of many shallow SDE groups, it is equally likely that salinity was as important a factor in determining their distribution, such as in deep assemblages, for which DISTLM selected salinity as a predictive factor. As mentioned above, the surface sediment grain size was rarely identified in shallow assemblage models. This was surprising, since several studies have demonstrated that grain size can influence species activities such as burrowing, tube construction and migration (Green 1968, Trueman and Ansell 1969, Alexander et al 1993, McLachlan et al 1993, de la Huz 2002) and frequently relationships have been observed between the sediment grain size and macrobenthic community composition (Davis 1925, Thorson 1957, Sanders 1958, Green 1968, Rhoads and Young 1970, Gray 1974, Thrush et al 2003, Anderson et al 2004). Snelgrove and Butman (1994) stressed, however, that sediment grain size often correlated with other abiotic factors that led more directly to the creation of the physical environment in which the biota reside. Warwick et al (1991) and Dyer (2000) both found evidence that inter-estuary differences in biota related to hydrodynamic regime, whereas within estuary variations in community composition had strong associations with sediment grain size and organic content. Freeman and Rogers (2003) also demonstrated that hydrodynamic forces needed to be included in any attempt to link benthic communities to physical forcing factors, concluding that sediment grain size was an important predictor variable when combined with other factors.

It may be that the current study did not cover a sufficiently large range of sediment types for the influence of particle size to be detected. Therefore, any further development of SDE group models should be designed to overcome this limitation. Equally surprising was the frequency with which sediment erosion rate was selected by DISTLM as a predictive factor in SDE distribution. Relationships between the macrobenthos and sediment erosion rates are uncommon in the literature on estuarine sediment dynamics (Le Hir et al 2007, but see Paterson et al 2000). Rather, the macrobenthos are more usually shown to have relationships with the sediment critical erosion threshold (Widdows et al 2000, Widdows et al 2002, Orvain et al 2003, Le Hir et al 2007). Both the sediment erosion rates and critical erosion thresholds are derived from the same procedure, yet there is rarely any evidence of a strong relationship between sediment erosion rates and sediment critical erosion thresholds (Le Hir et al 2007). Paterson et al (2002) suggested that sediment erosion rates were related more to within-sediment processes, rather than dynamics of the surficial layer.

The sediment critical erosion threshold was determined by considering the point at which sediment erosion commenced, whilst the maximum erosion rate was calculated from data obtained following this initial resuspension. Thus, it appears that sediment erosion rates may represent some property of the sediment layers below the sediment surface (Paterson et al 2000). Lundkvist et al (2007) suggested that diatoms stabilised sediments just below the surface sediment layer rather than the surface itself, for which the most influential factor appeared to be the ease with which algal mats were removed. For these estuaries the dynamics influencing the potential for sediment erosion to commence may not be the same as those influencing erosion of slightly deeper layers.

In Chapter 4 of this thesis, sediment erosion rates were shown to be weakly correlated with measures derived from down-core sediment profiles of Chl *a* consistent with the findings of Paterson et al (2000) suggesting relationships between sediment erosion rates and Chl *a* and EPS concentrations. Increased levels of Chl *a* removal from the near-surface layers might reflect increased biological activity, which may in turn be expected to promote sediment disturbance and hence increase sediment erosion rates. Nevertheless, the availability of Chl *a* in deeper layers, had a negative relationship with the sediment erosion rate, suggesting that the relationship between the two abiotic factors was not simply due to increased biological activity promoting higher erosion rates.

Sediment erosion rates had weak positive correlations with the percentage of fine sediment and the current flow at 10cm above the sediment surface, suggesting that sediment erosion rates may reflect a composite of interactions. It would be beneficial for future studies of sediment dynamics if links between sediment erosion rates and other abiotic factors could be elucidated. Sediment erosion rates are not convenient to measure: usually either a portable flume must be positioned in the field or sediment must be transferred to suitable laboratory testing equipment. Equipment to measure sediment erosion rates is not easily accessible for all researchers, and there is frequently a disparity between measurements obtained from different equipment such as Cohesive Sediment Meters and even between flumes of different construction (Tolhurst et al 2000, Widdows et al 2005). Thus, abiotic proxies for sediment erosion rates need to be found to circumvent these problems. Le Hir et al (2007) suggest that relationships may be found between erosion rates and the bottom shear stress induced by current flows.

The modelling exercises presented here did provide realistic predictions of biological functional groups by modelling the relationship of the SDE groups to the environmental variables when using a very restricted number of abiotic predictors. Even when not statistically significant, the developed models were still indicative of the abiotic-biotic relationships, when prediction of the abundance of individuals in SDE groups could be made. The confidence that can be placed upon predictions, however, is limited and could be greatly improved if new sites were sampled under a wider range of abiotic conditions to allow refinement of the models.

The high levels of co-linearity among the abiotic variables suggested that it might be possible to identify a reduced suite of abiotic parameters for consideration in future studies. As was shown in Chapter 4, sediment water content could be used to predict values for some of the other abiotic parameters such as sediment shear strength. If these relationships are developed further, then sampling could be restricted to a very few key variables.

5.4.3 The ability of the models to generalise the distribution of SDE groups and biotic effects.

The current study has shown that predictive models of functional group distributions can be derived for estuarine macrobenthos; based upon the infauna's ability to disturb and disrupt sediment. The challenge remains to now develop the models further to improve confidence in the models ability to accurately predict the structure in Macrobenthic assemblages and to allow testing across a wider range of environmental and biological variables.

The very nature of an infaunal existence necessitates biological interaction with the sediment matrix, thereby promoting sediment disturbance, if not through feeding activities then by the need to seek refuge from predation or sediment

resuspension and potential extirpation from the intertidal environment resulting form hydrodynamic forces (Hall 1994). This intimate association of the infauna with the sediment matrix should theoretically allow biological functional groups to be developed based on a physical and measurable effect realised by the biota. Although accurate direct measures of the overall levels of sediment disturbed are not readily available for many estuarine species, there are many studies into those species activities and traits that, as already mentioned, often promote sediment disturbance (Hall 1994, Snelgrove and Butman 1994). Thus, realistic estimates of the physical impact of the biota upon their environment should be possible from biological data alone.

Developing models that predict the distribution of functional groups within an ecosystem provides a means to link biotic activity to ecosystem processes (Hooper et al 2002, Fano et al 2003, Mouillot et al 2006). In some instances of assessment of ecosystem status, the functional contribution of the biota may be more informative than the taxonomic composition of the macrobenthic community (Diaz and Cabido 2001, Mouillot et al 2006). Many researchers and statutory bodies seek ways to assess whether ecosystems are "healthy" and whether processes or functions within the system are threatened by potential future species extinctions or invasions (Crooks 2004, Fano et al 2003, Wallentinus and Nyberg 2007) by establishing links between species and ecosystem processes. Models of functional group distribution provide such links.

Where the focus of interest is upon the distribution of a particular species, then generic models that can predict the distribution of functional groups could also provide a tool to assess the likely distribution of the component species from any one SDE group for any estuary. Using knowledge of the local species pool and

species' traits, it should be possible to prepare inventories of species that could contribute to each SDE group within a given locality.

Whilst macrobenthic species perform many "functional roles", not all roles are evident or quantifiable without extensive single species investigations. The direct contribution of many species to other ecosystem processes such as nutrient fluxes and the degradation of organic matter can be difficult to assess. Nevertheless, the influence of infaunal species on sediment disturbance might provide a useful proxy for some of these other biological functions. Nutrient cycling and pollutant burial within the sediment, and fluxes of solutes and matter across the sediment-water interface are influenced by macrobenthic species both directly and indirectly by their impact upon sediment mixing processes (Swift et al 1993, 1996, Levin et al 2001, Waldbusser et al 2004, Mermillod-Blondin et al 2005). Both the indirect and direct effects of each species are influenced greatly by the species' body size and abundance (Thrush et al 2003, Mouillot et al 2005). Therefore, where SDE groups are developed from a solid understanding of the activities and body size distributions of the component species, then it is likely that associations will be found between the distribution of the SDE groups and other processes occurring in soft sediments. The SDE groups developed in this thesis convey information about the magnitudes and depth ranges over which sediment disturbance is occurring. Therefore, by modelling the distribution of SDE groups through an estuary, the likely magnitude of processes allied to sediment disturbance can also be visualised. For ecosystem processes that are difficult to quantify accurately in the field, modelling SDE group distribution may provide a relatively cheap and robust proxy.

It is clearly crucial that for the SDE group approach to provide meaningful predictions and inform about ecosystem processes, the SDE groups themselves

must accurately characterize the macrobenthos. For some species, data can be found that describe activities and calculate reworking rates, e.g. *Nereis diversicolor* (Trevor 1977, Cammen 1980, Davey 1982) and *Calianssa* sp. (Rowden and Jones 1993, Rowden et al 1998). For others, relatively little is known, for example how far and how often do errant polychaetes such as *Nephtys hombergii* travel and in which directions? Do behaviours change with maturity? Even for well-studied species such as *N. diversicolor* the question of how to characterise its range of activities such as burrowing, deposit feeding and net-spinning can often only be resolved subjectively. For many of the species included in the model development in this chapter very little quantitative data was available and SDE values were inferred from morphology or estimated from similar species. This is a major shortcoming of the model development and calls into question the models' ability to represent the true structure of macrobenthic assemblages. If, however, some of these questions about species' activities can be answered and realistic estimates made for each species, then SDE groups could provide a means to model the functioning of estuaries.

Unlike many functional group classification systems (Diaz and Cabido 2001, Hooper et al 2002), the SDE groups developed in this study perform dual roles, providing information about biological *effects* upon the sedimentary environment, and facilitating the modelling of biological *responses* to environmental gradients. This dual performance of SDE groups provides a direct means to link ecosystem function and species activity, and hence to assess how changes in the environment could influence biological effects upon ecosystem processes.

Many researchers have emphasised the need to study trophodynamics to understand ecosystem functioning (Baird and Ulanoxicz 1993, Livingston 2002, Pasquaud et al 2007). By allocating all the biota in an ecosystem into

compartments according to their trophic activities, flows between compartments can be investigated and modelled. This approach was extended by Brown et al (2004) to include biomass as a proxy for body size effects. However, it was shown in Chapter 2, that functional groups developed according to trophic traits of the estuarine macrobenthos, whilst informative in their own right, did not perform well as *response* groups. Dangles and Malmqvsit (2004) were also unable to link the diversity of stream invertebrates to environmental variables. Although trophic functional group classification can be informative and applied to classify many different biotic components of an ecosystem, it appears that modelling the distribution of trophic functional groups in response to environmental forcing is unlikely to succeed in producing generic, predictive tools for general application in estuarine management, including research into sediment dynamics.

In contrast to trophic functional groups, modelling abiotic-biotic relationships based upon the distribution of SDE groups did provide generic algorithms that appear to have the potential to be applied to further estuarine systems. Thus, the present work provides the beginning of a common framework for modelling biologically-mediated sediment disturbance, with potential to generalise across estuaries and possibly across many research interests.

In summary, if the approach suggested in this thesis is developed further, in particular to overcome the difficulties arising from such a small dataset, there are potentially many important consequences of these findings:

- future predictions of the impact of biota upon sediment disturbance may be possible based upon only abiotic data for estuarine sites, circumventing the need to model species distribution for some research purposes;
- since biological sediment disturbance impacts upon many other sediment processes within estuaries, such as nutrient fluxes and the degradation of

organic matter, prediction of other estuarine functions may also be facilitated by modelling the distribution of sediment disturbance effect groups; and

- predictions of function may provide an indirect means to model infaunal macrobenthic species distributions within an estuary.

Therefore, the sediment disturbance effect groups developed in this thesis provide an important step forward in the search for links between broad scale abiotic drivers and smaller scale processes occurring within estuarine intertidal sediments.

CHAPTER 6

General Discussion

"Ecologists deal with systems of great complexity"

Shugart (1997)

6.1 Overview of the findings of this Thesis

The overarching aim of the research presented in this thesis was to link species activity to ecosystem processes. Using the estuarine ecosystem as a test bed, the impact of the activities of macrobenthic species upon sediment disturbance was investigated and novel functional groups were developed that theoretically described the magnitude of sediment disturbance promoted by the biota during their routine daily activities. This novel categorisation of species allowed modelling of the distribution of functional groups along an estuary in response to environmental variables. Predicted distributions were validated using independent data. Since the sediment disturbance effect (SDE) functional groupings theoretically convey information about the magnitude and distribution of effects within the sediment, inference can also be made as to activity occurring at any one site. Hence, inter-site comparisons can be based upon the relative abundance of different functional groups, including estimates of the overall magnitude of sediment disturbance. Successful development of such an approach would represent a step forward for environmental managers assessing the health of estuarine ecosystems, since it would provide a tool to compare sites according to an important ecological process and to estimate biological effects for parameterisation in other ecosystem models.

The ability to predict levels of biologically-mediated sediment disturbance also has potential to illuminate many other ecosystem processes that are allied to sediment dynamics, such as biochemical processes within the sediment and nutrient fluxes across the sediment-water interface (Aller 1982, Rice 1986, Berg et al 2001, Biles et al 2002, Mermillod-Blondin et al 2004, Waldbusser and Marinelli 2006); the physical stability of the sediment and its propensity to erode (Rhoads et al 1978, Grant et al 1982, Meadows et al 1990, Rowden et al 1998, Paterson and Black

1999, Herman et al 2001, Widdows and Brinsley 2002, Widdows et al 2004, Orvain 2005, Le Hir et al 2007); and the degradation of organic matter (Rhoads 1974, Aller 1982, Aller and Yingst 1985, Blair et al 1996, Boon and Duineveld 1998, Dauwe et al 1998, Nordstrom et al 2006). By predicting the location and relative strengths of sediment disturbance, the occurrence of processes that are themselves influenced by sediment disturbance may also be predicted *a priori*. In addition, functional groups that estimate contribution to overall effects allow links between biotic and abiotic ecosystem compartments to be explored, elucidating the relationships between ecosystem functioning, organisation and resilience.

Whilst the results of this study suggest that these goals are achievable, whether the existing SDE groups themselves can fulfil the functional group role is unknown. The accurate characterisation of the biota is crucial for the SDE groups to perform their task in describing the impact of the biota on sediment disturbance. The lack of any empirical testing to substantiate the estimated effects of each group severely limits the certainty that can be related to the estimates.

Any field survey of the macrobenthos has inherent errors due to sampling and processing those samples, as well as being subject to natural and stochastic variation in the biocoenosis. The processes involved in developing the SDE groups also had many other associated sources of error for example errors in body measurements, interpretation of the literature, estimation of the sediment depths exploited and the spatial extent of activity. For the SDE groups to accurately characterise each species' contribution to function, each species needed to be correctly identified, adequately sampled to reflect its true abundance, the depths at which the species were observed needed to reflect the true spatial exploitation of the sediment, the body measurements had to be accurate and there had to be adequate scientific knowledge about the species activities. In terms of

the type of motility, feeding and biogenic construction activities exhibited by the estuarine macrofauna, there is indeed a large body of scientific knowledge but the literature is heavily biased to a few well studied species, for example *Nereis diversicolor* (Trevor 1977, Davey 1994, Francois et al 2002) and Calianassa (Rowden and jones 1993, Rowden et al 1998), and for only a few species is there much information about the *frequency* with which activities occur e.g. sediment reworking rates for Callianassa (Rowden and Jones 1993) or *Hydrobia* (Orvain and Sauriau 2002). Little is known about how often tubes or burrows are rebuilt, how many unoccupied burrows persist in the sediment or the behaviour of commensals. None of the sources of error was investigated in terms of its influence on the SDE classification process, nor were any independent measures of actual sediment disturbance effects available and thus, the conceptual models of how each species interacts with the sediment lack validation. For the models to be generic and portable between estuaries it must also be assumed that the SDE group classification of a species does not change with locality. If this is not the case, then each species must be re-classified for each estuary, although it may be that the algorithms describing relationships between the SDE groups and environment remain unchanged. Body size, sediment depths exploited and activity are all inherently variable and hence for some species it is likely that re-classification must be considered for each new estuary. Body size varies with factors such as season, cohort, maturity and food supply (Basset et al 2004) and it may also vary with population, for example *Heteromsatus filiformis* is known to be much larger in the Schelde estuary than in the Tamar system (M.Kendall pers.comm.). Some species such as *Scrobicularia plana* and *Nereis diversicolor* are known to vary their position within the sediment seasonally, usually being at shallower depths in winter (Zwarts and Wanink 1993, Zwarts et al 1994). Activity

levels have also been shown to vary according to season, age, reproductive status, and ambient environmental conditions (Wheatcroft et al 1998).

The statistical procedures employed in this thesis have errors and implicit assumptions over and above the error sources already mentioned. Consequently it is perhaps surprising that any relationship existed between the SDE groups and the environment. Yet despite the very low number of sample locations, relationship were identified and validated. Although this could be a statistical artefact, the fact that more than one SDE group demonstrated relationships with the abiotic data gives weight to the case for further investigations to refine and extend the approach. The potential advantages of pursing the approach advocated in this Thesis are considered below.

6.2 Potential value of developing the SDE groups further.

Legislation and concerns about human impacts upon ecosystems are strong drivers of much of the research into ecosystem functioning (Rapport et al 1998 and the references therein, Dolédec et al 1999, Carignan and Villard 2002, Reiss and Kröncke 2005). For example, the European Water Framework Directive (WFD: 2000/60/EC) requires that the status of estuaries and coastal water bodies be determined. Various biotic elements require consideration under the WFD, including the macrobenthos, for which species composition must be quantified every three years (de Jonge et al 2006). There are many ongoing investigations to develop tools that can determine whether the structure of the biological communities (species composition and abundance) observed in the field have in fact deviated from the "natural composition" that would exist in the absence of human disturbance (Grall and Glèmarec 1997, Molvaer et al 1997, Weisberg et al 1997, Borja et al 2000, Frid and Hall 2001, Borja et al 2003, Rogers and

Greenway 2005). The current best practice to assess the impact of human activities is to select or combine the following approaches:

- use of historical data as a baseline;
- make comparisons with nearby "pristine" sites;
- use expert opinion;
- employ indices of estuarine health; or
- develop models that predict species distribution including the distribution of selected indicator species.

There are inherent problems with each of these approaches and each relies upon knowledge of how community structure relates to quality, or "good ecological status" (de Jonge et al 2006). Historical data and pristine sites are rarely available, and nearby systems may be so different in their physical and chemical properties that comparisons are unhelpful. Expert opinions rely on a conceptual model of the environment for which levels of uncertainty cannot be assessed (Halpern et al 2007) and conceptual models cannot be easily transferred to, and applied by, non-specialists. Much effort has been expended on the development of indices that infer ecosystem health from various combined measures of species abundance and tolerances to stress (Reiss and Kröncke 2005, Quintino et al 2006 and references therein). Whilst the benthic indices approach has some advantages over previously discussed practices, it can lack the ability to distinguish between change in the biota induced by either natural "stress" or human activities (Quintino et al 2006). For this reason, many investigators attempted to model species distributions (Ysebaert et al 2002, Thrush et al 2003, Rosa-Filho et al 2004, Ellis et al 2006), but these previous models have been labour intensive and lacked portability between estuarine systems (see review by Constable 1999 and references therein). De Jonge et al (2006) advocate that

monitoring strategies should be reviewed to incorporate elements of species functions as well as taxonomic identity and abundance.

Functional groups have long been seen as a means to reducing complexity within ecosystems (Simberloff and Dayan 1991, Mathieson et al 2000, Pearson 2001, Blondel et al 2003), hence providing a basis for generic predictions of functional effects and their distributions (Woodward and Diament 1991, Dolédec et al 1999, Statzner et al 2001, Fano et al 2003). Fairweather (1999) suggests, for environmental management purposes, that rather than simply asking "is this the healthiest assemblage that we can expect at this place?", scientists instead ask what the assemblage is "doing". Whilst the ability to answer the former question satisfies many legislative obligations (such as the WFD), the need to ask the question is prompted by a desire to promote ecosystem "health" and to minimise unavoidable detrimental effects upon ecosystem functioning. Simply determining degree of deviation from the "healthiest assemblage" does not automatically convey the consequences of such deviation for ecosystem processes and, as Fairweather (1999) points out, assemblage structure may not always relate directly to function. In addition, as Tett et al (2007) discuss, change from the reference condition does not automatically imply degradation of ecosystem status as the WFD would suggest. Tett et al (2007) reviewed the detection of eutrophication and defined "undesirable disturbance" as "a perturbation of an ecosystem that appreciably degrades health or threatens the sustainable human use of an ecosystem". Tett et al (2007) were unable to identify individual indicators of undesirable disturbance resulting from eutrophication and recommended a "multi-step" approach. Tett et al (2007) suggested that the health of the ecosystem should be assessed in terms of ecosystem "vigour" as well as structure, where the term "vigour" refers to fluxes of energy and materials and ecosystem resilience

(2006). Whilst Tett et al (2007) recognised the role that species diversity plays in ecosystem resilience, they suggested that a balance among functional groups and life traits had greater impact upon ecosystem health than species diversity *per se*. Tett et al (2007) focussed upon eutrophication but, by applying the term vigour in the wider context of *processes* occurring within the ecosystem, the SDE groups proposed in this thesis could be employed as a measure of "vigour" to allow Tett's approach to the identification of undesirable change to be applied to the estuarine macrobenthos.

Studies that model the levels at which function is performed, at different sites within an ecosystem, allow immediate comparison of changes in function with fluctuations in abiotic factors. Such an approach precludes the need for interpretation of the relationship between species composition and function, providing instead output that is interpretable and relevant to the process being investigated. Where discrepancies are noted, managers can trigger further investigation and the activation of management plans.

In the search for tools that provide a direct means to generalise the functional effect of macrobenthic species upon estuarine ecosystem functioning, this thesis:

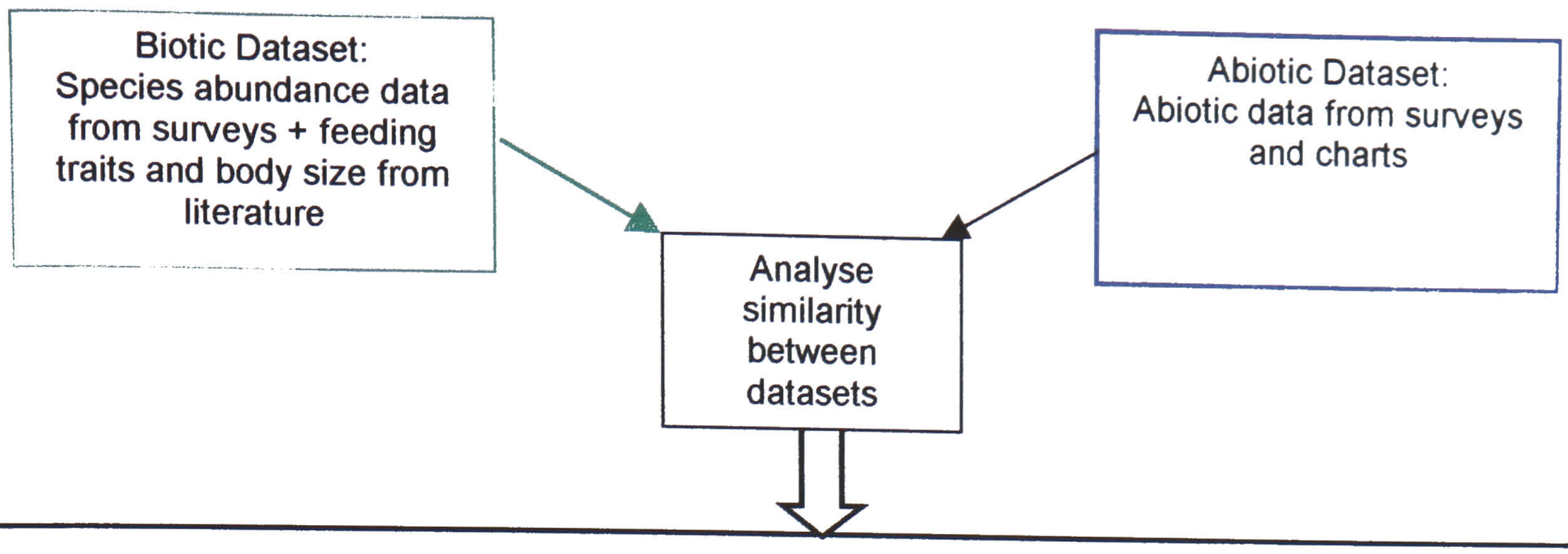
- investigated the responses of the macrobenthos to environmental factors, when the infauna was grouped according to either its feeding or bioturbatory functional attributes;
- examined the distribution of species activity within the sediment matrix;
- developed novel functional groups that incorporated:
  - those functional attributes shown by earlier chapters to have strong relationships with selected abiotic factors; and
  - the magnitude and location of the biological effect within the sediment; and

- developed and tested models that predicted the distribution of functional groups within an estuary.

6.3 The development of SDE groups.

The term "functional group" is ambiguous (Wright 1973, Gitay and Noble 1997, Padilla and Allen 2000, Blondel 2003, Gerino et al 2003). The concept that species share many traits and behaviours has been long been utilised in ecology to study community structure (see review by Pearson 2001 and references therein). For the purposes of this thesis, Pearson's (2001) approach, that functional groups share similar attributes, was adopted and functional groups defined as "any group of species that have been combined as a single biological unit according to their similarity in one or more trait or activity".

Within benthic ecology, most studies have characterised functional groups upon either feeding behaviours or bioturbatory characteristics of the fauna. Other attributes that merit consideration have been identified (Pearson 2001, Statzner et al 2001, Mouillot et al 2006), and several authors expound the virtues of multi-trait groupings (Fauchald and Jumars 1979, Swift 1993, Bonsdorff and Pearson 1999, Statzner et al 2001, Leung et al 2000). Describing the macrobenthic fauna in terms of feeding habits enables food webs to be constructed and hence, energy flows through ecosystems to be examined (Pearson 2001, Duffy 2002 and the references therein, Petchey et al 2004). However, results in Chapter 2 supported the use of functional groups describing bioturbatory activities, in preference to feeding behaviour, when linking species to several commonly measured abiotic variables as outlined in Figure 6.1. The findings of Chapter 2 revealed that



Biota characterised by

	Species abundance	Species abundance and body length	Species abundance and bioturbation score	Species abundance and trophic group
Evidence of relationships with environment?	Some	Some	Some	Not evident with abiotic data investigated
Relationships may be improved by?	More data points			
	Continuous rather than categorical abiotic data			
		More accurate estimates of body size	Accurately quantify each species' contribution to bioturbation	Identify alternative abiotic data to test. Review trophic groups to include sub-categories and introduce a means to quantify contribution to function
Potential to produce generic model?	Limited to a few estuaries	Limited to a few estuaries	Possible	Possible
Function contribution modelled directly?	No, models species distribution	Only if function directly proportional to body length	Possible if alter score to quantify effect	Possible if alter trophic groups to quantify effect
To investigate further?	No, cannot model function directly or produce generic model	Continue literature search to estimate body size to develop new functional groups	Explore ways to estimate amount of bioturbation occurring by using body size and species activity traits	Continue literature search for feeding traits that result in sediment disturbance. Do not pursue modelling of trophic function directly at this time

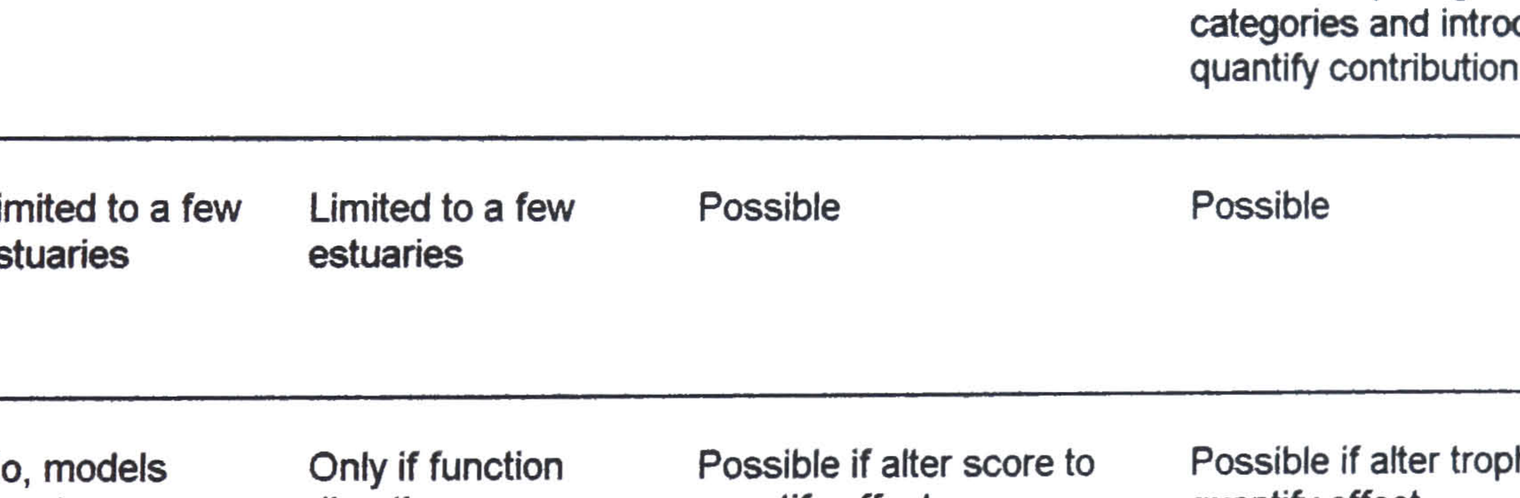


Figure 6.1. Summary of the findings of Chapter 2

characterising the biota by functional attributes altered the *perceived* relationships between the fauna and abiotic factors. Consequently, in estuarine systems, associations between bioturbatory functional groups and a suite of commonly measured abiotic parameters were easier to determine than associations between trophic groups and the same abiotic variables. Although this thesis found little evidence to link the trophic characteristics of the estuarine macrobenthos to possible environmental driving factors, this finding could have been heavily influenced by the choice of abiotic parameters investigated. The parameters included in the study showed little variation between sampling locations and the data were categorical rather than continuous. It may be that links between trophic functional groups and environmental factors can be identified if a different suite of abiotic factors was investigated, or if perhaps the trophic group classifications were expanded to include more descriptive sub-categories. This study, however, chose to focus on the bioturbatory characteristics of the biota in view of the relationships found with the existing abiotic data. For the determination of links between species activity and ecosystem processes, there is a need to identify the location of species activity within that ecosystem. This study suggested that greater confidence could be attached to any predictions of the distribution of macrobenthic species activity in an estuarine system, in response to the selected abiotic factors, if bioturbation was the function of interest.

Later chapters of this thesis therefore set out to characterise species by their ability to disturb sediment. Although there are many established classifications of species bioturbatory effects (Pearson 2001, Swift 1993, Swift et al 1996, Solan 2000, Francois et al 2002), several limitations were identified in existing schemes: many species display multiple behaviours and hence were not easily assigned to one functional category (Pearson 2001, Gerino et al 2003); many earlier schemes

were developed to describe sediment particle transfer processes and did not necessarily reflect other sediment disturbance effects (Pearson 2001); and few schemes made any allowance for the *magnitude* of a bioturbatory effect but rather concentrated simply on the *type* of effect.

The approach employed in the current study attempted to address all of these shortcomings by focussing on the *outcome* of *all behaviours* that promoted direct sediment disturbance. The aim was to estimate the total volume of sediment disturbed directly by each species according to body size and routine activities. Mouillot et al (2006) suggested that biotic contributions to ecosystem processes were largely dependent upon body size, consistent with links between function and biomass (see review by Mouillot et al (2006) and references therein, Gilbert et al 2007). However, the biomass of an individual macrobenthic species does not necessarily predict the mechanics of physical interaction with the sediment. Idiosyncrasies of each species' morphology will determine how movements, burrow construction and feeding behaviours combine to impact upon sediment dynamics. Thus, it was more intuitive to employ the volume of the species, rather than its biomass, to link species morphology to sediment disturbance effects. Since, however, not all species activities that have a direct impact upon sediment dynamics result from the physical displacement of the *whole* individual through the substratum, other aspects of species activity need to be enumerated, e.g. the volume of sediment scraped by the palps of surface deposit feeders and the volume of sediment occupied by tubes.

Although many species can contribute to sediment disturbance they will differ not only in the magnitude of their effect but also in the sediment region upon which the effect is realised. The findings of Chapter 3 (summarised in Figure 6.2) revealed that macrobenthic community responses to abiotic factors should not be

Schelde Dataset:

Mean species abundance for various sediment depth horizons at 5 different sites

Test using ANOSIM for any significant differences in structure of assemblages due to either site or depth

Tamar / Plym Biotic dataset:

Mean species abundance for various sediment depth horizons at 9 different sites

Examine pairwise similarities between assemblages at different depth horizons to look for boundaries between similar assemblages

Tamar/Plym Abiotic Dataset:

Erosion measures, current flows, sediment characteristics

Split Tamar/Plym dataset into shallow, mid level and deep assemblages, using boundaries suggested from Shelde data.

Correlations to examine relationships between the different abiotic factors. Abiotic dataset reduced accordingly

Examine relationship between abiotic data and Tamar/Plym shallow, mid and deep assemblages

Findings:

Depth is a significant factor in the structure of assemblages

Assemblages from different depths do not all have the same relationships with the abiotic data.

Individuals found in shallow assemblages tended to be smaller than conspecifics in the deeper assemblages

Future Investigations:

Need to assess whether patterns observed in macrofaunal assemblages hold for sub-tidal/high elevation sites and different types of estuary, and also must ensure better characterisation of deeper assemblages.

Re-examine depth boundaries, with particular attention to seasonal variation in depth ranges of species. Examine traits of deeper assemblage to seek alternative ways (rather than stating an artificial boundary) to identify longer-lived assemblage including investigation of body size distributions and species traits

Investigate using sediment water content as a proxy for other sediment characteristics and develop regression equations

Figure 6.2. Summary of the processes and findings described in Chapter 3

investigated as if the macrofauna were a single entity. Rather shallow and deep assemblages should be identified. Thus, in the development of functional group classifications, not only was the volume of disturbed sediment considered but also the depth ranges over which effects occurred. The resulting functional groups were novel in that they incorporated many traits, (e.g. body size, feeding, motility, biogenic construction) to reflect the volume of sediment influenced by a macrobenthic species during its activities and potentially provided managers with information on sediment disturbance and the depths to which it might extend. Properties such as burrow size and volume of sediment physically occupied by an animal do not themselves always strictly result in *bioturbation* defined as the displacement and mixing of the sediments. To avoid confusion with other bioturbatory classifications, however, the functional groups derived in this study were labelled "sediment disturbance effect groups".

6.4 Linking sediment disturbance effect (SDE) groups to ecosystem processes

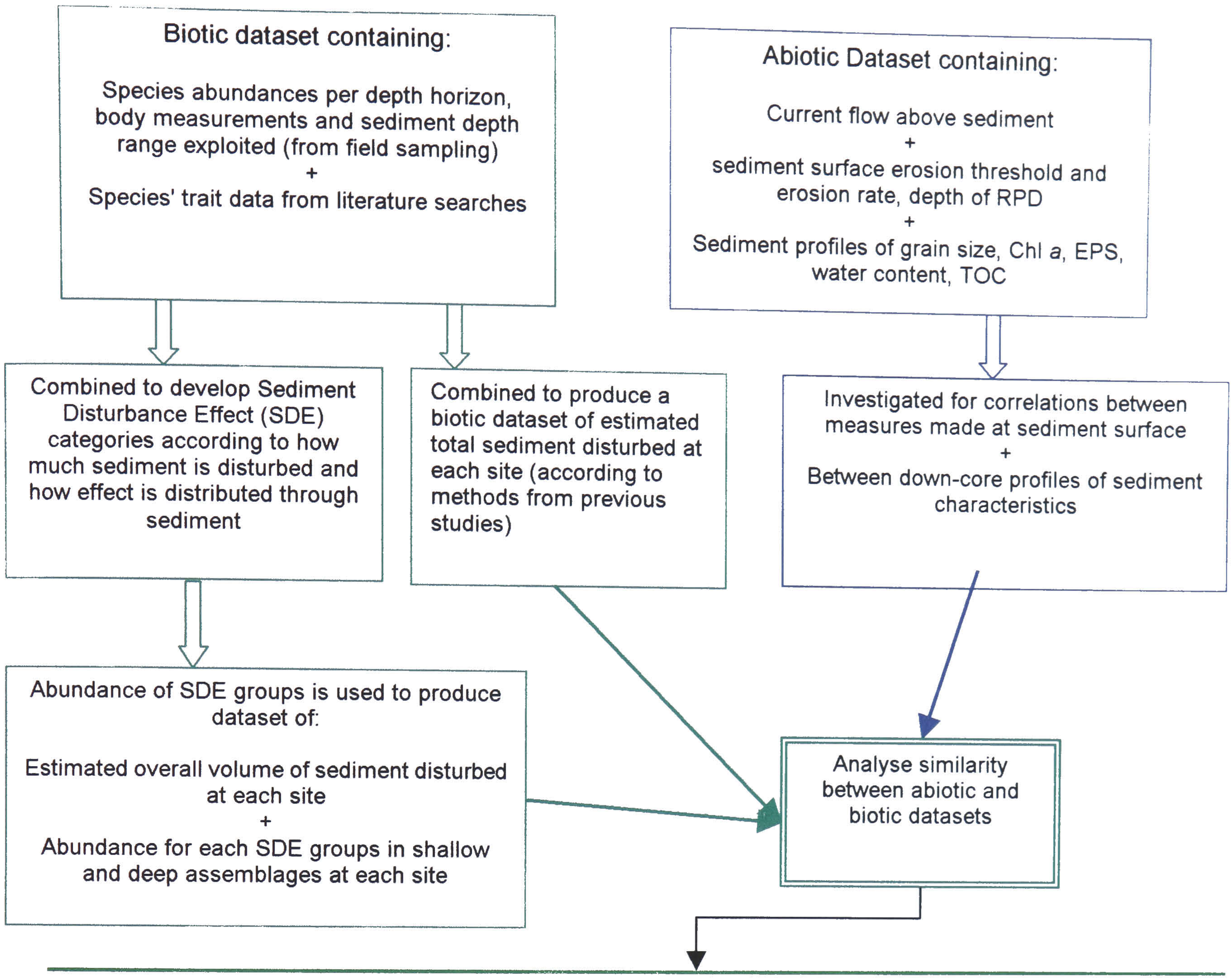
Hooper et al (2002) suggested that an improved understanding of relationships between species and ecosystem functioning could be achieved if links between top-down and bottom-up approaches to estimating "function" could be established. The major problems in linking these different approaches were identified in Chapter 1:

- the requirement to both identify accurately *and* quantify species' activities that contribute to the functions and processes of interest; and
- the need to quantify accurately the functions and processes occurring *at the ecosystem level*.

The estimation of total sediment disturbance effects for each species addressed the first hurdle to linking top-down and bottom-up approaches but a match between the patterns in sediment abiotic characteristics and *overall* biological effects was not convincing (see Figure 6.3). Although some strong associations were observed between overall sediment disturbance and certain sediment characteristics no abiotic proxy could be confidently identified for the level of biologically-mediated sediment disturbance occurring at a particular site, since the influence of the biota upon the sediment characteristics could not be clearly disentangled from the impact of abiotic variables. Constable (1999) stressed that interactions between processes occurring on different scales must be identified before linking "top-down" and "bottom-up" approaches. In this study such interactions were not determined. This inability to link processes occurring on different scales precluded consideration of many ecological questions about ecosystem organisation and regulation.

The absence of good evidence for connections between the overall biotic disturbance effect and abiotic patterns in sediment characteristics was due in part perhaps to the different scales at which each parameter was measured, and to the complex interactions between the biota and environment. For some abiotic variables, such as the distribution of organic carbon (TOC) with depth in the sediment, small-scale patterns were observed at the scale of sample but no longer evident at the scale of site. Conversely, other environmental factors were estimated across a broader scale than the biota, e.g. the current flows at 10cm across the sediment bed were based upon model predictions for a grid of dimensions 50m x 50m.

The abiotic patterns that characterised the estuarine soft sediments were not solely the product of biologically-mediated effects. Hydrodynamic, chemical and



	Estimate of total sediment disturbed at each site vs. abiotic data	Assemblage comprising all SDE groups in shallow depth horizons vs. abiotic data	Assemblage comprising all SDE groups in deep depth horizons vs. abiotic data	Each individual SDE group from shallow assemblages vs. abiotic data	Each individual SDE group from deep assemblages vs. abiotic data
Evidence of relationships?	Some	Some weak relationships	None	Some	Some
Problems	No actual values for total sediment disturbed available to validate estimates used to define SDE groups or calculate overall sediment disturbed Lack of certainty over whether correlations reflect genuine variation in sediment disturbance, or the responses of dominant species to abiotic forcing or are statistical artefacts				
Future investigations	Need to identify an independent means to quantify overall sediment disturbance. More studies needed to validate Gilbert et al's work linking biovolume to bioturbation or produce refined estimates. Wheatcroft's estimates based on body length to the power 4.25 appear unrealistic and should not be pursued. Investigate whether profiles of sediment water content can be used as a proxy for other abiotic factors. Need to improve estimates of each individual species' potential to disturb sediment and refine classifications. Need a larger dataset with more sample locations to test any associations for significance and improve sampling of deeper/larger organisms				

Figure 6.3 Summary of the processes and findings described in Chapter 4

climatic forces and also interactions between the biota on multiple spatial and temporal scales influenced the sediment characteristics. The interplay of abiotic processes alone could have provided many possible explanations for abiotic patterns observed in the sediment. Thus, although the effects of macrobenthic activities upon the sediment matrix were investigated, the influence of *abiotic* factors in driving the abiotic characteristics of the sediment was unknown. As a result of it was only possible to estimate the theoretical overall biotic effect. In addition, the assumptions that the biological effects were additive may have been simplistic. Accordingly, using the estimates of overall volumes disturbed as a parameter in other models of sediment dynamics, or for inter-site and inter-system comparisons, remains a theoretical possibility rather than a reality.

If the SDE groups developed in this thesis can be refined and shown to reflect natural levels of biotic activity, then they will not simply provide an inventory of species with similar biological effects. They would also convey information about the amount of sediment disturbance occurring and the sediment depths to which disturbance effects extend. By characterising the infauna according to SDE groupings, estimates could be made of overall sediment disturbance. Thus, the SDE groups have the potential to provide a rudimentary tool that could be applied in attempts to disentangle the relative contributions of the biotic and abiotic components to the *de facto* conditions observed at the time of sampling. Such tools are crucial to understanding ecosystem organisation and functioning (Hooper et al 2002, Sagoff 2003).

6.4.1 Linking sediment disturbance effect groups to environmental variables

In the search for practical management tools, researchers may seek to explain the distribution of the biota by reference to abiotic factors (Lavorel and Garnier 2002,

Ysebaert et al 2002, Thrush et al 2003). Within estuarine ecosystems there is strong evidence that the distribution of the macrobenthos relates to sediment grain size, salinity, tidal and river current flows and organic matter (Davis 1925, Thorson 1957, Sanders 1958, Rhoads and Young 1970, Gray 1974, Pearson and Rosenberg 1978, Wildish 1977, Warwick and Davies 1977, Wildish and Kristmanson 1979, Warwick and Uncles 1980, Constable 1999, Dyer 2000, Anderson et al 2004). Chapter 3, however, revealed that the responses of shallow assemblages to these abiotic factors were not the same as responses shown by the deep-living biota, for example the shallow assemblage had the strongest association with salinity (r_s=0.531) but for the deep assemblage TOC had the strongest relationship with biotic structure (r_s=0.386) (see Section 3.3.3 and Figure 6.2). There were stronger relationships between shallow assemblages and environmental data than between deeper assemblages and the abiotic factors, a pattern that recurred when considering the assemblages in terms of their SDE groups (see Section 4.3.3.1). Subsequent consideration of the *individual* SDE groups, however, demonstrated that both deep and shallow SDE groups had strong relationships with some of the abiotic factors but that the factors demonstrating the strongest associations with a specified SDE group varied according to the depth assemblage under considerations. For example the SDE group C3 had a strong association (ρ=0.72, $p<0.05$) with the sediment erosion rate for shallow assemblages but for deeper assemblages the association was much weaker (ρ=0.34, $p>0.05$) and a strong association was found with whole core shear strength (ρ=-0.94, $p<0.05$) (see Section 4.3.3.2)

6.4.1.1 Separating shallow and deep assemblages

Chapter 3 of this thesis demonstrated that vertical stratification of the infaunal

communities must be considered when examining abiotic-biotic relationships. Findings presented in Chapter 3 (summarised in Figure 6.2 above) suggested a tendency for individuals from shallower depth horizons to be smaller than those from deeper assemblages, in broad agreement with many other studies (Hines and Comtois 1985, Esselink and Zwarts 1989, Zwarts and Wanink 1989, Zwarts and Wanink 1993, Davey and Partridge 1998). It was argued in Chapter 3 that the cost of burrowing deeper into estuarine sediments is only outweighed by the benefits for larger bodied individuals: potential benefits include protection from predation (Holland 1980) and environmental fluctuations (Johnson 1965, Brotas et al 1990), improved feeding opportunities for deposit feeders (Rhoads 1974, Neira and Höpner 1993), and minimised disturbance from other biota (Rhoads 1974, Whitlach 1980, Josefson 1989, Myers 1977, Thistle 1981, Grant 1981).

Many of the species exploiting deeper sediment horizons were also characterised by longer life spans. Thus, it appeared that deeper assemblages were characterised by longer-lived and larger-bodied individuals than were found in shallower assemblages. If life history traits vary according to depth occupied in the sediment, then it is probable that each assemblage will display different relationships with environmental factors (Lavorel and Garnier 2002). By considering the macrobenthos as two separate assemblages, clearer patterns may emerge between the biota and abiotic forcing factors that, in turn, improve understanding as to how changes in the environment could impact upon the biota.

The effects of short-term "pulse" and sustained "press" disturbances (Bender et al 1984, Tett et al 2007) upon the biotic structure may be more evident if assemblages that are characterised by different traits are compared. Furthermore, many studies have linked species' traits with their response to disturbance regimes (Pearson and Rosenberg 1978, Levin 1984, Statzner et al 2001, Carignan

and Villard 2002, Norkko et al 2006). Dolédec et al (1999, 2006) suggested that variation of functional characteristics between communities could be used to infer levels of human disturbance. If deep and shallow assemblages have different responses to environmental change (and hence to human disturbance), then researchers could gain insight into different aspects of environmental change by considering both assemblages in turn, whereas grouping the biota as one response group would produce different interpretations. Thus, the deep and shallow assemblage structures at any one site may inform about a range of environmental conditions that have been experienced by the biota over both short and longer temporal time scales.

The variability in species' life histories and responses to environmental variables could have important ramifications for ecosystem resilience, persistence and any attempts to model these factors or detect adverse impacts upon the ecosystem. For example, species that have a trait of rapid reproduction may also respond more rapidly to disturbance than species with longer generation times. Consequently, species displaying short generation times may provide early warnings about disturbance effects (Carignan and Villard 2002), and their absence could be used to trigger management action plans. However, rapid reproduction is often associated with other opportunistic traits such as rapid growth, dispersal and exploitation of transient, favourable environments (Grassle and Grassle 1974, McCall 1977, Norkko et al 2006). Therefore, variation in the distribution of opportunistic, short-lived species is more likely to reflect responses to short-term environmental fluctuations than environmental conditions that have been sustained for more than a few months.

For example, the polychaete *Capitella sp* is an opportunistic species that exhibits cycles of rapid colonisation of recently disturbed areas followed by equally rapidly

decline, possibly due to resource limitation (Grassle and Grassle 1974, Phillips and Tenore 1984) or species interactions (McCall 1977, Bonsdorff and Pearson 1997). Any attempt to determine, and hence model, the distribution of *Capitella* will be confounded by the rapid fluctuations in abundance (Grassle and Grassle 1974, Chesney and Tenore 1985) and may also be heavily influenced by species interactions (Pearson and Rosenberg 1978, Gray 1981, Norkko et al 2006).

On the other hand, although longer-lived species may exhibit different traits to those displayed by more opportunistic species, the former are also likely to display some level of temporal variation in their relationships with abiotic factors due to different responses at different life stages (Whitlach et al 1998). In fact, for much of their early development, *deep* assemblage individuals may have resided in the *shallow* assemblages. The factors that influence successful settlement to the sediment may not be the same as those promoting a long-term residence in a more benign environment (i.e. at deeper sediment depth) at a given site. It would therefore appear that to assess the *long-term* integration of the biological and physical environment within an estuary, managers should investigate *older* assemblages. Within soft sediments, larger-bodied animals that occupy the deeper sediment regions best represent older infaunal assemblages. Assessment of ecosystem "health" or integrity (*sensu* Karr and Dudley 1981), by considering the shallow and deep assemblages as separate entities, allows inference of the likely influence of abiotic factors acting over different spatial and temporal scales upon community structure. Such information will allow greater insight into forces that *have driven* community assemblages and could be used to further ecological studies of resilience and patterns of recolonisation following disturbance within estuarine ecosystems. A greater understanding of the role of the timing and frequency of extreme events, the sediment depths to which environmental

fluctuations impact, local- versus broad-scale disturbances and species interactions could emerge from investigations that separate shallow and deep assemblages.

Separating the infaunal community into two, sediment depth-related assemblages may at first daunt some researchers. Nevertheless, this thesis has identified clear benefits in so doing:

- separating communities into "shallow " and "deep" assemblages allows investigators to consider the different temporal and spatial scales upon which species experience their environment and the influence of acute and chronic disturbance;
- modelling the distribution of each functional group within each assemblage independently allows for the selection of different abiotic forcing factors and improves the fit of the models to observed data, hence improving any predictive power of resulting relationships;
- the current study recommended that investigations into estuarine health should focus on the deeper assemblage *in the first instance* to obtain meaningful information about long-term site status that would help to inform where to focus subsequent investigations; and
- by focusing studies on a subset of the overall infaunal community, managers could make savings in time and effort, and interpretation of findings might be made easier. Investigating the forces structuring deeper-dwelling assemblages will focus attention on longer-term abiotic-biotic interactions that are more readily characterised by the relatively broad scale upon which most physical parameters are measured.

6.4.1.1.1 The problem of defining "deep" and "shallow"

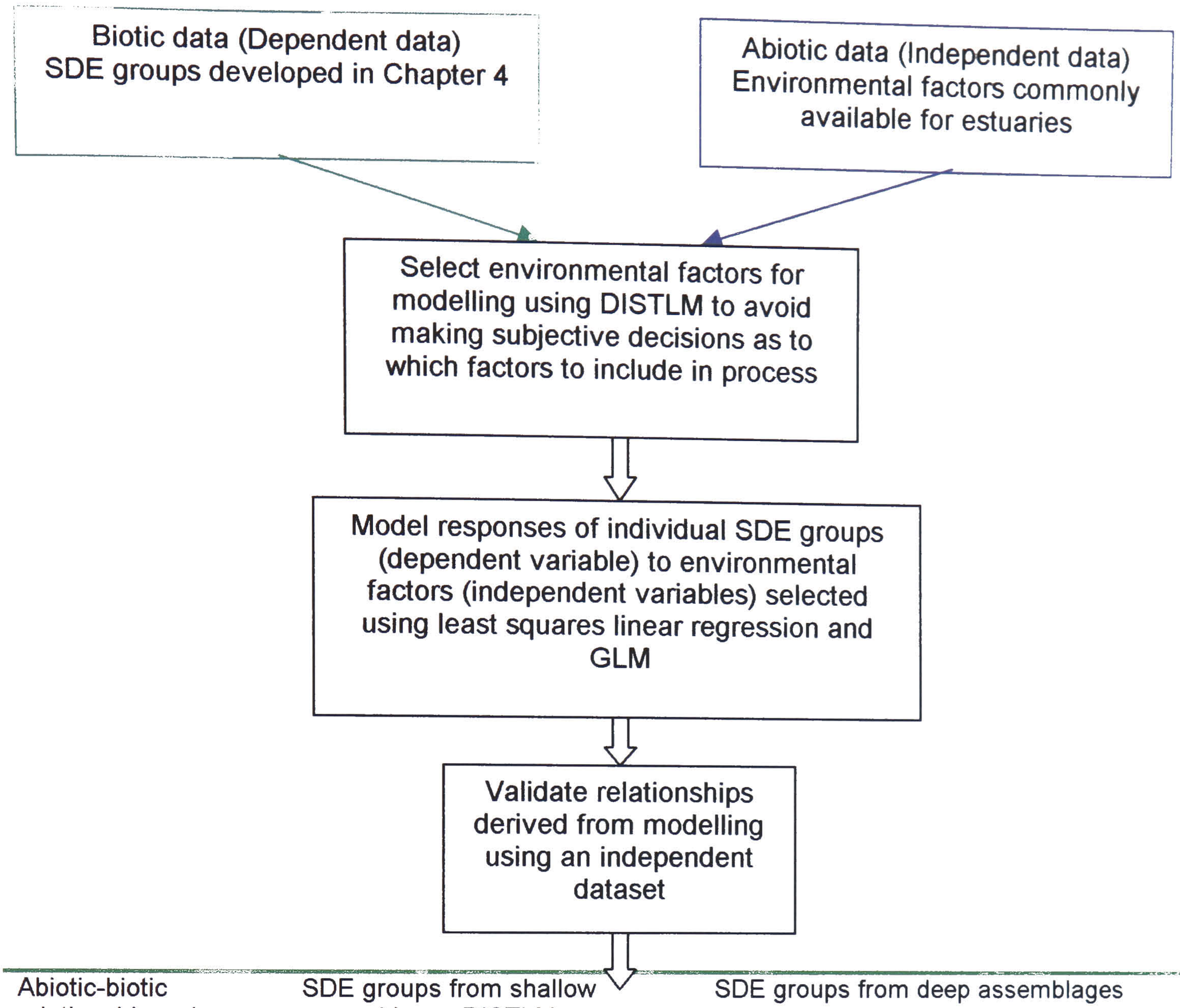
For the purposes of the present study a pragmatic view was taken that the boundary between shallow and deep assemblages should ensure that organisms that never exploit deeper regions of the sediment are excluded from the *deep* assemblage. The most practical way to achieve this was to re-examine the species abundance distribution data. Although the statistical results gave some insight into the relationships, the boundaries examined are all artificially imposed on the biota as was the original decision of where to actually section the sediment. A review of the biotic data, however, showed that whilst some species extended into the 8-10cm layer but not beyond, e.g. *Nemertea* indet. and *Sipunculidae indet.*, most of those species found in the 10-15cm layer were also found in deeper layers on occasion. As a result, a boundary of 10cm depth in the sediment was employed, although many others might have been chosen. If the interpretation that deeper assemblages comprise longer-lived species is correct and, as indicated in this study, longer-lived assemblages do have different relationships with environmental forces than do more ephemeral assemblages, then it is desirous to identify those "longer-lived" individuals. Since, it is the presence and abundance of longer-lived individuals that need to be identified, not species or individuals with the *potential* for longevity, then a simple examination of species abundance and traits is not enough. Including a measure of body size might allow some estimation of the numbers of longer-lived individuals but there is another reason for identifying the depths species exploit: to assess how the sediment disturbance effect is distributed through the sediment since this will affect other processes such as sediment stability, compaction and pollutant fluxes. The problem of what is *deep* and what is *shallow* needs further attention and a pragmatic decision may be needed to recommend a value that is useful for

practical purposes. Research is needed to assess the effects of setting the boundary too shallow or too deep on the relationships between assemblages and the environment, and to explore alternative means to identify subsections of the biota.

6.4.1.2 The role of SDE groups as functional response groups

Whilst the present SDE groups were developed to provide estimates of biotic *effects* upon sediment processes, they also appeared to perform as *response* groups, displaying strong relationships with abiotic driving factors. Hooper et al (2002) stressed that although most functional groups are developed with only one of these roles in mind, the need to develop links between biological *effects* groups, that link species to ecosystem processes, and biological *response* groups, that reflect biological distribution along environmental gradients, is paramount to answer questions about species roles in ecosystem functioning. Strong associations demonstrated in Chapter 4 between environmental variables and the abundance of most SDE groups suggested that SDE groups can perform both "effect " and "response" roles, and that prediction of future biotic effects upon sediment dynamic processes should be possible from environmental knowledge alone. Consequently, in Chapter 5, models were developed to describe the responses of the SDE groups to a range of abiotic variables that are commonly measured for biomonitoring and academic research purposes (see Figure 6.4). Modelling function, rather than specific species or diversity measures has many advantages:

- modelling selected "indicator" species may link the modelled species to a specific abiotic predictor variable, but may be insensitive to variation in



Abiotic-biotic relationships when modelling?	SDE groups from shallow assemblages DISTLM	SDE groups from deep assemblages
Using DISTLM	Yes (R^2 0.5 – 0.94)	Yes (R^2 0.47 – 0.92)
Using LM	Some	Some
Using GLM	Some	Some
Problems	Low number of sample sites and low representation of some SDE groups across those sites Some skewed data, outliers, high leverage data points and evidence of incorrect assumptions about error of variance Predictions generally over-estimates and estimates generally poorer for GLM with very large standard errors	
Future Investigations	Focus on linear regression and DISTLM or stepwise regression (provided number of abiotic variables does not exceed sample locations) Data from new sample locations needed to increase the number of data points and develop model further. A large increase in the number of data points would permit more abiotic factors and interaction terms to be considered for modelling and increase confidence in the statistical significance of any derived relationships.	

Figure 6.4 Summary of the processes and findings described in Chapter 5

other factors that can promote disturbance. For examples, responses to metal contamination of sediments may do little to predict the response to increased wave exposure. Models of single species' responses may lack portability between estuaries and geographic regions;

- measures of species diversity require all species to be accurately identified and do not display simple relationships in response to disturbance (Mouillot et al 2006);
- some indices of "health" that consider the species' responses to anthropogenic stresses may be inefficient at discriminating between different types of impact such that sites may be designated as being degraded when the "stress" is in fact natural (Dolédec et al 1999, Quintino et al 2006);
- within estuaries the "Estuarine Quality Paradox" precludes the useful interpretation of indices based upon relationships between organic enrichment and assemblage structure (Elliott and Quintino 2007). Estuarine fauna have the same characteristics (low diversity dominated by small-bodied, low-biomass, r-strategist individuals) as areas suffering from anthropogenic organic enrichment. Hence, Elliott and Quintino (2007) advocate combining measures of biological structure with those describing function:
- the development of species-specific distribution models is not practical for all species across all taxa that occur in every ecosystem (Shugart 1997, Steffen et al 1992, Carignan and Villard 2002) and individual models lack portability.

Particularly within estuaries, the infauna is frequently characterised by low species richness (Gray 2001), including high spatial and temporal heterogeneity (Mclusky

1981, Thrush et al 2003, Tagliapietra et al 2005). Attempts to model the distribution of macrobenthic species individually within an estuary are hence confounded by low representation across several sites for some species, necessitating a large sampling effort to collect sufficient data (Holme and M^{c}Intyre 1984, Tagliapietra et al 2005). In addition, the ability of statistical models to adequately and realistically describe the relationship between infaunal assemblages and environmental factors is greatly influenced by the ability of any sampling regime to accurately characterise the assemblage. When species are rare, sampling effects often result in greater uncertainty in estimates of mean abundance.

In this study, by grouping species according to functions, several more species were included in the modelling process than could have been considered individually. Provided there is a degree of functional redundancy within each SDE group, i.e. more than one species performing a specific function (Lawton and Brown 1993, Loreau 2004), then the *modelling of function* distribution is potentially less sensitive to low *species* numbers since it is the presence of the group and not the species that is being modelled. This does not make any assumptions about the significance or otherwise of the species that are poorly represented. Rather, the simple act of grouping species increases the likelihood of collecting sufficient data for that group to enable mathematical modelling. It is important to remember that SDE groups are a tool to aggregate species, and that the role of functional redundancy in community dynamics should not be confused with the role in data collection.

Any ecological significance of functional redundancy must be considered by reference to the full range of traits and activities performed by a species. Whilst the loss of a *species* may not necessarily result in the absence of a *functional*

group at a given site, the function may be occurring at a reduced level *overall* and the species may have been involved in other processes that impact upon other ecosystem processes (Purvis and Hector 2000). Indeed, some researchers question the true existence of functional redundancy (Pearson 2001, Loureau 2004), since although many species perform similar roles they may not all act on similar temporal scales, and may play a role in a variety of functional processes.

The SDE groups developed in this study could provide a tool to investigate the role of functional redundancy and ecosystem resilience in estuarine systems. Effects of removal of a species from an estuarine system upon sediment dynamics could be estimated, although care should be taken to discriminate between redundancy *as applicable to sediment disturbance* and that redundancy applicable to *all the other functions* to which the species may contribute.

Elliott and Quintino (2007) suggest that the highly variable environmental conditions found within estuaries should be regarded as a positive effect for species that can tolerate that level of variability. According to Elliott and Quintino (2007), species that are able to exploit estuarine sites can achieve high population because of the low levels of inter-specific competition. Consequently, since estuaries are frequently characterised by low biodiversity, it should be considered that natural estuarine functioning may not rely on high biodiversity. Instead, resilience within estuaries may arise from natural variability within the structure of the biota and hence measures to detect the impact of human disturbance upon ecosystem health must disentangle natural variability from that induced by human activity. Elliott and Quintino (2007) suggest that researchers seek ways to test how low-biodiversity, natural variability and function influence the resilience of the estuarine assemblages both naturally and under anthropogenic disturbance.

If the distribution of function across many sites in many estuaries can be predicted *a priori* from abiotic data, it will also be possible to examine some of these other fundamental ecological issues, such as the role of species diversity in levels of functioning (Tilman 1996, Levin et al 2001b). Peterson et al (1998) suggest that resilience of ecosystems is improved if species experience their environment on different spatial and temporal scales, which may indeed be a reality for the infauna of estuarine sediments.

In the study presented here, there were generally several species within each SDE group, suggesting that there may be elements of functional redundancy within most of the SDE groups. Only the larger biological effect groups contained very few species, and it is the large species, with large sediment disturbance effects, that were potentially least well sampled by the procedures used in this study. In addition to addressing the issues with SDE group development and establishing where the boundary lies between shallow and deep assemblages, as already discussed in sections above, any future development of the functional approach applied in this thesis would need to ensure that the larger-bodied infauna were adequately characterised by sampling procedures, and hence also by the models of their functional group distribution.

6.2.1.3 Predicting the distribution of SDE groups within an estuary

Chapter 5 confirmed that for many SDE groups the distribution of function could be predicted for new sites, provided adequate abiotic data were available. The same chapter also showed that many of the abiotic factors frequently considered by modelling studies (salinity, sediment grain size, current flows, sediment water content and sediment erosion rates (Constable 1999) were highly correlated. In addition, the strong relationships described in Chapter 4 between sediment water

content and many other abiotic parameters suggested that sediment water content may indeed act as a "universal master variable", as proposed by Flemming and Delafontaine (2000). A synthesis of these finding implies that the SDE groups could be predicted from a relatively small suite of environmental variables and that some of the abiotic variables could be predicted from knowledge of sediment water content profiles. Time spent developing predictive relationships between sediment water content and other abiotic factors could produce long-term savings in both time and effort expended in sampling.

Employing SDE groups to represent biotic effects allowed the levels of function across an estuary to be modelled, of potential benefit to managers, planners and researchers wishing to predict how sediment dynamics would be affected by future events including human activity and climate change. Anthropogenic activities have had far-reaching effects upon many ecosystems (Hobbs 1997, Rapport et al 2003, Hirst 2004) and which are likely to be exacerbated by climate change (Schindler 2001, Thrush et al 2003, Vinebrooke et al 2004, Parry et al 2007). However, predicting the future distribution of biota and important ecosystem functions under any changed climate scenario has been hampered by the lack of generic models that apply across estuaries (Carignan and Villard 2002, Thrush et al 2003, Cabral and Murta 2004). Nevertheless, by considering the likely responses of the component species of an SDE group to changed environmental conditions, the likely impacts of climate change upon function may be assessed.

Although many researchers doubt that functional response groups will display a monotonous response to broad scale changes such as global warming (Hobbs 1997), compiling inventories of those species able to contribute to each SDE group will provide the means to link ecosystem performance to species responses under long term alterations in environmental conditions. The tolerances of

different species to environmental parameters are unlikely to be consistent and environmental changes could impact a macrobenthic species in a multitude of ways for example by influencing:

- species geographical range;
- species metabolism;
- species reproduction and survival;
- non-benthic stages of development and life-cycle;
- sedimentation and resuspension processes;
- chemical processes in the sediment;
- the abundance and distribution of the microphytobenthos;
- current flows and turbidity levels;
- energy partitioning.

The position that a species occupies within the sediment provides some degree of protection from variations in environmental parameters although the majority of deeper-living, larger-bodied species do pass some time in the surface layers as juveniles and may also have a planktonic phase in their life cycle. For these reasons it is unlikely that either the deep or shallow benthic assemblages will be shielded from the effects of broad-scale changes in climate.

The UKCIP02 scenarios (Hulme et al 2002) make various predictions about future climate for the UK, based upon different potential levels of carbon emissions, including: increased annual-averaged temperatures of air and coastal waters, rising sea-level, increased frequency of storm surges, and altered rainfall patterns. The ramifications of changes in climate for estuary function are myriad. Changes in rainfall, particularly the increased frequency and duration of extreme events (Ekstrom et al 2005), could lead to higher river levels, flooding and increased runoff of soil and nutrients from inland areas. The combination of altered river

flows and rising sea-levels will influence the hydrodynamics of estuaries, and the heavy urbanisation of many estuarine regions hinders natural redistribution inland of features such as mudflats (Townend 2002, Crooks 2004). The challenge for managers and engineers is to provide new areas to accommodate the intertidal and floodplain functions of estuarine ecosystems (Crooks 2004), even though the conversion of alternate sites into new wetlands may not provide a truly functional replacement for the lost habitat (Elliott and Cutts 2004).

If the intertidal habitat is successfully sustained within estuaries despite climate change, it is still generally unclear how the fauna will respond to altered environmental conditions. Whilst there have been some studies into the potential for altered biological community structure, such as undertaken by the MONARCH project (Monitoring Natural Resource Response to Climate Change), (Kendall et al 2004, Lawrence and Soame 2004, Rehfisch and Austin 2006, Wallentinus and Nyberg 2007), climate change may induce some surprising changes in the biological functioning of estuaries. For example, recent work by Fulweiler et al (2007) revealed that marine sediments could switch from being a net sink of nitrogen to being sites for nitrogen fixation. In the face of such complexity, managers can only plan mitigation and action plans to deal with the effects of climate change by basing assessments of any likely impact upon *current* knowledge of how the system functions.

The SDE groups approach developed in this study may go some small way towards improving our current understanding of estuarine functioning in so far as it relates to sediment dynamics. Where information is available about individual species' environmental tolerances, comparisons could be made between the predicted abundance of functional groups within estuaries and those species that are known to have the potential to persist and fulfil that functional role under

different environmental regimes. In addition, where species are likely to become locally extinct or invasion by non-native species is possible, then estimations of changed sediment disturbance can be considered. Whilst such estimations can only be rudimentary, and cannot account for complex species interactions with the environment and with other living organisms, SDE groups could provide a simple initial method to assess the *potential* of individual species to contribute to sediment disturbance processes.

6.4.1.4 The relationship between SDE groups and ecosystem processes other than sediment disturbance

Employing SDE groups to represent macrobenthic activity levels may help to elucidate the links between the macrobenthic fauna and ecosystem processes other than *simple* sediment disturbance, in particular with processes that occur either within the sediment or across the sediment-water interface, for example nutrient fluxes between the sediment and overlying water and the release of sediment pollutants. Few researchers expect there to be any "universal" functional groups that can be applied across all levels of biotic organisation within an ecosystem, from microbe to whale (Gitay and Noble 1997). However, where functions are linked, then a single classification system may have several applications. Processes such as fluxes of matter and solutes between the unconsolidated sediment and overlying water bodies are linked to the activities of the macrobenthos within soft sediments (Aller 1980, 1982, Kristensen et al 1985, Rice 1986, Biles et al 2002, Timmermann et al 2003, Mermillod-Blondin et al 2004). Thus, the relative impact of a macrobenthic species upon fluxes across the sediment-water interface may also be characterised by the sediment disturbance effect of that species. So by predicting the magnitude and distribution of sediment

disturbance it may be possible to also infer the levels of fluxes occurring at different sites, facilitating inter-site and inter-system comparisons of functioning. Sediment reworking can also impact upon processes occurring within the sediment matrix for example, the distribution and fate of pollutants within the sediment (Lee and Swartz 1980, Swift 1993, Mulslow et al 2002, Banta and Anderson 2003, Timmermann et al 2003), nutrient cycling and the degradation of organic matter (Rhoads 1974, Blair et al 1996, Nordstrom et al 2006). Rates at which chemical processes occur within the sediments can alter according to changing levels of sediment disturbance (Aller and Yingst 1985, Mortimer et al 1999, Mermillod-Blondin et al 2004). Indeed, Chapter 5 describes strong associations between the distribution of some SDE groups and parameters related to chlorophyll *a* removal from the upper sediment layers. Such findings suggest that investigations into links between SDE groups and nutrient cycling within the sediment could prove fruitful.

6.5 Further development of SDE groups

The SDE groups and models developed in Chapters 4 and 5 of this thesis were based upon sample data from the Tamar and Plym estuaries only, and have not been tested in other estuarine systems. Estuaries are complex ecosystems that vary greatly in their geological, chemical and hydrological attributes (Levin et al 2001a, Ellis et al 20006, Mouillot et al 2006). Thus the ability of the SDE group models to generalise beyond the Tamar/Plym system is uncertain. It would now be desirable to extend this study to include other estuaries by testing the original model's abilities to predict the distribution of SDE groups elsewhere and subsequently incorporating the new data into model development and refinement.

Any such further work should ensure that data are collected from additional sites covering a wide range of interstitial salinities and sediment types. A range of estuary "types" should also be included in any additional investigations. Sanders (unpublished data) showed that the taxonomic structure of the estuarine macrobenthos at various locations around the UK varied with the geomorphology of the estuarine system. Estuarine geomorphology influences the hydrodynamic regime of an estuary with consequent implications for the biota in terms of factors such as current flow, sedimentation rate, sediment erosion and the supply of organic matter.

In addition, the geographic location of an estuary determines the species pool from which estuarine macrobenthic species are recruited. Hence, further model development and subsequent validation would benefit if samples were obtained from various geographic locations.

The development of the SDE groups presented in this thesis was dependent upon sufficient information about species behaviours being available in the literature, as would the future development of any other functional classifications based upon species activity. Undoubtedly, the utility of any functional classification is limited by its ability to truly characterise the type and levels of biotic effect. Further studies to characterise sediment disturbance would greatly improve the accuracy of SDE group classification for many species, for example little is known about the distances moved through the sediment by errant species such as *Nephtys sp*, and many small species found at depth, such as *Tubificoides sp.*, were treated as moving up and down the sediment but may in fact have been associated with burrows of other organisms. There is an increasing interest in relationships between species traits and environmental parameters for both flora and fauna (Dolédec et al 1999, Statzner et al 2001, Bremner et al 2003, Usseglio-Polatera et

al 2004, Poff et al 2006). For many life history and feeding activity traits, greater access to species data is becoming available, for instance by initiatives such as BIOTIC (www.marlin.ac.uk/biotic, accessed 23/11/2007) for marine invertebrates, ELMR (http://ccmaserver.nos.noaa.gov/ecosystems/estuaries/elmr.html, accessed 23/11/2007) for estuarine fauna, and LEDA (Knevell et al 2003) and BIOFLOR (www.bio.unc.edu/faculty/peet/vegdata/iavs2003/kuehn.ppt, accessed 23/11/07) for flora. Improved access to species trait data for the estuarine macrobenthos will allow the SDE groups developed in this thesis to be refined as more accurate information becomes available.

6.6 Conclusions

The current work has provided the foundations for further development of models that predict contributions of macrobenthic species' to sediment-disturbance related functions in estuaries. Model refinement should lead to improved confidence in predictions. There is the potential that a generic model, based upon SDE groups, could be applied to any estuary, and the results combined with local knowledge of the macrobenthic species pool to predict species distributions where required. In addition, this current study has provided new insights that could help researchers examine the role of spatial and temporal scales upon the structure of estuarine infaunal assemblages. By modelling the differential responses of shallow and deep macrobenthic assemblages in terms of a functional contribution, a greater understanding of the complexity of estuarine ecosystems will start to emerge.

The approach developed in this thesis merits extension to other biological components and ecosystems. By considering the overall impact of each species' activities upon a single ecosystem process, researchers can quantify and compare relative contributions to ecosystem functioning, regardless of the mechanism by

which the effect is realised. Such an approach makes no assumptions about each species' influence upon other processes. Further, where several different "overall effects" are examined, inclusion under one functional scheme does not preclude consideration of others. For example, SDE groups consider only the direct influence of species upon sediment disturbance. However, were an additional scheme to be developed, according to each species' influence upon sediment stabilising processes, then the original allocation of species into SDE groups would not determine *a priori* the new group membership. Rather, the latter would be considered from a fresh examination of species traits.

As discussed above, to successfully employ the approach advocated in this thesis there are some serious difficulties to overcome (see Section 6.1 and 6.2.1.1.1), not least of which is quantifying the true levels of species activity. Species activity type and levels can vary according to seasonality, maturity, inter- and intra-species interactions, climate and food supply amongst other factors (Cammen 1989, Zwarts and Wanink 1993, Whitlach et al 1998). Activity can also vary between cohorts, populations and according to geographic location. Future laboratory studies might provide useful information although these often do not reflect levels of activity observed in the field. However, to move forward and link species activity to the environment, biotic contributions to function need to be quantified. This will require a combination of field and laboratory studies and also a classification system that incorporates variability in activity levels and type. The SDE groups developed in this Thesis are a rudimentary first step and produced surprisingly good results. The large number of sources of potential errors, combined with high degrees of uncertainty attached to SDE group development, limit the usefulness of the existing models. To improve upon both the models and our ability to confidently interpret the observed relationships, both the models and

the SDE development processes need to be reviewed in the light of new sample data that covers a wider range of environmental conditions and permits better characterisation of the spatial distribution of larger, deeper-living organisms. In addition SDE group classification could be improved if research were undertaken to identify the type and frequency of sediment modifying activities for many more infaunal species, particularly the larger or more abundant species.

Work presented in this thesis has provided strong evidence that species activity can be quantitatively linked to ecosystem processes. There is potential for increased understanding of the contribution of species to ecosystem functioning if: careful consideration is given to the selection of abiotic factors to characterise the function of interest; species are grouped according to their overall impact upon a particular function rather than the mechanisms by which those species realise any effect; and due consideration is given to any differential responses to abiotic forcing displayed by components of the biota with distinctly different life history traits. Whilst all ecosystems are complex, not all functional grouping approaches to characterising biota are equal. If researchers focus upon quantifying the relative contribution of species to the overall level of ecosystem functioning, a greater understanding of biotic-abiotic interactions will emerge.

REFERENCES

Alexander RR, Stanton RJ, Dodd JR (1993) Influence of Sediment Grain Size on the Burrowing of Bivalves: Correlation with Distribution and Stratigraphic Persistence of Selected Neogene Clams. PALAIOS 8(3):289-303

Aller RC (1980) Relationships of tube-dwelling benthos with sediment and overlying water chemistry. In: Tenore KR, Coull BC (eds) Marine benthic dynamics. University South Carolina Press, Columbia, p285-308

Aller RC (1982) The effects of macrobenthos on chemical properties of marine sediments and overlying waters. In: McCall PL, Tevesz MJS (eds) Animal-sediment relations. Plenum Publishing Corp. New York, p 53-102

Aller RC, Yingst JY (1985) Effects of the marine deposit-feeder *Heteromastus filiformis* (Polychaeta), *Macoma balthica* (Bivalvia) and *Tellina texana* (Bivalvia) on averaged sedimentary solute transport, reaction rates and microbial distributions. J Mar Res 43:615-645

Amos CL, Sutherland TF, Cloutier D, Patterson S (2000) Corrasion of a remoulded bed by saltating littorinid shells. Cont Shelf Res 20:1291-1315

Andersen FO, Kristensen E (1991) Effects of burrowing macrofauna on organic matter decomposition in coastal marine sediments. Symp Zool Soc London 63:69-88

Anderson MJ (2001) A new method for nonparametric multivariate analysis of variance. Austral Ecol 26:32-46

Anderson MJ (2004) DISTLM v.5: a FORTRAN computer program to calculate a distance-based multivariate analysis for a linear model. Department of Statisitc, University of Aukland, New Zealand.

Anderson MJ, Ford RB, Feary DA, Honeywell C (2004) Quantitative measures of sedimentation in an estuarine system and its relationship with intertidal soft-sediment infauna. Mar Ecol Prog Ser 272:33-48

Andersen TK (2001) Seasonal variation in erodability of two temperate, microtidal mudflats. Est Coast Shelf Sci 53:1-12

Attrill M J, Power M, Thomas RM (1999) Modelling estuarine Crustacea population fluctuations in response to physico-chemical trends. Mar Ecol Prog Ser 178:89-99

Attrill MJ (2002) A testable linear model for diversity trends in estuaries. J Animal Ecol 71:262-269

Austin MP (2002) Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. Ecol Model 157:101-118

Baird D, Ulanowicz RE (1993) Comparative study on the trophic structure, cycling and ecosystem properties of four tidal estuaries. Mar Ecol Prog Ser 99:221-237

Bale AJ, Widdows J, Harris CB and Stephens JA (2006) Measurements of the critical erosion threshold of the surface sediments along the Tamar Estuary using a mini-annular flume. Cont Shelf Res 26:1206-1216

Banta GT, Anderson O (2003) Bioturbation and the fate of sediment pollutants. Experimental case studies of selected infauna species. Vie Milieu 53(4):233-248

Barnes RD (1974) Estuarine Biology. Studies in biology no 49. Edward Arnold, London.

Barnes RD (1987) Invertebrate Zoology, 5th edition. Saunders College Publishing

Barnes RSK, Hughes R (1988) Speciation and Biogeography. In: An Introduction to Ecology Oxford, pp351

Basset A, Sangiorgio F, Pinna M (2004) Monitoring with benthic macroinvertebrates: advantages and disadvantages of body size descriptors. Aquatic Conserv: Mar Freshw Ecosyst 14:S43-S58

Basset A, Angelis DL (2007) Body size mediated coexistence of consumers competing for resources in space. Oikos 116(8):1363-1377

Belyea LR, Lancaster J (1999) Assembly rules within a contingent ecology. Oikos 86:402-416.

Berg P, Rysgaard S, Funch P, Sejr MK (2001) Effects of bioturbation on solutes and solids in marine sediments. Aquat Microb Ecol 26:81-94

Biles CL, Paterson DM, Ford RB, Solan M, Raffaelli DG (2002) Bioturbation, ecosystem functioning and community structure. Hydrology and Earth System Science 6(6):999-1005

Bilyard GR (1987) The value of benthic infauna in marine pollution studies. Mar Pollut Bull 18(11):581-585.

Black KS, Paterson DM (1997) Measurement of the erosion potential of cohesive marine sediments: a review of current in situ technology. J Marine Env Engg 4: 43-86

Black KS, Tolhurst TJ, Paterson DM and Hagerthey SE (2002) Working with natural cohesive sediments. J Hydraul Eng Jan 2002:2-8

Blair NE, Levin LA, DeMaster DJ, Plaia G (1996) The short-term fate of fresh algal carbon in continental slope sediments. Limnol Oceanogr 41(6):1208-1219

Blondel J (2003) Guilds or functional groups: does it matter? Oikos 100:223-231

Bolam SG, Whomersley P, Schratzberger M (2004) Macrofauna recolonisation on intertidal mudflats: effect of sediment organic and sand content. J Exp Mar Biol Ecol 306:157-180

Bonsdorff E, Ostermann CS (1985) The establishment, succession and dynamics of a zoobenthic community: an experimental study. In Gibbs PE (ed) Proceedings of the 19th European Marine Biology Symposium, Plymouth, Devon, 16-21 September 1984, pp287-298

Bonsdorff E, Pearson TH (1997) The relative impact of physical disturbance and predation by *Crangon crangon* on populations density in *Capitella capitata*: an experimental study. Ophelia 46:1-10.

Bonsdorff E, Pearson TH (1999) Variation in the sublittoral macrozoobenthos of the Baltic Sea along environmental gradients: a functional group approach. Aust J Ecol 24: 312-326

Boon AR, Duineveld GCA (1998) Chlorophyll *a* as a marker for bioturbation and carbon flux in southern and central North Sea sediemnts. Mar Ecol Prog Ser 162:33-43

Borja A, Franco J, Perez V (2000) A marine Bioitc Index to establish the ecological quality of soft-bottom benthos within European estuaries and coastal environments. Mar Pollut Bull 40:1100-1114

Borja A, Muxika I, Franco J (2003) The application of a Marine Biotic Index to different impact sources affecting soft-bottom benthic communities along European coasts. Mar Pollut Bull 46:835-845

Boudreau BP, Marinelli R (1994) A modelling study of discontinuous biological irrigation. J Mar Res 52: 947-968

Brenchley GA (1981) Disturbance and community structure: an experimental study of bioturbation in a soft-bottom environment. J Mar Res 39(4):767-790

Bremner J, Frid CLJ, Rogers SI (2003) Assessing Marine Ecosystem Health: The long-term effects of fishing on functional diversity in the North Sea benthos. Aquatic Ecosystem Health and Management 6(2):131-137

Brotas V, Amorim-Ferreira A, Vale C, Catarino F (1990) Oxygen profiles in intertidal sediments of Ria Formosa (S. Portugal) . Hydrobiologia 207:123-130.

Brown JH, Marquet PA, Taper ML (1993) Evolution of body size: consequences of an energetic definition of fitness. Am Nat 142(4): 573-584

Brown JH, Gillooly JF, Allen AP, van Savage M, West GB (2004) Toward a metabolic theory of ecology. Ecology 85(7):1771-1789

Bryan GW, Uysal H (1978) Heavy metals in the burrowing bivalve *Scrobicularia plana* from the Tamar Estuary in relation to environmental levels. J Mar Biol Ass UK 59:89-108

Cabral HN, Murta AG (2004) Effect of sampling design on abundance estimates of benthic invertebrates in environmental monitoring studies. Mar Ecol Prog Ser 279:19-24

Cadee GC (1976). Sediment reworking by *Arenicola marina* on tidal flats in the Dutch Wadden Sea. Neth J Sea Res 10:440-460

Cammen LM (1989) The relationship between ingestion rate of depsoit feeders and sediment nutritional value. In: Lopez G, Taghon G, Levington J (eds) Ecology of marine deposit feeders, Springer-Verlag pp 201-222

Carignan V, Villard M-A (2002) Selecting indicator species to monitor ecological integrity: a review. Environ Monit Assess 78:45-61

Carson R (1962) Silent Spring. Houghton Mifflin

Chapin III FS, Zavaleta ES, Eviners VT, Naylor RL, Vitousek PM, Reynolds HL, Hooper DU, Lavorel S, Sala OE, Hobbie SE, Mack MC, Diaz S (2000) Consequence of changing biodiversity. Nature 405:234-242

Chapman MG, Tolhurst TJ (2007) Relationships between benthic macrofauna and biogeochemical properties of sediment at different spatial scales and among different habitats in mangrove forests. J Exp Mar Biol Ecol 343:96-109

Chesney EJ, Tenore KR (1985) Oscillations of laboratory populations of the polychaete *Capitella capitata* (Type 1): their cause and implications fro natural populations. Mar Ecol Prog Ser 20:289-296

Christie MC, Dyer KR, Blanchard G, Cramp A, Mitchener HJ, Paterson DM (2000). Temporal and spatial distributions of moisture and organic contents across a macro-tidal mudflat. Cont Shelf Res 20:1219-1241

Clarke KR, Gorley RN (2001) Primer v5: User manual/tutorial. PRIMER-E Ltd, Plymouth.

Clarke KR, Warwick RM (2001) Change in marine communities: An approach to statistical analysis and interpretation. 2nd edition, PRIMER-E Ltd.

Clarke KR, Somerfield PJ, Chapman MG (2006) On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray-Curtis coefficient for denuded assemblages. J Exp Mar Biol Ecol 330:55-80

Clavier J (1984) Macrofauna vertical distribution within a fine sediment. Cah Biol Mar 25(2): 141-152

Clements FE (1916) Plant succession: an analysis of the development of vegetation. Carnegie Institution of Washington, Washington, DC.

Cohen JE, Jonsson T, Carpenter SR (2003) Ecological community description using the food web, species abundance, and body size. PNAS 100(4):1781-1786

Commito JA (1982) Importance of predation by infaunal polychaetes in controlling the structure of a soft-bottom community in Maine, USA. Mar Biol 68(1):77-81

Connell JH (1978) Diversity in tropical rain forests and coral reefs. Science 199:1302-1309

Connolly SR, Roughgarden J (1999) Theory of marine communities: Competition, predation and recruitment-dependent interaction strength. Ecol Monog 69(3):277-296

Connor D (1999) Marine Nature Conservation Review Guidance Notes for completion of recording forms. JNCC, UK

Constable AJ (1999) Ecology of benthic macro-invertebrates in soft sediment environments: A review of progress towards quantitative models and predictions. Aust J Ecol 24: 452-476

Coulson MG, Budd JTC, Withers RG, Nicholls DN (1980) Remote sensing and field sampling of mudflat organisms in Langstone and Chichester harbours, Southern England. In Price JH, Irvine DEG, Farnham WF (eds) Systematics Association Special Volume No 17a "The Shore Environment, Vol 1: Methods", pp.241-263. Academic Press, London and New York.

Crawley MJ (2005) Statistics: An introduction using R. John Wiley and Sons, Chichester.

Crooks S (2004) The effect of sea-level rise on coastal geomorphology. Ibis 146 (supplt1):18-20

Dangles O, Malmqvist B (2004) Species richness decomposition relationships depend on species dominance. Ecol Lett 7:395-402

Darwin C (1859) The origin of species.

Dauer DM (1984) Functional morphology and feeding behaviour of *Streblospio benedicti* (Polychaeta; Spionidae). Proceedings of the First International Polychaete Conference, Sydney. In Hutchings PA (ed) Linnean Society of New South Wales pp418-429

Dauer DM (1993) Biological criteria, environmental health and estuarine community macrobenthic structure. Mar Pollut Bull 26(5):249-257

Dauwe B, Herman PMJ, Heip CHR (1998) Community structure and bioturbation potential of macrofauna at four North Sea stations with contrasting food supply. Mar Ecol Prog Ser 173:67-83

Davey JT, Partridge VA (1998) The macrofaunal communities of the Skeffling muds (Humber estuary) with special reference to bioturbation. Geological Society Special Publications 139:115-124

Davis FM (1925) Quantitative studies of the fauna of the sea-bottom. Part II Fish Invest London, Ser 2 8(4):1-50

de Deckere EMGT, Herman PMJ, Sandee AJJ, van der Wal P and Heip CHR (2002) The effect of *Corophium volutator* on sediment stability: a flume study. In: de Deckere EMGT Faunal influence on sediment stability in intertidal mud NIOO Thesis 20.

de Jonge VN, Elliott M, Brauer VS (2006) Marine monitoring: its shortcomings and mismatch with the EU Water Framework Directive's objectives. Mar Pollut Bull 53(1-4):5-19

Dernie KM, Kaiser MJ, Richardson EA, Warwick RM (2003) Recovery of soft sediment communities and habitats following physical disturbance. J Exp Mar Biol Ecol 285-286:415-434

de Sylva DP (1975) Nektonic food webs in estuaries. In Cronin LE (ed) Estuarine Research: Chemistry, Biology and the Estuarine System. Vol. 1. Academic Press, New York, pp. 420–447.

Diaz S and Cabido M (2001) Vive la difference: plant functional diversity matters to ecosystem processes. Trends Ecol Evol 16(11):646-655

Dolédec S, Chessel D, ter Braak CJF, Champely S (1996) Matching species traits to environmental variables: a new three-table ordination method. Environmental and ecological statistics 3: 43-166

Dolédec S, Statzner B, Bournard M (1999) Species traits for future biomonitoring across ecoregions: patterns along a human-impacted river. Freshw Biol 42:737-758

Dolédec S, Phillips N, Scarsbrook B, Riley RH, Townsend CR (2006) Comparison of structural and functional approaches to determining landuse effects on grassland stream invertebrate communities. J N Am Benthol Soc 25(1):44-60

Doncaster CP, Pound GE, Cox SJ (2003) Dynamics of regional coexistence for more or less equal competitors. J Animal Ecol 72:116-126

Duffy JE (2002) Biodiversity and ecosystem function: the consumer connection. Oikos 99:201-219

Dyer KR, Christie MC, Feates N, Fennessy MJ, Pejrup M, van der Lee W (2001) An investigation into processes influencing the morphodynamics of an intertidal mudflat, the Dollard Estuary, The Netherlands: I. Hydrodynamics and Suspended Sediment. Est Coast Shelf Sci 50(5):607-625

Eagle, RA (1975) Natural fluctuations in a soft bottom benthic community. J Mar Biol Ass UK 55:865-878

Ehrlich P, Ehrlich A (1981) Extinction. The causes and consequences of the disappearance of species. Random House. New York.

Ehrlich PR, Raven PH (1964) Butterflies and plants – a study in coevolution. Evolution 18:58-608

Ekström M, Fowler HJ, Kilsby CG, Jones PD (2005) New estimates of future changes in extreme rainfall across the UK using regional climate model integrations. 2. Future estimates and use in impact studies. J Hydrol 300:234-251

Elliott M, O'Reilly MG (1991) The variability and prediction of marine benthic community parameters. In Elliott M, Ducrotoy J-P (eds) Estuarine & Coasts: spatial and temporal intercomparisons. Olsen & Olsen , Fredensborg, Denmark 231-238

Elliott M, Dewailly F (1995) Structure and components of European estuarine fish assemblages. Neth J of Aquatic Ecol 29, 397–417.

Elliott M, Nedwell S, Jones NV, Read SJ, Cutts ND, Hemingway KL (1998) Intertidal sand and mudflats & subtidal mobile sandbanks (volume II). An overview of dynamic and sensitivity characteristics for conservation management of marine SACs. Scottish Association for Marine Science (UK Marine SACs Project). 151 Pages.

Elliott M, Cutts ND (2004) Marine habitats: loss and gain, mitigation and compensation. Mar Pollut Bull 49:671-74

Elliott M, Burdon D, Hemingway K L (2006) Marine ecosystem structure, functioning, health and management and potential approaches to marine ecosystem recovery: a synthesis of current understanding. Unpublished report: YBB092-F-2006 for the Countryside Council of Wales, by the Institute of Estuarine and Coastal Studies. University of Hull, UK 102pp

Elliott M, Quintino V (2007) The Estuarine Quality Paradox, Environmental Homeostasis and the difficulty of detecting anthropogenic stress in naturally stressed areas. Mar Pollut Bull 54: 640-645

Elliott M, Whitfield AK, Potter IC, Blaber SJM, Cyrus DP, Nordlie FG, Harrison TD (2007a) The guild approach to categorizing estuarine fish assemblages: a global review. Fish and Fisheries 8, 241-268

Elliott M, Burdon D, Hemingway KL, Apitz SE (2007b) Estuarine, coastal and marine ecosystem restoration: Confusing management and science – A revision of concepts. Est Coast Shelf Sci 74:349-366

Ellis J, Ysebaert T, Hume T, Norkko A, Bull T, Herman P, Thrush S, Oldamn J (2006) Predicting macrofaunal species distributions in estuarine gradients using logistic regression and classifications systems. Mar Ecol Prog Ser 316:69-83

Elton, C (1933) Ecology of animals. Methuen, London

Emlen JM, Freeman DC, Kirchhoff MD, Alados CL, Escos J, Duda JJ (2003) Fitting population models from field data. Ecol Model 162:119-143

Emmerson MC, Solan M, Emes C, Paterson DM, Raffaelli D (2001) Consistent patterns and the idiosyncratic effects of biodiversity in marine ecosystems. Nature 411:73-77

Engelberg J, Boyarsky LL (1979) The noncybernetic nature of ecosystems. Am Nat 114(3):317-344

Esselink P, Zwarts L (1989) Seasonal trend in burrow depth and tidal variation in feeding activity of *Nereis diversicolor*. Mar Ecol Prog Ser 56:243-254

Fairweather PG (1999) Determining the "health" of estuaries: Priorities for ecological research. Aust J Ecol 24:441-451

Fano EA, Mistri M, Rossi R (2003) The ecofunctional quality index (EQI): a new tool for assessing lagoonal ecosystem impairment. Est Coast Shelf Sci 56:709-716

Faraway JJ (2002) Practical Regression and ANOVA using R. Chapman Hall

Faraway JJ (2006) Extending the linear model with R: generalized linear, mixed effects and non-parametric regression models. Chapman and Hall

Fauchald K, Jumars PA (1979) The diet of worms: a study of polychaete feeding guilds. Oceanogr Mar Biol Annu Rev 17:193-284

Fischlin A, Midgley GF, Price JT, Leemans R, Gopal B, Turley C, Rounsevell MDA, Dube OP, Tarazona J, Velichko AA (2007) Ecosystems, their properties, goods, and services. Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of WorkingGroup II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, Parry ML, Canziani OF, Palutikof JP, van der Linden PJ, Hanson CE (eds) Cambridge University Press, Cambridge, 211-272.

Field JG, Clarke KR, Warwick RM (1982) A practical strategy for analysing multi-species distribution patterns. Mar Ecol Prog Ser 8:37-52

Flach EC (1996) The influence of the cockle, *Cerastoderma edule*, on the macrozoobenthic community of tidal flats in the Wadden Sea. In: Dworschak, PC et al (eds) (1996). Influences of Organisms on their Environment, the Role of Episodic Events: Proceedings of the 29th European Marine Biology Symposium Vienna, 29 August-2 September 1994. PSZN I: Marine Ecology, 17(1-3). European Marine Biology Symposia, 29: pp. 87-98.

Flach E, Heip C (1996) Vertical distribution of macrozoobenthos within the sediment on the continental slope of the Goban Spur area (NE Atlantic). Mar Ecol Prog Ser 141:55-66

Flemming BW, Delafontaine MT (2000) Mass physical properties of muddy intertidal sediments: some applications, misapplications and non-applications. Cont Shelf Res 20:179-1197

Folk RL, Ward WC (1957) Brazos River bar, a study in the significance of grain-size parameters. J Sediment Petrol 27: 3-27

Forget G, Lebel J (2001) An ecosystem approach to human health. Int J Occup Environ Health 7 (2Suppl): S3-38

Forster RM, Crach V, Sabbe K, Vyverman W, Stal LJ (2006) Biodiversity-ecosystem function relationship in microphytoenthic diatoms of the Westerschelde estuary. Mar Ecol Prog Ser 311:191-201

Fox J (2002) An R and S-plus companion to applied regression. Thousand Oaks, CA, Sage

Francois F, Gerion M, Stora G, Durbec J-P, Poggiale J-C (2002) Functional approach to sediment reworking by gallery-forming macrobenthic organisms: modelling and application with the polychaete *Nereis diversicolor*. Mar Ecol Prog Ser 229:127-136

Freeman SM, Rogers SI (2003) A new analytical approach to characterisation of macro-epibenthic habitats: linking species to the environment. Est Coast Shelf Sci 56:749-764

Frid C, Hall S (2001) Ecological quality objectives for benthic communities: If we protect the habitat do we need more? ICES COM 2001/IT:06

Fulweiler RW, Nixon BA, Granger SL (2007) Reversal of the net dinitrogen gas flux in coastal marine sediments. Nature 448:180-182

Gergel SE, Turner MG, Mille JR, Melack JM, Stanley EH (2002) Landscape indicators of human impacts to riverine systems. Aquat Sci 64:118-128.

Gerino M, Stora G, Gontier G, Weber O (1993) Quantitative approach of bioturbation on continental margins. Annales de l'Institut Oceanographique 63: 177-181

Gerino M, Stora G, Francois-Carcaillet F, Gilbert F, Poggiale JC, Mermillod-Blondin F, Desrosiers G, Vervier P (2003) Macro-invertebrate functional groups in freshwater and marine sediments: a common mechanistic classification. Vie Milieu 53(5):221-231

Gessner MO, Inchausti P, Persson L, Raffaelli DG, Giller PS (2004) Biodiversity effects on ecosystem functioning: insights from aquatic systems. Oikos 104:419-422

Gibson R, Hextall B, Rogers A (2001) Photographic guide to the sea and shore life of Britain and North-west Europe, Oxford

Gilbert F, Hulth S, Grossi V, Poggiale J-C, Desrosiers G, Rosenberg R, Gerino M, Francois-Carcaillet F, Michaud E, Stora G (2007) Sediment reworking by marine benthic species from the Gullmar Fjord (western Sweden): Importance of faunal biovolume. J Exp Mar Biol Ecol 348:133-144.

Gitay H, Noble IR (1997) What are functional types and how should we seek them? In Smith M, Shugart HH, Woodward FI (eds) Plant Functional Types: Their Relevance to Ecosystem Properties and Global Change pp 3-19, Cambridge University press, Cambridge UK

Goosen NK, van Rijswijk P, Kromkamp J, Peene J (1997) Regulation of annual variation in heterotrophic bacterial production in the Schelde estuary (SW Netherlands). Aquat Microb Ecol 12:223-232

Grall J, Glèmarec M (1997) Using biotic indices to estimate macrobenthic community perturbations in the Bay of Brest. Est Coast Shelf Sci 44(suppl A):43-53

Grant J (1981) Sediment transport and disturbance on an intertidal sandflat: Infaunal distribution and recolonization. Mar Ecol Prog Ser 6:249-255

Grant WD, Boyer LF, Sanford LP (1982) The effects of bioturbation on the initiation of motion of intertidal sands. J Mar Res 40:659-677

Grassle JF, Grassle JP (1974) Opportunistic life histories and genetic systems in marine benthic polychaetes. J Mar Res 32:235-284

Grassle JF, Morse-Porteous LS (1987) Macrofaunal colonisation of disturbed deep-sea environments and the structure of the deep-sea benthic communities. Deep Sea Res A 34(12):1911-1950

Gray JS (1974) Animal-sediment relationships. Oceanogr Mar Biol Annu Rev 12:223-261

Gray JS (1981) The ecology of marine sediments. Cambridge University Press, Cambridge.

Gray JS (2000) The measurement of marine species diversity, with an application to the benthic fauna of the Norwegian continental shelf. J Exp Mar Biol and Ecol 250: 23-49

Gray JS (2001) Marine diversity: the paradigms in patterns of species richness examined. Sci Mar 65 (Suppl2):41-56

Green J (1968) The biology of estuarine animals. Sidgwick and Jackson, London

Green MO, Oldman JW (1999) Deposition of flood-borne sediment in Okura estuary. Report No. ARC90242/2 National Institute of Water and Atmospheric research, Hamilton New Zealand

Grehan AJ, Scaps P, Desrosiers G, Juniper K, Stora G (1994) Vertical macrofauna distribution in the soft sediments of the Gulf of St. Lawrence and the Scotian continental margin: a preliminary assessment of intersite differences in bioturbation potential. Vie milieu 44(2):101-107

Guidetti P, Modena M, La Mesa G, Vacchi M (2000) Composition, abundance and stratification of macrobenthos in the marine area impacted by tar aggregates derived from the Haven oil spill (Ligurian Sea, Italy). Mar Pollut Bull 40(12):1161-1166

Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. Ecol Model 135:147-186

Gutierrez D, Gallardo VA, Mayor S, Neira C, Vasquez C, Sellanes J, Rivas M, Soto A, Carrasco F and Baltazar M (2000) Effects of dissolved oxygen and fresh organic matter on the bioturbation potential of macrofauna in sublittoral sediments off Central Chile during 1997/1998 El Nino. Mar Ecol Prog Ser 202:81-99

Hagberg J, Jonzen N, Lundberg P, Ripa J (2003) Uncertain biotic and abiotic interactions in benthic communities. Oikos 100:353-361

Hall SJ (1994) Physical disturbance and marine benthic communities: Life in unconsolidated sediments. Oceanogr Mar Biol Annu Rev 32:179-239

Halpern BS, Selkoe KA, Mitcheli F, Kappel CV (2007) Evaluating and ranking the vulnerability of global marine ecosystems to anthropogenic threats. Conserv Biol 21(5):1301-1315

Hayward PJ, Ryland JS (1995) The Marine Fauna of the British Isles and North-West Europe, Oxford Scientific Publications

Herman PMJ, Middleburg JJ, Koppel van de J, Heip CHR (1999) Ecology of estuarine macrofauna. Adv Ecol Res 29:195-240

Herman PMJ, Middelburg JJ, Widdows J, Lucas CH, Heip CHR (2000) Stable isotopes as trophic tracers: combining field sampling and manipulative labelling of food resources for macrobenthos. Mar Ecol Prog Ser 204:72-92

Herman PMJ, Middelburg JJ, Heip CHR (2001) Benthic community structure and sediment processes on an intertidal flat results from the ECOFLAT project. Cont Shelf Res 21:2055-2071

Hewitt JE, Thrush SF, Cummings VJ, Pridmore RD (1996) Matching patterns with processes: predicting the effect of size and mobility on the spatial distributions of the bivalves *Macomona liliana* and *Austrovenus stutchburyi*. Mar Ecol Prog Ser 135:57-67

Hilty J, Merenlender A (2000) Faunal indicator taxa selection for monitoring ecosystem health. Biol Conserv 92:185-197

Hines AH, Comtois KL (1985) Vertical distribution of infauna in sediments of a sub-estuary of central Chesapeake Bay. Estuaries 8 (3):296-304

Hirst AJ (2004) Broad-scale environmental gradients among estuarine benthic macrofaunal assemblages of south-eastern Australia: implications for monitoring estuaries. Mar Freshw Res 55:79-92

Hobbs R (1997) Future landscapes and the future of landscape ecology. Landscape and Urban Planning 37(1-2):1-9

Holland AF, Mountford NK, Hiegel MH, Kaumeyer KR, Mihursky JA (1980) Influence of predation on infaunal abundance in Upper Chesapeake Bay, USA Mar Biol 57P:221-235

Holme NA, McIntyre AD (1984) Methods for the study of marine benthos. IBP handbook, Volume 16. Oxford UK, Blackwell

Holme NA (1964) Methods of sampling the benthos Adv Mar Biol 2:171-260.

Hols DR (1996) National Biomonitoring Programme for Riverine Ecosystems. Framework document for the programme. NBP Report Series No 1. Institute for Water Quality Studies. Department of Water Affairs and Forestry, Pretoria, South Africa.

Hooper DU, Solan M, Symstrad A, Diaz S, Gessner MO, Buchmann N, Degrange V, Grime P, Hulot F, Mermillod-Blondin F, Roy J, Spehn E, van Peer L (2002) Species diversity, functional diversity and ecosystem functioning. In Loreau M, Naeem S, Inchausti P (eds) Chapter 17 Biodiversity and ecosystem functioning. Synthesis and perspectives. Oxford University Press

Houghton JT, Ding Y, Grissp DJ (2001) Climate Change 2001: The Scientific Basis. Contribution of working party 1 to the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC) Cambridge University Press.

Hulme M, Jenkins GJ, Lu X, Turnpenny JR, Mitchell TD, Jones RG, Lowe J, Murphy JM, Hassell D, Boorman P, McDonald R, Hill S (2002) Climate change scenarios for the UK: the UKCIP02 scientific report, Tyndall Centre UEA, Norwich, UK

Hulme M, Turnpenny J (2004) Understanding and managing climate change: the UK experience. The Geographical Journal 170(2):105-115

Hulot FD, Lacroix G, Lescher-Moutoue F, Loreau M (2000) Functional diversity governs ecosystem response to nutrient enrichment. Nature 405:340-344

Huz de la R, Lastra M, Lopez J (2002) The influence of sediment grain size on burrowing, growth and metabolism of *Donax trunculus* L (Bivalvia. Donacias). J Sea Res 47: 85-95

Jax K (1998) Holocoen and ecosystem. On the origin and historical consequence of two concepts. Journal on the History of Biology 31:113-42

Johnson RG (1965) Temperature variation in the infaunal environment of a sand flat. Limnol Oceanogr 10:114-120

Johnson RG (1967) The vertical distribution of the infauna of a sand flat. Ecology 48(4):571-578

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69: 373-386

Jones NS (1976) Synopses of the British Fauna (New Series) No. 7 British Cumaceans, Linnean Society of London/Estuarine & Brackish Water Society

Jordan CF (1981) Do ecosystems exist? Am Nat 118(2):284-287

Jorgensen SE (1994) Review and comparison of goal functions in system ecology. Vie Milieu 44(1):11-20

Josefson AB (1989) Do subsurface deposit-feeders partition resources by vertical stratification in the sediment? Sci Mar 52 (2-3):307-313

Jumars PA, Nowell ARM (1984) Effects of benthos on sediment transport: difficulties with functional groups. Cont Shelf Res 3(2):115-130

Karr JR, Dudley DR (1981) Ecological perspective on water quality goals. Environ Manage 5:55-68

Kendall MA, Burrow MT, Southward AJ, Hawkins SJ (2004) Predicting the effects of marine climate change on the invertebrate prey of the birds of rocky shores. Ibis 146(Suppl1):40-47

Kinne O (1971) Salinity: animal-invertebrates p 821-996 O.Kinne (ed) Marine Ecology Vol 1, Environmental factors part 2 John Wiley ad Sons New York

Knevell C, Bekker RM, Bakker JP, Kleyer M (2003) Life-history traits of the Northwest European Flora: The LEDA database. J Vegetation Sci 14(4):611-614

Kramer KJM, Brockman WH, Warwick RM (1994) Tidal estuaries: Manual of sampling and analytical procedures. AA Balkema, Rotterdam

Kristensen E, Jenasen MH, Andersen K (1985) The impact of polychaete (*Nereis virens* Sars) on nitrification and nitrate reduction in estuarine sediments. J Exp Mar Biol Ecol 85:75-91

Lampert W, Sommer U (1997). The Ecology of Lakes and Streams. Oxford University Press.

Lavelle P, Bignell D Lepage M (1997) Soil function in a changing world: the role of invertebrate ecosystem engineers. Eur J of Soil Biol 33:159-193

Lavoral S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Funct Ecol 16:545-556

Lawrence AJ, Soame (2004) The effects of climate change on the reproduction of coastal invertebrates. Ibis 146 (Suppl1):29-39

Lawton J H (1994) What do species do in ecosystems? Oikos 71:367-374

Lawton JH, Brown VK (1993) Redundancy in ecosystems. In Schulze ED, Mooney HA (eds) Biodiversity and Ecosystem Functioning. Springer pp255-270

Le Hir P, Monbert Y, Orvain F (2007) Sediment erodibility in sediment transport modelling: can we account for biota effects? Cont Shelf Res 27:1116-1142

Lee H II, Swartz RC (1980) Biological processes affecting the distribution of pollutants in marine sediments. In: RA Baker (ed) Contaminants and Sediments, Ann Arbor, Michigan Volume 2 p 555-605.

Legendre P, Anderson MJ (1999) Distance-based redundancy analysis: Testing multispecies responses in multifactorial ecological experiments. Ecol Monogr 69(1):1-24

Leung B, Forbes MR, Houle D (2000) Fluctuating asymmetry as a bio-indicator of stress: comparing efficacy of analyses involving multiple traits. Am Nat 155:101-1115

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

Levin LA, Blair NE, Martin CM, DeMaster DJ, Plaia G, Thomas CJ (1999) Macrofaunal processing of phytodetritus at two sites on the Carolina margin: in-situ experiments using 13C-labeled diatoms. Mar Ecol Prog Ser 181:37-54

Levin LA, Boesch FF, Covich A, Dahm C, Erseus C, Ewel KC, Kneib RT, Moldenke A, Palmer MA, Snelgrove P, Strayer D, Weslawski JM, (2001a) The function of marine critical transition zones and the importance of sediment biodiversity. Ecosystems 4: 430-451

Levin SA, Dushoff J, Keymer JE (2001b) Community assembly and the emergence of ecosystem pattern. Sci Mar 65 (Suppl 2):171-179

Lincoln R (1979) British Marine Amphipoda. British Museum (Natural History), London

Lindsay SM, Woodin SA (1996) Quantifying sediment disturbance by browsed spionid polychaetes: implications for competitive and adult-larval interactions. J Exp Mar Biol Ecol 196(1-2):97-112

Lindsay SM, Woodin SA (1992) Tissue loss induces switching of feeding mode in spionid polychaetes. Mar Ecol Prog Ser 125(1-3):159-169

Livingston RJ (2002) Trophic organization in coastal systems. CRC Press, Florida pp 412

Loreau M (2004) Does functional redundancy exist? Oikos 104(3):606-611

Lundkvist M, Grue M, Friend PL, Flindt MR (2007) The relative contributions of physical and microbiological factors to cohesive sediment stability. Cont Shelf Res 27:1143-1152

Margalef, R. (1997) Our biosphere. ECI. Oldendorf.

Matthews WJ, Bek J, Surat E (1982) Comparative ecology of the darters *Etheostoma podostemone*, *E. flabellare* and *Percina roanoka* in the upper Roanoke River drainage, Virginia. Copeia 1982:805-814.

Mathieson S, Cattrijsse A, Costa MJ, Drake P, Elliott M, Gardner J, Marchand J (20002) Fish assemblages of European tidal marshes: a functional guilds-based comparison. Mar Ecol Prog Ser 204:225-242

Mattiessen P, Law RJ (2002) Contaminants and their effects on estuarine and coastal organisms in the United Kingdom in the late twentieth century. Environ Pollu 120:739-757

Mauer D, Keck RT, Tinsman JC, Leathem WA, Wethe C, Lord C, Church TM (1986) Vertical migration and mortality of marine benthos in dredged material: a synthesis. Int Rev Gesamten Hydrobiol 71(1):49-63

May RM (1995) The cheetah controversy. Nature 374:309-310

Mayer LM (1994) Surface area control of organic carbon accumulation in continental shelf sediments. Geochim Cosmochim Acta 58:1271-1284

Mazik K, Elliott M (2000) The effects of chemical pollution on the bioturbation potential of estuarine intertidal mudflats. Helgol Mar Res 54:99-109

Mazik K, Curtis N, Fagan MJ, Taft S, Elliott M (2008) Accurate quantification of the influence of benthic macro- and meio-fauna on the geometric properties of estuarine muds by micro computer tomography. J Exp Mar Biol Ecol 354: 192-201

McArdle BH, Anderson MJ (2001) Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology 82(1):290-297

McArdle BH, Blackwell RG (1989) Measurement of density variability of the bivalve *Chione stutchburyi* using spatial autocorrelation. Mar Ecol Prog Ser 52:245-252

McCall PL (1974) Community patterns and adaptive strategies of the infaunal benthos of Long Island Sound. J Mar Res 35:221-266

McCann KS (2000) The diversity-stability debate. Nature 405:228-233

McIntosh RP (1985) The background of ecology: Concept and theory. Cambridge University Press, England

McClachlan A, Jaramillo E, Donn TE, Wessels F (1993) Sandy beach macrofauna communities and their control by the physical environment: a geographical comparison. J Coastal Res Spec Issue 15:27-38

Mclusky DS (1981) The estuarine ecosystem. Glasgow Blackie

McLusky DS, Elliott M (2004) The Estuarine Ecosystem. Ecology, Threats and Management. Oxford University Press.

McMaster RL (1967) Compactness variability of estuarine sediments: an in situ study in estuaries, pp 261-267. In Lauff GH (ed) American ASS Advance Sci 83

Meadows PS, Reid A (1966) The behaviour of *Corophium volutator* (Crustacea: Amphipoda). J Zool Lond 150:387-399

Meadows PS, Tait J, Hussain SA (1990) Effects of estuarine infauna on sediment stability and particle sedimentation. Hydrobiologia 190:263-266.

Mermillod-Blondin F, Marie S, Desrosiers G, Long B, Montety LDE, Michaud E, Stora G. (2003). Assessment of the spatial variability of intertidal benthic communities by axial tomodensitometry: importance of fine-scale heterogeneity. J Exp Mar Biol Ecol 287:193-208

Mermillod-Blondin F, Rosenberg R, François-Carcaillet F, Norling K, Mauclaire L (2004) Influence of bioturbation by three benthic infaunal species on microbial communities and biogeochemical processes in marine sediment. Aquat Microb Ecol 36:271-284

Mermillod-Blondin F, Francois-Carcaillet F, Rosenberg R (2005) Biodiversity of benthic invertebrates and organic matter processing in shallow marine sediments: an experimental study. J Exp Mar Biol Ecol 315:187-209

Millennium Ecosystem Assessment (2005) Ecosystem and Human Well-being: Synthesis. Island Press, Washington DC.

Miller DC, Bock MJ, Turner EJ (1992) Deposit and suspension feeding in oscillatory flows and sediment fluxes. J Mar Res 50(3):489-520

Molvaer J, Knutzen J, Magnusson J, Rygg B, Skey JM, Sorensen J (1997) Classification of environmental quality in fjords and coastal water. A guide. Veiledning 97:02. Norwegian Pollution Control Authority, Oslo

Moore HB (1931) The muds of the Clyde Sea area III: Chemical and physical conditions: rate of sedimentation and fauna. J Mar Biol Ass UK 17:325-358

Morris AW, Bale AJ, Howland RJM (1982) Chemical variability in the Tamar Estuary, south-west England. Est Coast Shelf Sci 14:649-661

Mortimer RJG, Davey JT, Krom MD, Watson PG, Frickers PE, Clifton RJ (1999) The effect of macrofauna on porewater profiles and nutrient fluxes in the intertidal zone of the Humber estuary Est Coast Shelf Sci 48:683-699

Mouillot D, Spatharis S, Reizopoulou S, Laugier T, Sabetta L, Basset A, Do Chi T (2006) Alternatives to taxonomic-based approaches to assess changes in transitional water communities. Aquatic Conservation: Marine and Freshwater Ecosystems16(5):469-482

Mulsow S, Landrum PF, Robbins JA (2002) Biological mixing responses to sublethal concentrations of DDT in sediments by *Heteromastus filiformis* using a ^{137}Cs marker technique. Mar Ecol Prog Ser 239:181-191

Muylaert K, Tackx M, Vyverman W (2005) Influences of changes in salinity and light intensity on growth of phytoplankton communities from the Schelde river and estuary (Belgium/Netherlands). Hydrobiologia 540(1-3):105-115

Myers AC (1977) Sediment processing in a marine subtidal sandy bottom community: I. Physical aspects. J Mar Res 35:609-647

Naeem S, Thompson LJ, Lawler SP, Lawton JH, Woodfin RM (1994) Declining biodiversity can alter the performance of ecosystems. Nature 368:734-736

Naeem S, Wright JP (2003) Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. Ecol Lett 6:567-579

Naeem S, Loreau M, Inchausti P (2002) Biodiversity and ecosystem functioning: the emergence of a synthetic ecological framework. In: Loreau M, Naeem S, Inchausti P (eds) Biodiversity and ecosystem functioning. Synthesis and perspectives. Oxford University Press.

Nedwall DB, Walker TR (1995) Sediment-water fluxes of nutrients in an Antarctic coastal environment: influence of bioturbation. Polar Biology 15: 57-64

Neira C, Höpner T (1993) Fecal pellet production and sediment reworking potential of the small polychaete *Heteromastus filiformis* show a tide dependent periodicity. Ophelia 37(3): 175-185

Nelder J, Wedderburn R (1972) Generalised linear model. J Royal Statistical Soc A 132:370-384

Norberg J (2004) Biodiversity and ecosystem functioning: A complex adaptive systems approach. Limnol Oceanogr 49(4):1269-1277

Nordstrom M, Bonsdorff E, Salovius S (2006) The impact of infauna (*Nereis diversicolor* and *Saduria entemon*) on the redistribution and biomass of macroalgae on marine soft bottoms. J Exp Mar Biol Ecol 333:58-70

Norkko A, Rosenberg R, Thrush SF, Whitlach RB (2006) Scale- and intensity-dependent distubance determines the magnitude of opportunistic response. J Exp Mar Biol Ecol 330:195-207

Nybakken JW (1993) Marine Biology: an ecological perspective. 3rd edition. Harper-Collins. New York

Odum E.P (1969) The strategy of ecosystem development. Science 164:262-270

Olive PJW, Garwood PR (1981) Gametogenic cycle and populations structures of *Nereis (Hediste) diversicolor* and *Nereis (Nereis) pelagica* from North-East England. J Mar Biol Ass UK 61:191-213

Orvain F, Sauriau P-G (2002) Environmental and behavioural factors affecting activity in the intertidal gastropod *Hydrobia ulvae*. J Exp Mar Biol Ecol 272 (2):191-216

Orvain F, le Hir P, Sauriau PG (2003) A model for initial resuspension of bioturbated layers and ensuing bed erosion. J Mar Res 61:821-849

Orvain F (2005) A model of sediment transport under the influence of bioturbation activities: generalisation to a key species *Scrobicularia plana*. Mar Ecol Prog Ser 286: 43-56

Ouellette D, Desrosiers G, Gagne J-P, Gilbert F, Poggiale J-C, Blier PU, Stora G (2004) Effects of temperature on in vitro sediment reworking processes by a gallery biodiffusor, the polychaete *Neanthes virens*. Mar Ecol Prog Ser 266:185-193

Padilla DK, Allen BJ (2000) Paradigm lost: reconsidering functional form and group hypotheses in marine ecology. J Exp Mar Biol Ecol 250:207-221

Parry ML, Canziani OF, Palutikof JP, Linden van der PJ, Hanson CE (eds) (2007) IPCC, 2007: Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment. Report of the Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge, UK, 976pp.

Pasquaud S, Lobry J, Elie P (2007) Facing the necessity of describing estuarine ecosystems: a review of food web ecology study techniques. Hydrobiologia 588(1):159-172

Paterson DM, Black KS (1999) Water flow, sediment dynamics and benthic biology. Adv Ecol Res 29:155-193

Paterson DM, Tolhurst TJ, Kelly JA, Honeywill C, de Deckere EMGT, Huet V, Shayler SA, Black KS, de Brouwer J, Davidson I (2000) Variations in sediment properties, Skeffling mudflat, Humber Estuary, UK. Cont Shelf Res 20:1373-1396

Pearson TH, Rosenberg R (1978) Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanogr Mar Biol Annu Rev 16:229-311

Pearson TH (2001) Functional Group Ecology in soft sediment marine benthos: The role of bioturbation. Oceanogr Mar Biol Annu Revu 39:233-267

Perillo GME (1995) Geomorphology and Sedimentology of estuaries. Elsevier, Amsterdam.

Perkins EJ (1974) The biology of estuaries and coastal waters. Academic Press, London.

Petchey OL, Downing AL, Mittelbach GG, Persson L, Steiner CF, Warren PH, Woodward G (2004) Species loss and the structure and functioning of multitrophic aquatic systems. Oikos 104 (3), 467–478.

Peters RH (1987) Ecological Implications of Body Size. Cambridge Univ. Press, Cambridge, UK

Peterson CH (1977) Competitive organization of the soft-bottom macrobenthic communities of southern California lagoons. Mar Biol 43:343-359

Peterson G, Allen CR, Holling CS (1998) Ecological Resilience, Biodiversity and Scale. Ecosystems 1: 6-18

Phillips NW, Tenore KR (1984) Effects of food-particle size and pelletization on individual growth and larval development of the deposit feeding polychaete *Capitella capitata*. Mar Ecol Prog Ser 16:241-247

Pianka ER (1978) Evolutionary Ecology. Harper and Row, New York.

Pickett STA, Cadenasso, ML (2002) The ecosystem as a multidimensional concept: meaning, model and metaphor. Ecosystems 5:1-10

Platell ME, Potter IC (1996) Influence of water depth, season, habitat and estuary location on the macrobenthic fauna of a seasonally closed estuary. J Mar Biol Ass UK 76:1.21

Poff NL, Olden JD, Vieira NKM, Finn DS, Simmons MP, Kondratieff BC (2006) Functional trait niches of North American lotic insects: traits-based ecological applications in light of phylogenetic relationships. J N Am Benthol Soc 25(4):730-755

Purvis A, Hector A (2000) Getting the measure of biodiversity. Nature 405:212-219

Quintino V, Elliott M, Rodrigues AM (2006) The derivation, performance and role of univariate and multivariate indicators of benthic change: Case studies at differing spatial scales. J Exp Mar Biol and Ecol 34:368-382

R Development Core Team R: A Language and Environment for Statistical Computing R Foundation for Statistical Computing Vienna, Austria 2007 ISBN3-900051-07-0 url http://www.R-project.org

Rapport DJ, Constanza R, McMichael AJ (1998) Assessing ecosystem health. Trends Ecol Ecol 13(10): 397-402

Reed DC, Huang K, Boudreau BP, Meysman FJR (2006) Steady-state tracer dynamics in a lattice-automaton model of bioturbation. Geochimica and Cosmochimica Acta 70: 5855-5867

Rehfisch MM, Austin GE (2006) Climate change and coastal waterbirds: the United Kingdom experience reviewed. In: Galbraith GC, Stroud DA (eds) Waterbirds around the world. The Stationary Office, UK pp 398-404

Reid DM (1930) Salinity interchange between seawater in sand and overflowing fresh-water at low water. J Mar Biol Ass UK 16:609-614

Reise K (1979) Spatial configurations generated by motile benthic polychaetes. Helgolander Wiss Meersunters 32:55-72

Reiss H, Kröncke I (2005) Seasonal variability of benthic indices: an approach to test the applicability of different indices for ecosystem quality assessment. Mar Pollut Bull 50:1490-1499

Reizopoulou S, Nicolaidou A (2007) Index of size distribution (ISD): a method of quality assessment fro coastal lagoons. Hydrobiologia 577:141-149

Remane A (1934) Die Brackwasserfauna. Verhandlungen der Deutsche Zoologischen Gesellschaft 35:34-74

Reynolds CS (2001) Emergence in pelagic communities. Sci Mar 65 (suppl 2):5-30

Rhoads DC (1974) Organism-sediment relations on the muddy sea floor. Ocenaogr Mar Biol Annu Rev 12:223-300

Rhoads DC, Boyer LF (1982) The effects of marine benthos on physical properties of sediments. A successional perspective. In: McCall PL, Tevesz MJS (eds) Animal-sediment relations New York: Plenum Press, p 3-52

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

Rhoads DC, Yingst JY, Ullmann WJ (1978) Seafloor stability in Central Long Island Sound. Part 1. Temporal changes in erodibility of fine grained sediment. In: Wilet ML (ed) Estuarine Interaction. Academic Press pp 221-244

Rice DL (1986) Early diagenesis in bioadvective sediments: Relationships between the diagenesis of beryllium-7, sediment reworking rates, and the abundance of conveyor-belt deposit-feeders. J Mar Res 44:149-184

Rice DL, Rhoads DC (1989) Early diagenesis of organic matter and the nutritional value of sediment. In: Lopez G, Taghon G, Levington J (eds) Ecology of Marine Deposit Feeders, Springer-Verlag, pp 59-97

Richardson DM, MacDonald IAW, Hoffmann JH, Henderson L (1997) Alien plant invasions. In: Cowling RM, Richardson DM, Pierce SM (eds) Vegetation of Southern Africa. Cambridge University Press, Cambridge, pp 535-570

Robinson PF, Riddle AM (2004) Tamar estuary BELLPLUME model description and validation. Report BL7970/B. Brixham Environmental Laboratory, Brixham, UK

Rogers SI, Greenway B (2005) A UK perspective on the development of marine ecosystem indicators. Mar Pollut Bull 50:9-19

Rojo C, Ortega-Mayagoitia E, Lavarez-Cobela MA (2000) Lack of pattern among phytoplankton assemblages. Or, what does the exception to the rule mean? Hydrobiologia 424:133-139

Rosa-Filho JS, Bemvenuti CE, Elliott M (2004) Predicting biological parameters of estuarine benthic communities using models based on environmental data. Brazilian Archives of Biology and Technology 47(4):613-627

Rosenfeld JS (2002) Functional redundancy in in ecology and conservation. Oikos 98:156-162

Rowden AA, Jago CF and Jones SE (1998) Influence of benthic macrofauna in the geotechnical and geophysical properties of surficial sediments, North Sea. Cont Shelf Res 18:1347-1363

Rowden AA, Jones MB (1993) Critical evaluation of sediment turnover estimates for Callianasidae (Decapoda: Thalassinidea). J Exp Mar Biol Ecol 173 (2): 265-272.

Ruesink JL, Feist BE, Harvey CJ, Hong JS, Trimble AC, Wisehart LM (2006) Changes in productivity associated with four introduced species: ecosystem transformation of a 'pristine' estuary. Mar Ecol Prog Ser 311: 203-215

Rysgaard S, Thamdrup B, Risgaard-Petersen N, Fossing H, Berg P, Christensen PB, Dalsgaard T (1998) Seasonal carbon and nitrogen mineralization in a high-Arctic coastal marine sediment, Young Sound Greenland. Mar Ecol Prog Ser 175:261-276

St Onge P, Miron G, Moreau G (2007) Burrowing behaviour of the softshell clam (*Mya arenaria*) following erosion and transport. J Exp Mar Biol Ecol 340:103-111

Sagoff M (2003) The plaza and the pendulum: Two concepts of ecological science. Biology and Philosophy 18:529-552

Sanders HL (1968) Marine benthic diversity. A comparative study. Am Nat 102(925):243-282

Schindler DW (2001) The cumulative effects of climate warming and other human stresses on Canadian freshwaters in the new millennium. Can J Fish Aquat Sci 58(1):18–29

Schwartz MW, Brigham CA, Hoeksema JD, Lyons KG, Mills MH, van Mantgem PJ (2000) Linking biodiversity to ecosystem function: implications for conservation ecology. Oecologia 122:297-305

Shirayama Y, Horikoshi M (1982) Vertical distribution of smaller macrobenthos and larger meiobenthos in the sediment profile in the deep-sea system of Suruga Bay (Central Japan). J Oceanogr Soc Japan 38:273-280

Shugart HH (1997) Plant and ecosystem functional types. In: Smith TM, Shugart HH, and Woodward FI (eds.) Plant Functional Types: Their Relevance to Ecosystem Properties and Global Change. Cambridge, UK: Cambridge University Press pp. 20–43.

Simberloff D, Dayan T (1991) The guild concept and the structure of ecological communities. Annu Rev Ecol Syst 22:115-143

Simboura N, Zenetos A (2002) Benthic indicators to use in Ecological Quality classification of Mediterranean soft bottom marine ecosystems, including a new Biotic Index. Mediterranean Marine Science 3/2: 1-35

Skriver J (2001) Biological Monitoring in Nordic Rivers and Lakes. Report to Nordic Council of Ministers. National Environment Research Institute Report 2001:513, Denmark.

Smaal AC, Nienhuis PH (1992) The Eastern Scheldt (The Netherlands), from an estuary to a tidal bay: a review of responses at the ecosystem level. Neth J Sea Res 30 (1):161-173

Smith KL, Howard JD (1972) Comparison of a grab sampler and large volume corer. Limnol Oceanogr 17:142-145

Smith M, Shugart HH, Woodward FI (1997) Plant Functional Types: Their Relevance to Ecosystem Properties and Global Change, Cambridge University press, Cambridge UK

Snelgrove PVR, Butman CA (1994) Animal-sediment relationships revisited: Cause versus effect. Oceanogr Mar Biol Annu Rev 32:111-177

Solan M (2004) The concerted use of traditional and sediment profile imagery (SPI) methodologies in marine benthic characterisation and monitoring. PhD Thesis. National University of Ireland, Galway.

Solan M, Wigham BD, Hudson IR, Kennedy R, Coulon CH, Norling K, Nilsson HC, Rosenberg R (2004) In situ quantifiaction of bioturbation using time-lapse fluorescent sediment profile imaging (f-SPI), luminophore tracers ad model simulation (2004) Mar Ecol Prog Ser 271:1-12

Spies RB, Davis PH (1979) The infaunal benthos of a natural oil seep in the Santa Barbara Channel. Mar Biol 50: 227-237

Statzner B, Bis B, Dolédec S, Usseglio-Polatera P (2001) Perspectives for biomonitoring at large spatial scales: a unified measure for the functional composition of invertebrate communities in European running water. Basic Appl Ecol 2:73-85

Steffen WL, Walker BH, Ingram JSI, Koch GW (1992) Global change and terrestrial ecosystems: The operational plan. IGBP Report No. 21. IGBP Secretariat, Stockholm.

Strasser M, Walensky M, Reise K (1999) Juvenile-adult distributions of the bivalve Mya arenaria on intertidal flats in the Wedden Sea: why are there so few year classes. Helgol Mar Res 53:45-55

Suess E (1875) Die Entstehung der Alpen

Sun M-Y, Lee C, Aller RC (1993) Anoxic and oxic degradation of ^{14}C-labeled chloropigments and a ^{14}C-labeled diatom in Long Island Sound sediments. Limnol Oceanogr 38(7):1438-1451

Swift DJ (1993) The macrobenthic infauna off Sellafield (north-eastern Irish Sea) with special reference to bioturbation. J Mar Biol Ass U K 73:143-162

Swift DJP, Stull JK, Niedoroda AW, Reed CW, Wong GTF (1996) Contaminant dispersal on the Palos Verdes continental margin II. Estimates of the biodiffusion coefficient D_B, from composition of the benthic infaunal community. Sci Total Environ 179:91-107

Tagliapietra D, Cornello M and Ghrardinin AV (2005) Monitoring transitional waters using reduced benthic assemblages. Environment International 31:1089-1093

Tamar EA Report (1996) Local Environment Agency Plan: Tamar Estuary and Tributaries. July 1996

Tansley AG (1935) The use and abuse of vegetational concepts and terms. Ecology 16:284-307

Tett P, Gowen R, Mills D, Fernandes T, Gilpin L, Huxham M, Kennington K, Read P, Service M, Wilkinson M, Malcolm S (2007) Defining and detecting undesirable disturbance in the context of marine eutrophication. Mar Pollut Bull 55: 282-297

Thayer CW (1983) Sediment-mediated biological disturbance and the evolution of marine benthos. In: Tevesz MJS, McCall PL (eds) Biotic interactions in recent and fossil benthic communities. Plenum Press New York, pp. 479-625

Thiel M (1998) Nemertines as predators on tidal flats – High noon at low tide. Hydrobiologia 265:241-250

Thistle D (1981) Natural physical disturbances and communities of marine soft bottoms. Mar Ecol Prog Ser 6:223-228

Thorson G (1957) Bottom communities (sublittoral or shallow shelf). Geological Society of America Memoirs 67:461-564

Thrush SF, Hewitt JE, Norkko A, Nicholls PE, Funnell GA, Ellis JI (2003) Habitat change in estuaries: predicting broad-scale responses of intertidal macrofauna to sediment mud content. Mar Ecol Prog Ser 263:101-112

Thrush SF, Hewitt JE, Herman PMJ, Ysebaert T (2005) Mutli-scale analysis of species-environment relationships. Mar Ecol Prog Ser 302:13-26

Tidal Stream Atlas for Plymouth Harbour and Approaches (1991) Hydrographic Office, Taunton

Tilman D (1996) Biodiversity: Population versus ecosystem stability. Ecology 77(2):350-363

Timmermann K, Banta GT, Larsen J, Andersen O (2003) Modelling particle and solute transport in sediments inhabited by *Arenicola marina*. Effects of pyrene on transport processes. Vie milieu 53(4):187-200

Tolhurst TJ, Reithmuller R, Paterson DM (2000) *In situ* versus laboratory analysis of sediment stability from intertidal mudflats. Cont Shelf Res 20 (10/11):1317-1344

Townend I (2002) Identifying change in estuaries. Littoral 2002. The changing coast. EUROCOAST / EUCC, Porto, Portugal

Trevor JH (1977) The burrowing of *Nereis diversicolor* OF Muller, together with some observations on *Arenicola*(L) (annelida: Polychaeta). J Exp Mar Biol Ecol 30:129-145

Trueman ER, Ansell AD (1969) The mechanisms of burrowing into soft substrata by marine animals. Oceanogr Mar Biol Ann Re. 7: 315-366.

Uncles RJ, Stephens JA, Smith RE (2002) The dependence of estuarine turbidity on tidal intrusion length, tidal range and residence time. Cont Shelf Res 22:1835-1856

Underwood GJC, Paterson DM, Parkes RJ (1995) The measurement of microbial carbohydrate exopolymer from intertidal sediments. Limnol and Oceanogr 40:1243-1253

Usseglio-Polatera P, Bournaud M, Richoux P, Tachet H (2004) Biomonitoring through biological traits of benthic macroinvertebrates: how to use species trait databases? Hydrobiologia 422-433:153-162

Vader WJM (1964) A preliminary investigation into the reactions of the infauna of the tidal flats to tidal fluctuations in water level. Neth J Sea Res 2(2):189-227

Vernadsky VI (1926) Biosfera (The Biosphere). Translated by D.Langmuir, revised by M. McMonamin. Neuraumont/Copernicus 1997, New York

Vinebrook R, Cottingham KL, Norberg J, Scheffer M, Dodson SI, Maberly SC, Sommer U (2004) Impacts of multiple stressors on biodiversity and ecosystem functioning: The role of species co-tolerance. Oikos 104:451-457

Von Humboldt A, Bonpland A (1807) Essai sur la géographie des plantes. Librarie Lebrault Schoell, Paris.

Waldbusser GG, Marinelli RL, Whitlach RB, Visscher PT (2004) The effects of infaunal biodiversity on biogeochemistry of coastal marine sediments. Limnol Oceanogr 49:1482-1492

Waldbusser GG, Marinelli RL (2006) Macrofaunal modification of porewater advection: role of species function, species interaction, and kinetics. Mar Ecol Prog Ser 311: 217-231

Walker BH (1992) Biodiversity and ecological redundancy. Biol Conserv 6:18-23

Wallentinus I, Nyberg CD (2007) Introduced marine organisms as habitat modifiers. Mar Pollut Bull 55:323-332

Warwick RM (1986) A new method for detecting pollution effects on marine macrobenthic communities. Mar Biol 92(4):557-562

Warwick RM, Davies JR (1977) The distribution of sublittoral macrofauna communities in the Bristol Channel in relation to the substrate. Est Coast Mar Sci 5:267-288

Warwick RM, Uncles RJ (1980) Distribution of benthic macrofauna associations in the Bristol Channel in relation to tidal stress. Mar Ecol Prog Ser 3:97-103

Warwick RM, Goss-Custard JD, Kirby R, George CL, Pope ND, Rowden AA (1991) Static and dynamic environmental factors determining the community structure of estuarine macrobenthos in SW Britain: Why is the Severn estuary different? J Appl Ecol 28:329-345.

Watson PG, Frickers PE and Goodchild CM (1985) Spatial and seasonal variations in the chemistry of sediment interstitial waters in the Tamar estuary. Est Coast Shelf Sci 21:105-119

Weisburg SB, Ranasinghe JA, Dauer DM, Schaffner LC, Diaz RJ, Frithsen JB (1997) An estuarine benthic index of biotic integrity (B-IBI) for Chesapeake Bay. Estuaries and Coasts 20(1):149-159

Welschmeyer NA (1994) Fluorometric analysis of chlorophyll a in the presence of chlorophyll b and phaeopigments. Limnol Oceanogr 39:1985-1992.

Weltzin JF, Loik, M.E., Schwinning, S., William, D.G., Fay, P.A., Haddad, B.M., Harte, J., Huxman T.E, Knapp A.K, Lin G, Pockman WT, Shaw MR, Small EE, Smith MD, Smith SD, Tissue DT, Zak JC (2003) Assessing the response of terrestrial ecosystems to potential changes in precipitation. BioScience 53(10):941-952

Wheatcroft RA, Jumars PA, Smith CR, Nowell ARM (1990) A mechanistic view of the particulate diffusion coefficient: step lengths, rest periods and transport directions. J Mar Res 48:177-207

Wheatcroft RA, Olmez I, Pink FX (1994) Particle bioturbation in Massachusetts Bay: preliminary results using a new deliberate tracer technique. J Mar Res 52:1129-1150

Wheatcroft RA, Martin WR (1996) Spatial variation in short-term (234Th) sediment bioturbation intensity along an organic-carbon gradient. J Mar Res 54:763-792

Wheatcroft RA, Starczak VA, Butman CA (1998) The impact of population abundance on the deposit-feeding rate of a cosmopolitan polychaete worm. Limnol. Oceanogr 43(8):1948-1953

Wheeler, D.P. (1990) Rediscovering ecology. EPA Journal 16(5) 34-36

Whitehouse RJS, Bassoullet P, Dyer KR, Mitchener HJ, Roberts W (2000) The influence of bedforms on flow and sediment transport over intertidal mudflats. Cont Shelf Res 20:1099-1124

Whitlach RB, Lohrer AM, Thrush SF, Pridmore RD, Hewitt JE, Cummings VJ, Zajac RN (1998) Scale-dependent benthic recolonization dynamics: life stage-based dispersal and demographic consequences. Hydrobiologia 376:217-226

Whitlach RB (1980) Patterns of resource utilization and coexistence in marine intertidal deposit-feeding communities. J Mar Res 38 (4): 743-765

Widdows J, Brinsley M (2002) Impact of biotic and abiotic processes on sediment dynamics and the consequences to the structure and functioning of the intertidal zone. J Sea Res 48:143-156

Widdows J, Brinsley MD, Salkeld PN, Lucas CH (2000) Influence of biota on spatial and temporal variation in sediment erodibility and material flux on a tidal flat (Westerschelde, The Netherlands). Mar Ecol Prog Ser 194:23-37

Widdows J, Blauw A, Heip CHR, Herman PMJ, Lucas CH, Middelburg JJ, Schmidt S, Brinsley MD, Twisk F, Verbeek H (2004) Role of physical and biological processes in sediment dynamics of a tidal flat in Westerschelde Estuary, SW Netherlands. Mar Ecol Prog Ser 274:41-56

Widdows J, Friend PL, Bale AJ, Brinsley MD, Pope ND, Thompson CEL (2007) Inter-comparison between five devices for determining erodability of intertidal sediments. Cont Shelf Res 27:1174-1189

Wiesner D (1995) EIA the environmental impact assessment process. What it is and what it means to you. Prism Press, Bridport

Wildish DJ (1977) Factors controlling marine and estuarine sublittoral macrofauna. Helgolander Wiss Meersunters 30:445-454

Wildish DJ, Kristmanson D (1979) Benthic suspension feeders and flow. Cambridge University Press

Wilson EO (1996) Biophilia and the environmental ethic. In E.O Wilson "In search of nature", p165-179. Penguin Group, London

Winberg PC, Lynch TP, Murray A, Jones AR, Davis AR (2007) The importance of spatial scale for the conservation of tidal flat macrobenthos: An example from New South Wales, Australia. Biol Conserv 134:310-320

Woodward FI, Diament AD (1991) Functional approaches to predicting the ecological effects of global change. Funct Ecol 5:202-212

Wright L (1973) Functions. Phil Rev 82:139-168

Wright JF (2000) An introduction to RIVPACS. In Wight JF, Sutcliffe DW, Furse MT (eds), Assessing the biological quality of fresh waters: RIVPACS and other techniques. Freshwater Biological Association, Ambleside, UK

Yingst JY, Rhoads DC (1978) Carbonate dissolution and temporal abundances of Foraminifera in Long Island Sound sediments. Limnol Oceanogr 38(2):331-345

Ysebaert T (2000) Macrozoobenthos and waterbirds in the estuarine environment: spatio-temporal patterns at different scales. PhD Thesis, University of Antwerp, Communication of the Institute of Nature Conservation, Belgium.

Ysebaert T, Herman PMJ (2002) Spatial and temporal variation in benthic macrofauna and relationships with environmental variables in an estuarine, intertidal soft-sediment environment. Mar Ecol Prog Ser 244:106-124

Ysebaert T, Meire P, Herman PMJ, Verbeek H (2002) Macrobenthic species response surfaces along estuarine gradients: prediction by logistic regression. Mar Ecol Prog Ser 225:79-95.

Zajac RN (2004) Macrofaunal responses to pit-mound patch dynamics in an intertidal mudflat: local versus patch-type effects. J Exp Mar Biol Ecol 313:297-315

Zajac RN, Whitlach RB (1982) Response of estuarine infauna to disturbance. I Spatial and temporal variation of initial recolonization. Mar Ecol Prog Ser 10:1-14

Ziegler S, Benner R (1998) Ecosystem metabolism in a subtropical, sea-grass dominated lagoon. Mar Ecol Prog Ser 173:1-12

Zwarts L, Wanink J (1989) Siphon size and burying depth in deposit- and suspension-feeding benthic bivalves. Mar Biol 100:227-240

Zwarts L, Wanink JH (1993) How the food supply harvestable by waders in the Wadden Sea depends on the variation in energy density, body weight, biomass, burying depth and behaviour of tidal-flat invertebrates. Neth J Sea Res 31(4):441-476

Zwarts L, Blomert A-M, Spaak P and de Vries B (1994) Feeding radius, burying depth and siphon size of *Macoma balthica* and *Scrobicualria plana*. J Exp Mar Biol Ecol 183:193-212

APPENDIX 1

	Swift Score	Length (mm)	Trophic Group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Abludomelita gladiosa	2	9	SDF	0	0	0	0	0	0	0	1	0	1	0	0	389	227	14	0	0
Abra alba	4	25	SDF	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	19	61
Abra tenuis	6	13	SDF	0	0	0	0	0	0	0	0	2	0	0	2	0	0	1	0	0
Adyte pellucida	6	20	GEN	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Aequipecten opercularis	2	90	SUSP	0	0	0	0	0	5	0	0	0	0	0	0	0	1	0	0	0
Ampelisca brevicornis	5	12	SDF	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5
Ampelisca typica	5	10	SDF	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	6
Amphicteis gunneri	3	55	SDF	0	0	0	0	0	2	13	0	1	3	1	4	15	1	0	0	0
Amphictene auricoma	10	40	SSDF	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	3
Amphilochus neapolitanus	2	4	SDF	0	0	0	0	0	1	0	1	1	2	0	0	5	6	1	0	0
Amphipholis squamata	1	5	OMNI	0	0	0	0	0	0	1	3	1	0	1	4	49	90	104	0	0
Amphiura brachiata	1	13	OMNI	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Anaitides longipes	2	150	GEN	0	0	0	0	0	0	0	0	0	0	0	0	12	2	1	0	0
Anaitides mucosa	2	150	GEN	0	0	0	1	0	7	3	3	1	7	7	12	6	56	255	26	24
Anapagurus hyndmanni	2	10	OMNI	0	0	0	0	0	0	1	0	0	0	0	0	15	5	9	0	2
Antedon bifida	0	100	SUSP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Anthura gracilis	3	11	SDF	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
Aonides oxycephala	3	45	SDF	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0
Aonides paucibranchiata	3	15	SDF	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Aora sp.	1	9	FF	0	0	0	0	0	0	0	0	0	0	0	0	34	53	101	0	2
Aphelochaeta marioni	8	100	SDF	5	5	2	2	2	1758	3177	110	636	1280	653	1914	27	64	36	0	66
Apseudes latreillii	3	7	SDF	0	0	0	0	0	1	1	0	0	421	1	4	87	2711	3431	0	4
Astacilla	1	30	SUSP	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
Asterias rubens	1	300	GEN	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Atylus vedlomensis	2	8	SDF	0	0	0	0	0	0	0	0	0	0	0	0	1	2	1	0	0
Buccinum undatum	0	110	GEN	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Calyptraea chinensis	0	15	SUSP	0	0	0	0	0	0	2	3	0	4	0	0	3	46	0	0	0
Capitella capitata	9	100	SSDF	0	1	0	0	0	5	17	3	2	49	1	1	3	12	368	7	0
Carcinus maenas	0	73	GEN	0	1	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0
Caulleriella sp.	7	7	SDF	6	8	0	4	4	209	260	18	45	456	812	336	36	35	39	23	280
Cerastoderma edule	2	50	SUSP	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0
Cerianthus lloydii	2	150	SUSP	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	4	4
Chamelea gallina	0	40	FF	0	0	0	0	0	0	1	0	0	0	1	1	1	0	0	0	0
Cirratulus sp.	5	300	SDF	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Cirriformia tentaculata	5	200	SDF	0	0	0	0	0	0	1	1	0	11	0	1	0	0	0	0	0
Clausinella fasciata	2	25	SDF	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0

	Swift Score	Length (mm)	Trophic Group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Corbula gibba	2	15	SUSP	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	2	2
Corophium sextonae	9	4.5	SDF	4	4	1	37	1	18	12	273	164	35	1	91	1687	581	519	0	26
Crepidula fornicata	0	50	SUSP	0	0	0	0	0	3	0	0	0	0	0	0	1	0	0	0	0
Diastylis laevis	8	11	SDF	0	0	0	0	0	0	0	0	0	4	0	0	4	1	0	0	1
Dosinia exoleta	5	60	SUSP	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0
Ebalia cranchii	2	11	OMNI	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Ensis siliqua	2	200	GEN	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Epitonium clathrus	2	40	GEN	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0
Eteone flava	4	120	GEN	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Eulalia bilineata	4	90	GEN	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Eumida sp.	6	150	GEN	0	0	0	0	0	0	0	0	0	0	0	0	1	2	1	1	3
Eumida sanguinea	6	60	GEN	0	0	0	0	0	25	58	6	1	60	4	13	42	45	7	0	2
Exogone hebes	4	10	GEN	0	0	0	0	0	0	0	0	0	0	0	0	6	14	0	0	0
Exogone naidina	4	4	GEN	0	0	0	0	0	19	2	1	0	5	0	0	30	18	2	0	0
Flabelligera affinis	4	60	SUSP	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Gammarella fucicola	2	10	SDF	0	0	0	0	0	0	0	0	0	1	0	0	114	1589	1150	0	2
Gammaropsis cornuta	2	8	SDF	0	0	0	0	0	0	0	0	0	0	0	0	59	68	2	0	0
Gammaropsis palmata	2	3	SDF	0	0	0	0	0	0	0	0	0	0	0	0	33	14	0	0	0
Gammarus locusta	4	33	OMNI	0	0	0	0	0	0	0	0	0	0	0	0	0	3	8	0	0
Glycera lapidum	4	75	GEN	0	0	0	0	0	0	0	0	0	0	0	0	7	2	0	0	0
Glycera tridactyla	5	100	GEN	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Gnathia oxyuraea	5	5.4	OMNI	0	0	0	0	0	0	0	0	0	4	0	0	13	27	4	0	1
Gnathiidae	5	35	OMNI	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
Goniada sp.	4	100	GEN	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Harmothoe fragilis	3	25	GEN	0	0	0	0	0	0	0	1	0	0	0	0	2	0	0	0	0
Harmothoe impar	3	25	GEN	0	0	0	0	0	1	2	0	1	0	0	3	23	6	3	0	0
Harpinia crenulata	3	5	SDF	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	2
Hediste diversicolor	9	200	GEN	3	0	0	0	0	5	7	6	3	8	0	4	0	0	0	0	0
Heteromastus filiformis	11	100	SSDF	3	0	0	1	1	14	8	9	9	63	6	33	223	821	14	36	35
Hinia pygmaea	3	14	OMNI	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Hydrobia ulvae	6	6	SDF	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Hydroides norvegica	0	75	SUSP	0	0	0	0	0	0	0	0	0	0	0	0	27	34	7	0	7
Iphimedia minuta	2	6	SDF	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Janira maculosa	2	10	OMNI	0	0	0	0	0	1	0	0	0	0	0	1	100	146	29	0	0
Jasmineira elegans	4	20	SUSP	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0
Kefersteinia sp.	4	75	GEN	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	4
Lagis koreni	9	50	SSDF	0	0	0	0	0	0	1	0	0	2	11	4	3	1	0	2	18

	Swift Score	Length (mm)	Trophic Group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Lanice conchilega	0	300	SDF	0	1	0	0	0	0	0	0	0	1	1	2	0	0	0	0	0
Lasaea adansoni	0	3	SUSP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0
Leptocheirus pilosus	6	5	SDF	0	0	0	0	0	0	1	0	0	0	0	0	13	29	2	0	0
Leptochiton asellus	0	19	OMNI	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leucothoe lilljeborgi	2	12	SDF	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Liocarcinus pusillus	2	40	OMNI	0	0	0	0	0	0	0	0	0	0	0	0	6	5	6	0	0
Lucinoma borealis	2	41	SUSP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	3
Lumbrineris sp.	5	400	GEN	0	0	0	0	0	0	0	0	0	0	0	0	9	1	1	0	0
Lysianassa ceratina	2	10	SDF	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1
Maera grossimana	9	10	SDF	0	0	0	0	0	0	0	0	0	3	0	1	154	10	35	0	1
Magelona alleni	9	170	SDF	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	24
Marphysa bellii	9	200	SSDF	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9
Melinna palmata	5	20	SDF	2	1	3	3	2	24	120	13	39	32	141	894	1	0	1	93	415
Melita palmata	2	16	SDF	0	1	0	0	0	8	0	0	0	12	0	0	0	0	0	0	0
Mya arenaria	2	150	SUSP	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	3
Myriochele heeri	7	30	SDF	0	0	0	0	0	0	0	0	0	3	117	57	0	2	0	60	94
Mysella bidentata	5	3	SUSP	0	0	0	0	0	0	1	0	0	0	0	0	2	3	69	0	6
Mytilus edulis	0	200	SUSP	0	0	0	0	0	0	1	0	0	0	0	2	0	0	0	0	0
Naididae	5	100	SSDF	0	1	2	2	2	55	37	0	8	147	77	35	24	48	5	16	6
Nebalia bipes	5	12	SDF	0	0	0	0	0	0	0	0	0	0	0	0	3	1	15	0	0
Nematonereis unicornis	2	200	GEN	0	0	0	0	0	0	2	0	0	1	0	0	9	3	2	0	2
Nemertea	5	100	GEN	0	3	0	1	0	24	86	1	1	16	2	20	67	293	554	2	4
Nephtys hombergii	6	200	GEN	57	41	73	55	78	43	40	36	33	23	110	123	2	0	0	27	105
Nephtys kersivalensis	6	100	GEN	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	15
Nereis longissima	4	500	GEN	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	4
Nicolea venustula	3	70	SDF	0	0	0	0	0	6	0	0	14	0	0	7	5	0	1	0	0
Notomastus latericeus	7	300	SSDF	0	0	0	0	0	0	0	0	0	0	0	1	1	4	7	6	9
Nucula nitidosa	2	13	SUSP	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1
Nucula nucleus	2	13	SUSP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Nucula sulcata	2	20	SUSP	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	1
Odontosyllis ctenostoma	4	20	GEN	0	0	0	0	0	1	6	0	0	0	0	4	1	1	0	0	0
Odontosyllis gibba	4	25	GEN	0	0	0	0	0	0	0	0	0	0	0	0	5	4	1	0	0
Oligochaeta	5	100	SSDF	0	0	0	1	137	0	0	9	0	3	0	0	0	1	0	0	0
Onoba semicostata	2	4	SUSP	0	0	0	0	0	0	0	0	0	2	2	0	18	49	766	8	1
Ophiothrix fragilis	2	20	GEN	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Ophryotrocha gracilis	4	4	OMNI	0	0	0	0	0	0	0	0	0	0	0	0	2	2	7	0	0
Orbinia sertulata	8	400	SSDF	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0

	Swift Score	Length (mm)	Trophic Group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Orchomene nanus	1	5	GEN	0	0	0	0	0	0	0	0	0	0	0	2	7	0	0	0	0
Owenia fusiformis	0	100	SDF	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1
Parametaphoxus fultoni	2	3	SDF	0	0	0	0	0	1	0	0	0	0	0	0	49	3	2	0	0
Pariambus typicus	0	7	SUSP	0	0	0	0	0	0	0	2	0	4	0	5	0	57	3	27	17
Parvicardium exiguum	3	13	SUSP	3	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Parvicardium ovale	3	14	SUSP	0	0	0	1	0	0	0	2	0	3	0	0	0	0	0	0	0
Parvicardium scabrum	3	12	SUSP	0	0	3	0	0	4	0	0	0	0	0	0	1	5	0	0	0
Perioculodes longimanus	5	5	SDF	0	0	0	0	0	0	0	0	0	0	0	0	15	0	0	0	0
Phaxas pellucidus	2	40	SUSP	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Philine aperta	0	70	GEN	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Pholoe inornata	4	20	GEN	0	0	0	0	0	0	0	1	0	4	0	5	10	3	2	0	0
Phoronis sp.	0	120	SUSP	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	4
Photis longicaudata	2	6	SDF	0	0	0	0	0	0	0	2	1	1	0	0	0	0	20	0	16
Phtisica marina	2	25	OMNI	0	0	0	0	0	1	0	1	0	0	0	0	5	50	93	0	3
Pisidia longicornis	0	100	SUSP	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0
Pista cristata	3	100	SDF	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1
Platynereis dumerilii	7	60	GEN	0	0	0	0	0	0	0	0	0	0	0	4	11	41	782	0	1
Podarkeopsis capensis	2	100	GEN	0	0	0	0	0	0	0	0	0	0	0	0	20	4	5	4	4
Pododesmus patelliformis	1	60	SUSP	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0
Poecilochaetus serpens	4	11	SSDF	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Polinices sp.	2	30	GEN	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Polycirrus plumosus	9	36	SDF	0	0	0	0	0	0	0	0	2	0	0	1	2	2	3	0	0
Polydora caeca	3	40	SDF	0	0	0	0	0	2	6	0	1	13	2	0	5	1	2	0	0
Polydora ciliata	3	30	SDF	6	4	0	14	0	0	0	2	0	18	1	0	1	0	0	0	0
Praxillella affinis	7	42	SSDF	0	0	0	0	0	0	0	0	0	0	0	0	30	8	0	1	98
Protodorvillea kefersteini	2	15	GEN	0	0	0	0	0	0	1	0	0	1	0	0	4	3	33	0	0
Psammechinus miliaris	2	50	OMNI	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Pseudopolydora pulchra	3	9	SDF	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Pseudoprotella phasma	2	25	SDF	0	0	0	0	0	4	0	4	0	0	0	1	3	1	0	0	0
Pygospio elegans	3	15	SUSP	2	2	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Sabellaria spinulosa	0	40	SUSP	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Scalibregma inflatum	9	100	SSDF	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Sphaerodorum gracilis	2	60	SUSP	0	0	0	0	0	0	0	0	0	0	0	0	15	7	3	0	0
Sphaerosyllis	4	6	GEN	0	0	0	0	0	21	14	21	0	45	0	0	47	90	176	0	0
Stenothoe marina	2	6	OMNI	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0
Stenothoe monoculoides	2	3	OMNI	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Sthenelais boa	3	200	GEN	0	0	0	0	0	0	4	0	0	0	0	1	3	1	0	0	0

	Swift Score	Length (mm)	Trophic Group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Streblospio shrubsolii	4	15	SDF	73	116	3	1	24	0	0	0	0	1	0	1	1	0	0	0	0
Syllidia armata	2	15	GEN	0	0	0	0	0	60	29	25	1	198	5	4	81	124	91	1	2
Syllis gracilis	2	50	GEN	0	0	0	0	0	0	2	1	3	21	0	3	9	1	15	0	0
Tanaopsis graciloides	3	1.3	FF	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	3
Tapes rhomboides	2	10	FF	0	0	0	0	0	0	0	0	0	0	0	0	3	0	2	0	0
Thyasira flexuosa	2	10	SDF	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Tritaeta gibbosa	2	6	SDF	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Tubificoides benedii	5	55	SDF	0	2	1	3	7	44	2537	44	23	502	91	153	48	761	1489	137	155
Typosyllis hyalina	2	50	CARN	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Unciola crenatipalma	2	7	SDF	0	0	0	0	0	0	0	0	0	0	0	0	41	4	0	0	0
Upogebia deltaura	10	150	SDF	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Venerupis senegalensis	2	50	SUSP	0	0	0	0	0	0	0	0	1	0	0	0	1	3	15	0	3

APPENDIX 2

	a Volume occupied by burrow / to reach surface	b Volume moved due to movement through sediment	c Volume moved due to movement across surface	d Volume moved by sediment ingestion	e Volume moved by surface deposit feeding		Total volume calculated as	References
		distance moved	distance moved		Feeding radius	depth		
Nemertea	Method 1		100*body length				a+c	Thiel (1998)
Sipunculidae	Method 1			= 0.82/5*body length			a+d	Dobbs (1983)
Phyllodoce sp.	Method 1		100*body length				a+c	errant calculate as per ***Nephtys***
Syllidae	Method 1		100*body length				a+c	errant calculate as per ***Nephtys***
Exogone sp	Method 1		100*body length				a+c	errant calculate as per ***Nephtys***
Nereis diversicolor	Method 2				= 0.5 * body length	=0.5* body width	a+e	Tevor (1977), Cammen (1980), Davey (1994)
Nephtys hombergii	Method 1		100*body length				a+c	Lee and Swartz (1980), Rhoads and Boyer (1982)
Spionidae indet	Method 1				= 0.5* body length	0.4mm	a+e	calculate as per ***Streblopsio***
Polydora ciliata (agg.)	Method 1				= 0.5* body length	0.4mm	a+e	calculate as per ***Streblopsio***
Tharyx sp	Method 1							calculate as per ***Streblopsio***
Pseudopolydora	Method 1				= 0.5* body length	0.4mm	a+e	calculate as per ***Streblopsio***
Pygospio elegans	Method 1				= 0.5* body length	0.4mm	a+e	Wilson (1981), Dauer (1984), Linday and Woodin (1992), Lindsay and Woodin (1996)
Streblospio ***shrubsolii***	Method 1				= 0.5* body length	0.4mm	a+e	
Magelona indet	Method 1				= 0.5* body length	0.4mm	a+e	calculate as per ***Streblospio***

Appendix 2 The calculations employed to determine the volume of sediment disturbed by activities.

Method 1= body volume * (no. of body lengths to reach mean depth at which found)

Method 2 = assume a minimum of U shaped tube volume = 2.5 * (mean no. body lengths to reach depth)*body volume

(estimate that a shape of u = 2 sides of equal length and horizontal of 1/2 depth)

	a Volume occupied by burrow / to reach surface	b Volume moved due to movement through sediment	c Volume moved due to movement across surface	d Volume moved by sediment ingestion	e Volume moved by surface deposit feeding		Total volume calculated as	References
Cirratulid	**Method 1**				**= 0.82/5 * body length**		a + c	
---wide thorax, ribbed, fine chaetae directed backwards	**Method 1**				**= 0.82/5 * body length**		a + c	
---long thin, thorax wider than rest	**Method 1**				**= 0.82/5 * body length**		a + c	**Treat as disturbing sediment in proportion to body size and use estimate from Dodds (1983). Other refs: Fauchald and Jumars (1979) Shull and Yasuda (2001), "BIOTIC"**
---slender head pointed prostonium, ribbed thorax, rest as wide/wider than thorax	**Method 1**				**= 0.82/5 * body length**		a + c	
Caulleriella zetlandica	**Method 1**				**= 0.82/5 * body length**		a + c	
Chaetozone sp.	**Method 1**				**= 0.82/5 * body length**		a + c	
Aphelochaeta marioni	**Method 1**				**= 0.82/5 * body length**		a + c	
Aphelochaeta sp	**Method 1**				**= 0.82/5 * body length**		a + c	
Cossura sp.	**Method 1**	**= 0.82/5 * body length**					a+d	**Calculate as per *Capitellidae***
Capitellidae	**Method 1**	**= 0.82/5 * body length**					a+d	**Lee and Swartz (1980) Dodds (1983), Neira and Hopner (1993)**
Heteromastus filiformis	**Method 1**	**= 0.82/5 * body length**					a+d	
Mediomastus sp.	**Method 1**	**= 0.82/5 * body length**					a+d	
Galathowenia sp	**Method 1**				**= 0.5* body length**	**0.4mm**	a + e	**Calculate as per *Streblospio***
Melinna palmata	**Method 1**				**= 0.5* body length**	**0.6mm**	a + e	**Fauchald and Jumars (1979), Lee and Swartz (1980)**
Ampharete sp	**Method 1**				**= 0.5* body length**	**0.6mm**	a + e	

Appendix 2 (continued, The calculations employed to determine the volume of sediment disturbed by activities.

Method 1= body volume * (no. of body lengths to reach mean depth at which found)

Method 2 = assume a minimum of U shaped tube volume = 2.5 * (mean no. body lengths to reach depth)*body volume

(estimate that a shape of u = 2 sides of equal length and horizontal of 1/2 depth)

	a Volume occupied by burrow / to reach surface	b Volume moved due to movement through sediment	c Volume moved due to movement across surface	d Volume moved by sediment ingestion	e Volume moved by surface deposit feeding		Total volume calculated as	References
Manayunkia aestuarina	Method 1						a	Haywood and Ryland (1995)
Oligochaeta indet	Method 1			= 0.82/5 * body length			a+d	
Heterochaeta costata (Tubifex costatus)	Method 1			= 0.82/5 * body length			a+d	Calculate as per *Tubificoides*
Tubificoides indet	Method 1			= 0.82/5 * body length			a+d	
Tubificoides amplivasatus	Method 1			= 0.82/5 * body length			a+d	Treat as disturbing sediment in proportion to body size and use estimate from Dodds (1983).
Tubificoides benedii	Method 1			= 0.82/5 * body length			a+d	
Tubificoides pseudogaster	Method 1			= 0.82/5 * body length			a+d	
Tubificoides galliciensis	Method 1			= 0.82/5 * body length			a+d	
Tubificoides insularis	Method 1			= 0.82/5 * body length			a+d	
Portunidae megalopa/juvenille	Method 1				5* body length	0.3mm	a + e	
Amphipoda	Method 1						a	Calculate as per *Ampelisca*
Ampelisca sp	Method 1						a	Lincoln (1979), Hayward and Ryland (1998)
Corophium sp.	Method 2				= 0.75*body length	1mm	a+e	Meadows and Reid (1966), de Deckere et al (2002)
Cumacea	Method 1		10*body length				a + c	Jones (1976)
Crangon crangon	Method 1						a	treat as only burrowing for protection "BIOTIC" database
Callianassidae	Method 1	estimated from Rowden and Jones (1993)					a + c	Rowden and Jones (1993)

Appendix 2 (continued) The calculations employed to determine the volume of sediment disturbed by activities.

Method 1= body volume * (no. of body lengths to reach mean depth at which found)

Method 2 = assume a minimum of U shaped tube volume = 2.5 * (mean no. body lengths to reach depth)*body volume

(estimate that a shape of u = 2 sides of equal length and horizontal of 1/2 depth)

	a Volume occupied by burrow / to reach surface	b Volume moved due to movement through sediment	c Volume moved due to movement across surface	d Volume moved by sediment ingestion	e Volume moved by surface deposit feeding	Total volume calculated as	References
Hydrobia ulvae	Method 1		assume coverage $2*10^{-4}$			a + c	Sauriau (2002), Orvain et al (2003)
Tragula fenestrata	Method 1		assume coverage $2*10^{-4}$			a + c	calculate as per *Hydrobia*
Retusa sp	Method 1						use same as prey - *Hydrobia*
Nucula nitidosa	Method 1						calculate as per *Abra*
Thyasira sp	Method 1						calculate as per *Abra*
Parvicardium exiguum	Method 1	calculate as per *C.edule*					calculate as per *Cerastoderma edule*
Cerastoderma edule	Method 1	estimated shaking and ploughing effect from Flach (1996)				a + b + c	Flach (1996), Mermillod-Blondin et al (2005)
Phaxus pellucidus	Method 1					a	Perkins (1974), "BIOTIC"
Macoma balthica	Method 1			= 1.9403	depth = 1mm	a + e	
Scrobicularia plana	Method 1			=0.8986	depth = 1mm	a + e	Green (1968), Lee and Swartz (1980), Zwarts et al (1994)
Abra alba	Method 1	estimate from Eagle (1975)				a + b	1 individual reworks area 7cm diameter in 4 weeks. Eagle (1975)
Mya arenaria	Method 1			=0.8986	depth = 1mm	a + e	"BIOTIC" treat as *Scrobicularia*, minimal effect on surface
Pyramidellidae	Method 1		assume coverage $2*10^{-4}$			a + c	calculate as per *Tragula*

Appendix 2 (continued) The calculations employed to determine the volume of sediment disturbed by activities.

Method 1= body volume * (no. of body lengths to reach mean depth at which found)

Method 2 = assume a minimum of U shaped tube volume = 2.5 * (mean no. body lengths to reach depth)*body volume

(estimate that a shape of u = 2 sides of equal length and horizontal of 1/2 depth)

APPENDIX 3

Summary of the number of sites at which each species was found

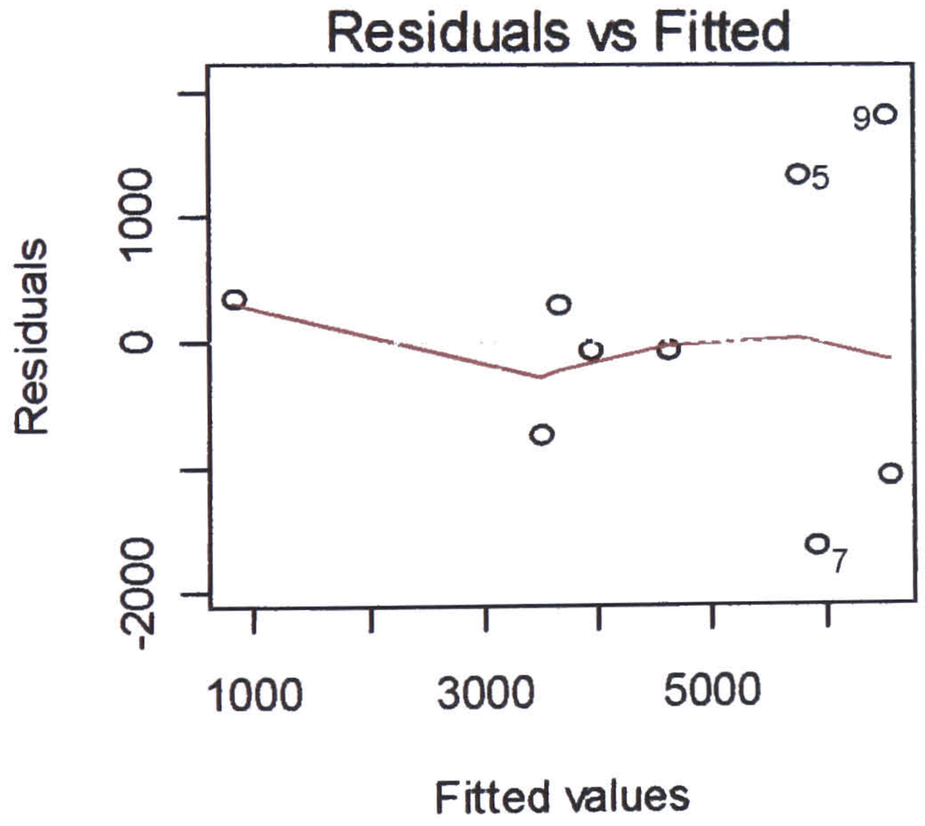
Species	Number of sites where species found
Tharyx sp	1
Magelona sp.	1
Mediomastus sp.	1
Lanice conchilega	1
Paranais littoralis	1
Heterochaeta costata (Tubifex costatus)	1
Amphipoda	1
Calianassa	1
hermit crab	1
Pyramellid gastropod	1
Nucula nitidosa	1
Mysella bidentata	1
Parvicardium exiguum	1
Phaxus pellucidus	1
Abra alba	1
Nemertea	2
syllidae	2
Exogone sp	2
Pseudopolydora	2
Caulleriella zetlandica	2
Capitellidae	2
Isopoda indet	2
Cumacea	2
Phoronidae	2
Ampelisca sp	3
Corophium sp.	3
Crangon crangon	3
Tragula fenestrata	3
Bivalve indet	3
Thyasira sp	3
Macoma balthica	3
Polyc indet	4
Phyllodoce sp.	4
Polydora ciliata (agg.)	4
Aphelochaeta sp	4
Galathowenia sp.	4
Oligochaeta indet	4
Copepoda	4
C.edule	4
Mya sp.	4

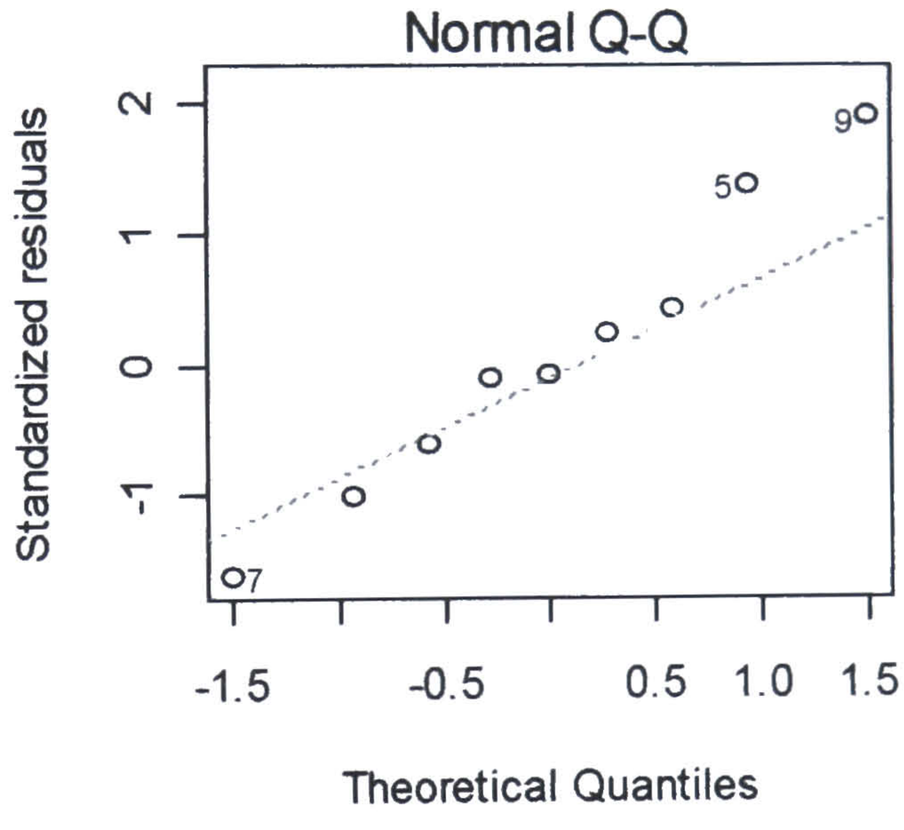
Species	Number of sites where species found
Sipunculidae	5
Cirratulid Type 1	5
Cirratulid Type 2	5
Heteromastus filiformis	5
Ampharete sp	5
juv crab	5
Retusa sp	5
Cossura sp.	6
Manayunkia aestuarina	6
Scrobicularia plana	6
Nephtys hombergii	7
Pygospio elegans	7
Melinna palmata	7
Nereis diversicolor	8
Cirratulid Type 3	8
Portunidae indet	8
Spionidae indet	9
Streblospio shrubsolii	9
Chaetozone sp.	9
Tubificoides indet	9
Hydrobia ulvae	9

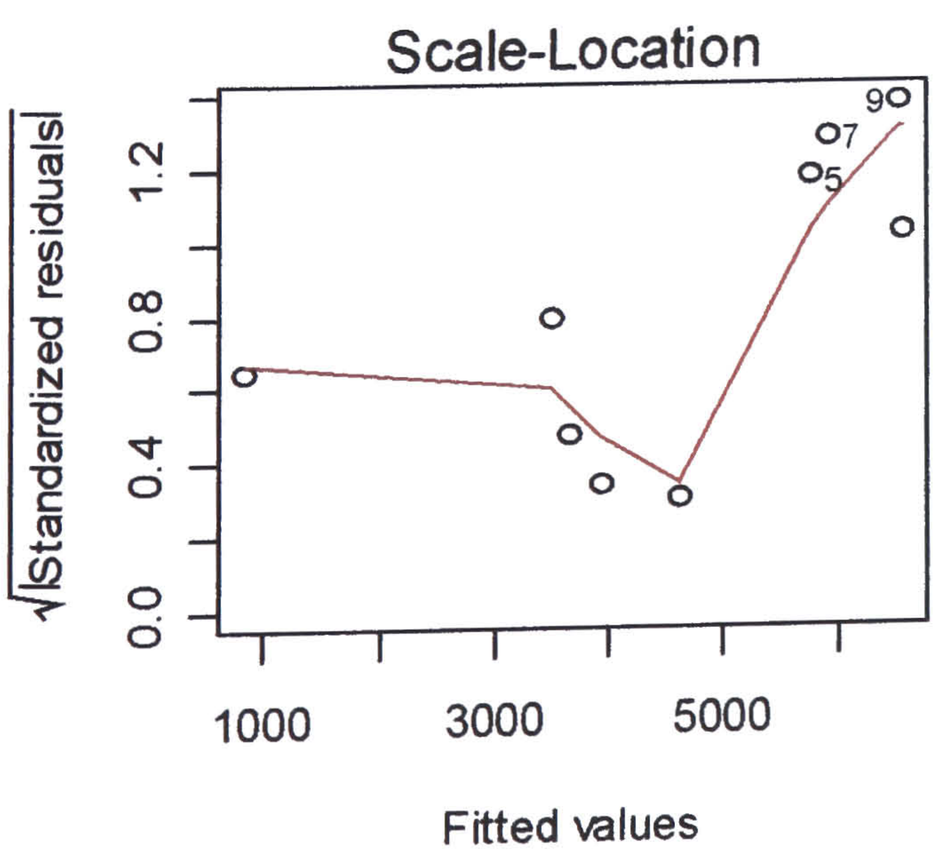
APPENDIX 4

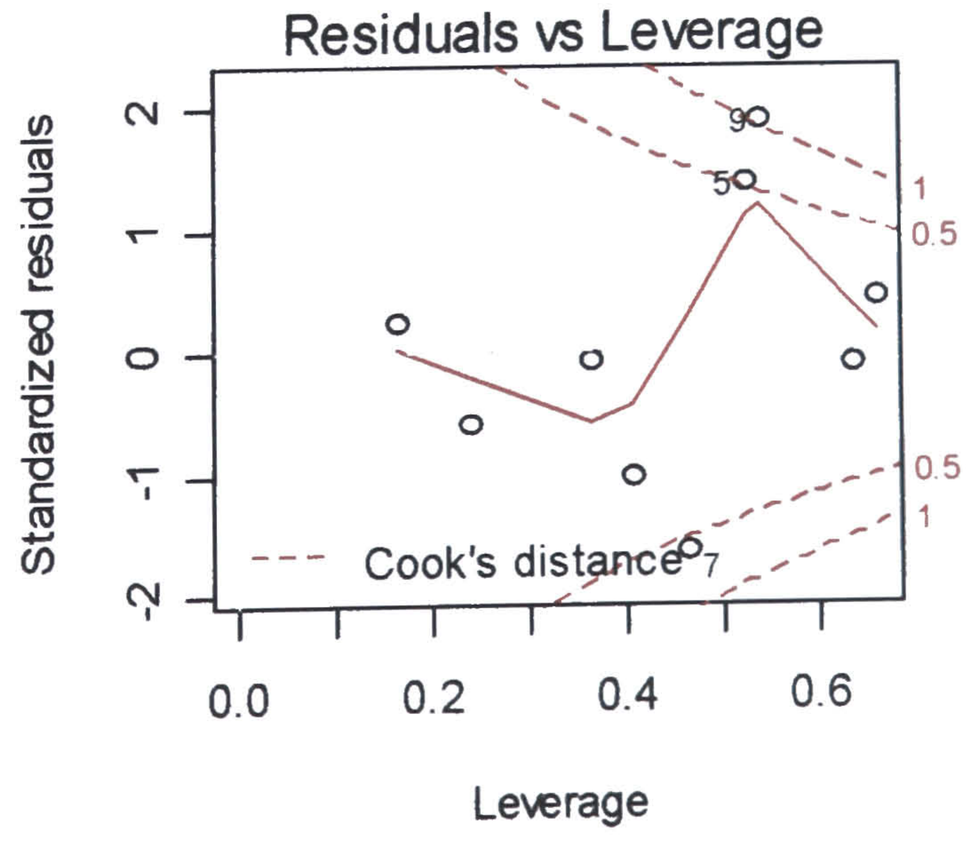
SDE Group "A1" lm Results

```
lm(formula = sa1 ~ sediment shear + current flow at 10cm + mean
burrow depth)

Residuals:
      1       2       3       4       5       6       7       8
-1106.16   336.91   -94.63   277.50  1314.54   -93.67 -1668.07  -757.72
      9
 1791.32
Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept)  3679.07    1502.98   2.448   0.0581 .
xTorq       -4186.36    1160.58  -3.607   0.0154 *
O7            -40.62      15.17  -2.677   0.0440 *
cur10cm     21577.15    6382.64   3.381   0.0197 *

Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
Residual standard error: 1395 on 5 degrees of freedom
Multiple R-Squared: 0.7385,     Adjusted R-squared: 0.5815
F-statistic: 4.706 on 3 and 5 DF,  p-value: 0.06423
```



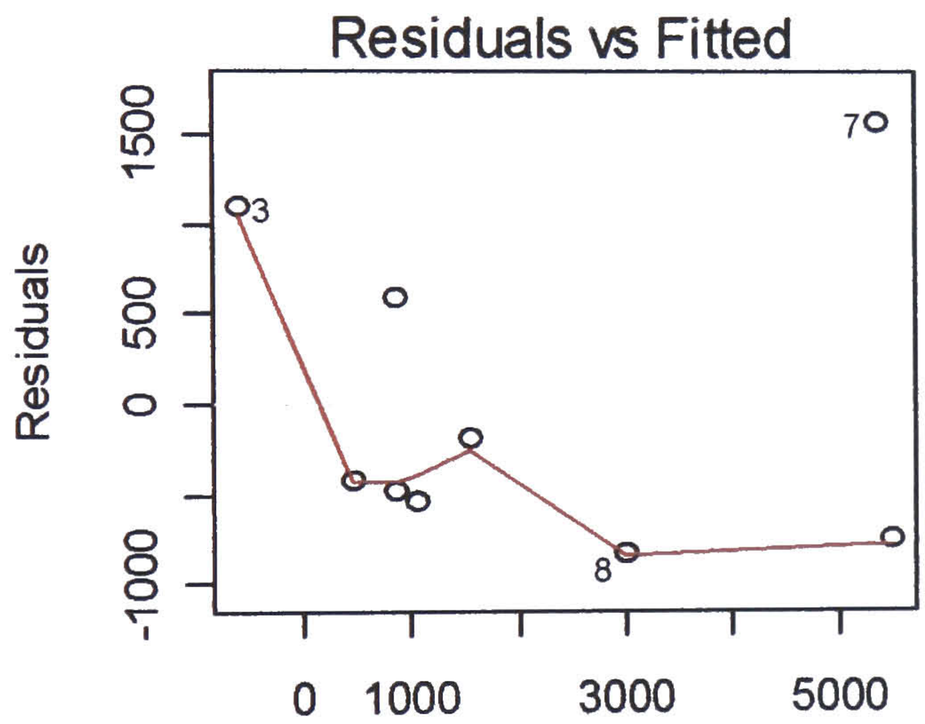


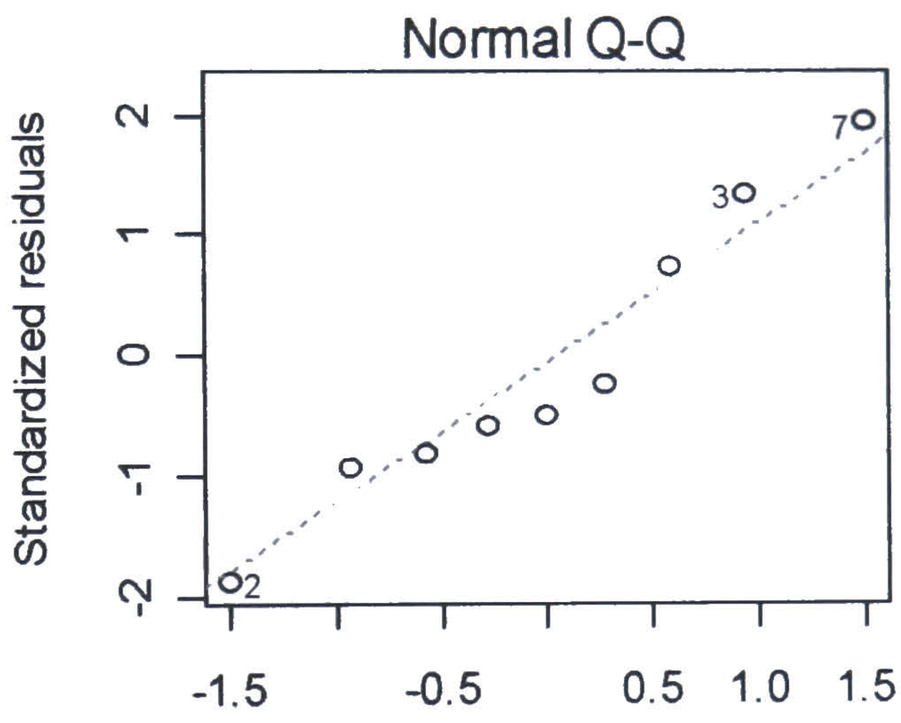


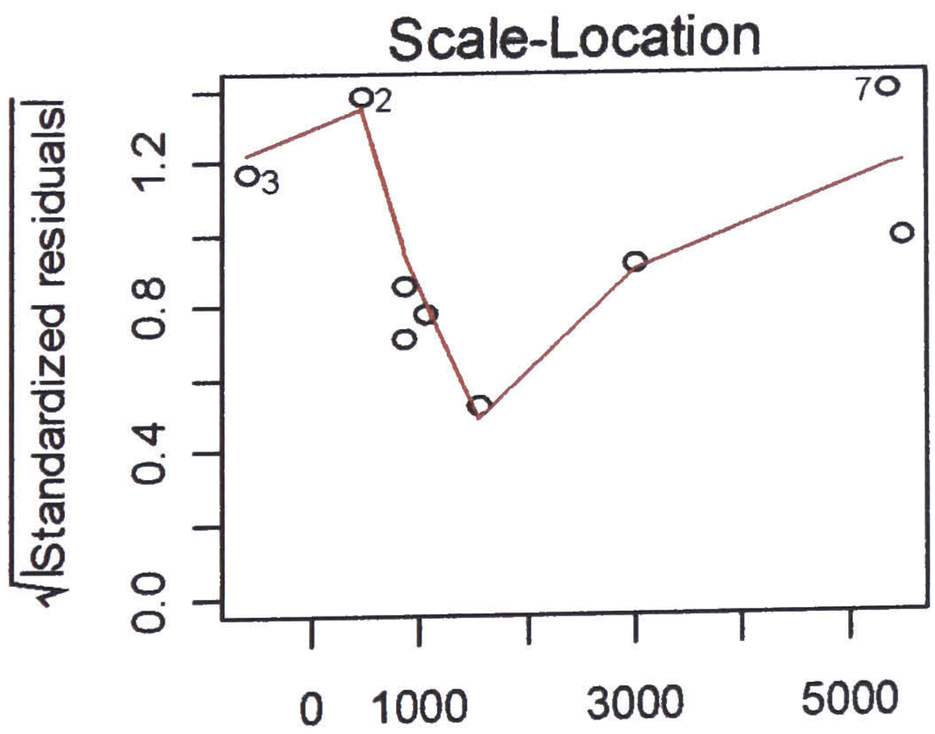


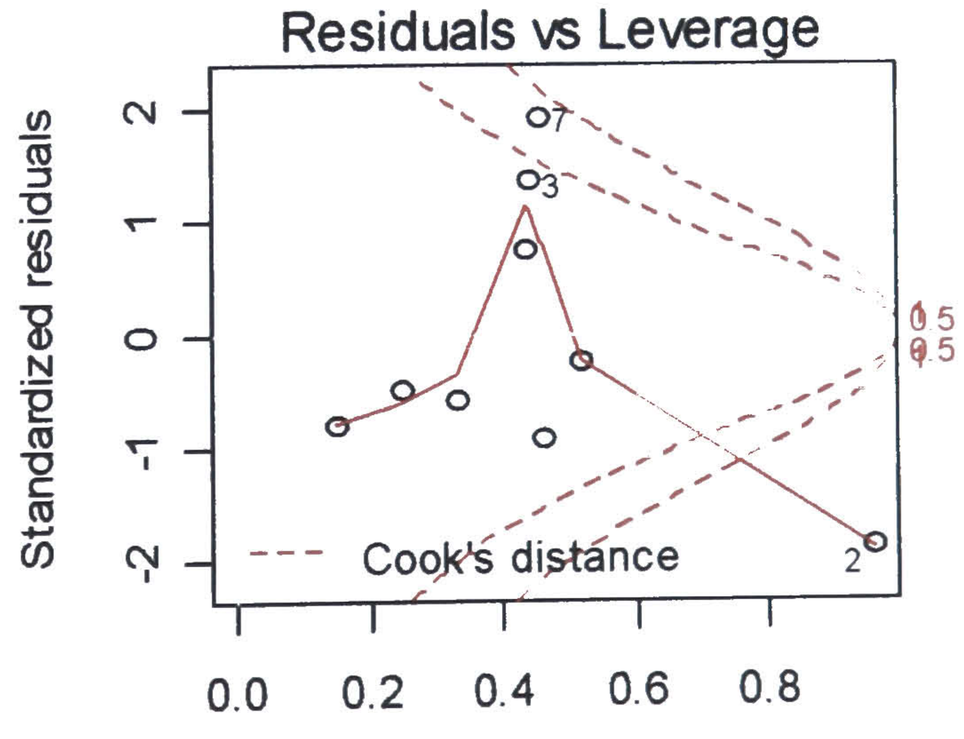
SDE Group "A2" lm Results

```
lm(formula = a2 ~ EPS + sediment shear + mean depth of RPD)

Residuals:
    1     2     3     4     5     6     7     8     9
595.7 -423.3 1101.4 -478.6 -202.4 -540.5 1553.8 -840.3 -765.8

Coefficients:
              Estimate Std. Error t value Pr(>|t|)
(Intercept)   230.9278  1163.2414   0.199  0.85046
Ed              0.5124     7.1387   0.072  0.94556
xTorq       -3212.3688   643.1104  -4.995  0.00412 **
O2           -130.3289   330.3820  -0.394  0.70949
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 1097 on 5 degrees of freedom
Multiple R-Squared: 0.8604,     Adjusted R-squared: 0.7766
F-statistic: 10.27 on 3 and 5 DF,  p-value: 0.01407
```



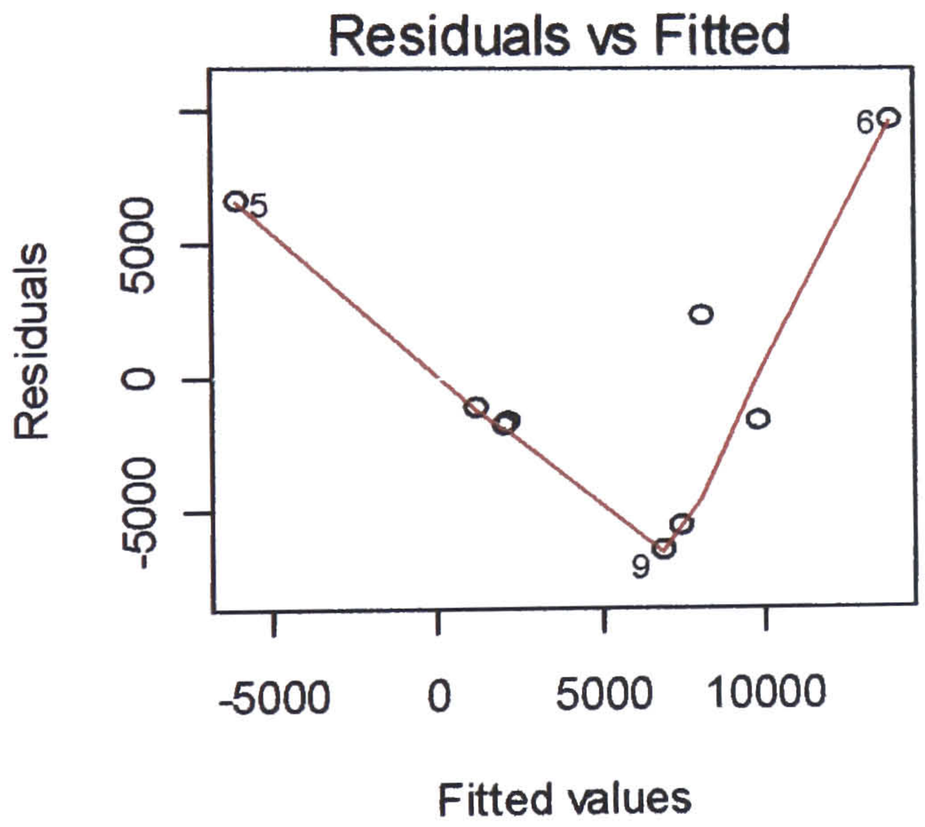


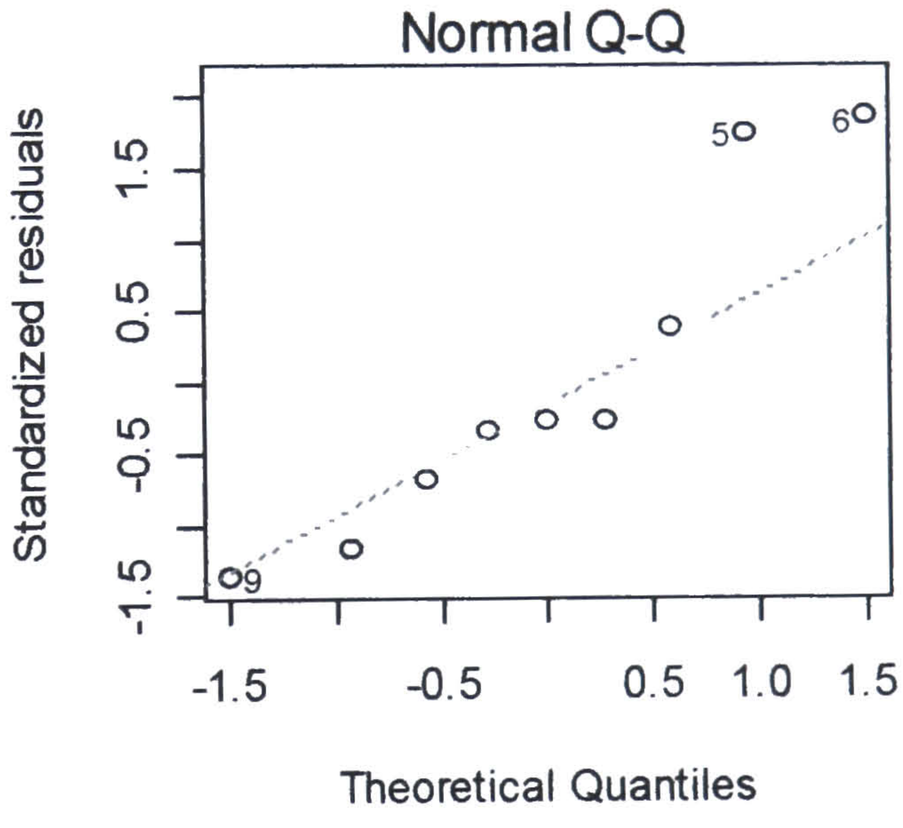


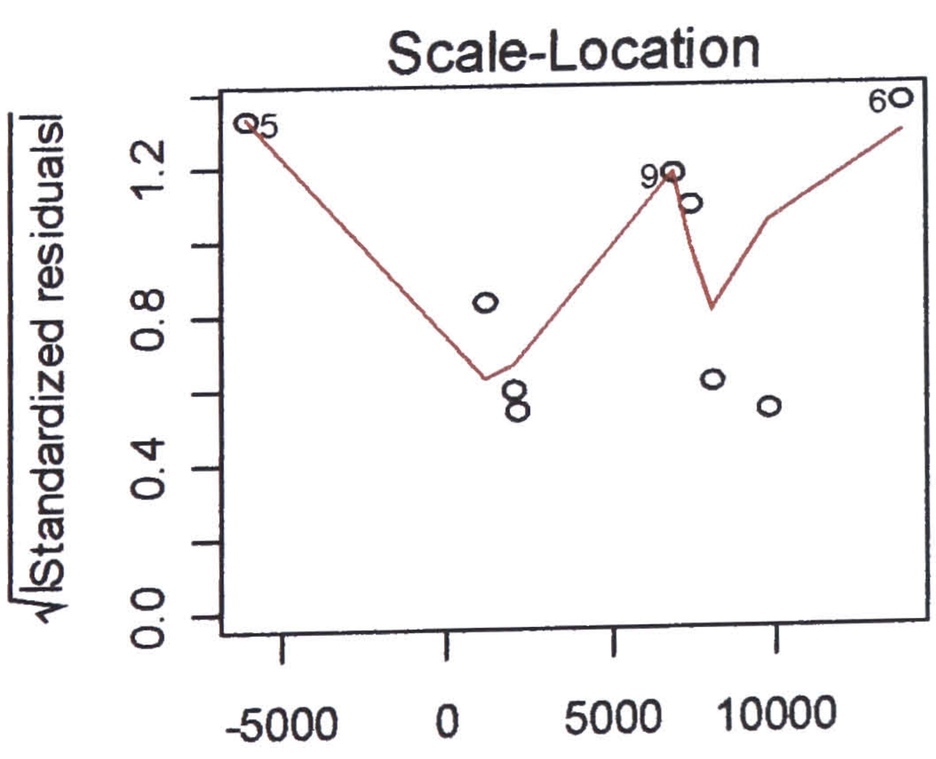


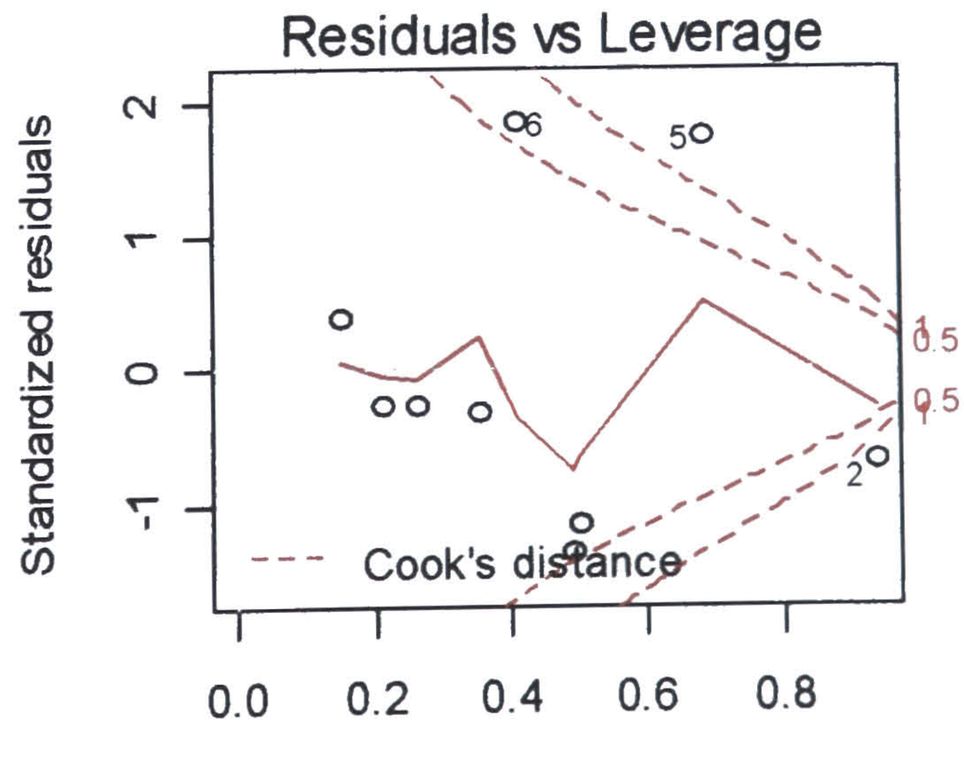
SDE Group "B1" lm Results

```
lm(formula = b1 ~ sediment water content + mean depth of RPD + current at
10cm)

Residuals:
    1     2     3     4     5     6     7     8     9
-1709 -1163 -5623 -1646  6654  9624  2299 -1845 -6590

Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept)  37089.2    15020.9   2.469   0.0566 .
water         -671.4      422.1  -1.591   0.1726
O2             1314.8     2655.0   0.495   0.6414
cur10cm      -31856.2    19899.1  -1.601   0.1703

Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
Residual standard error: 6747 on 5 degrees of freedom
Multiple R-Squared: 0.5455,     Adjusted R-squared: 0.2729
F-statistic: 2.001 on 3 and 5 DF,  p-value: 0.2325
```



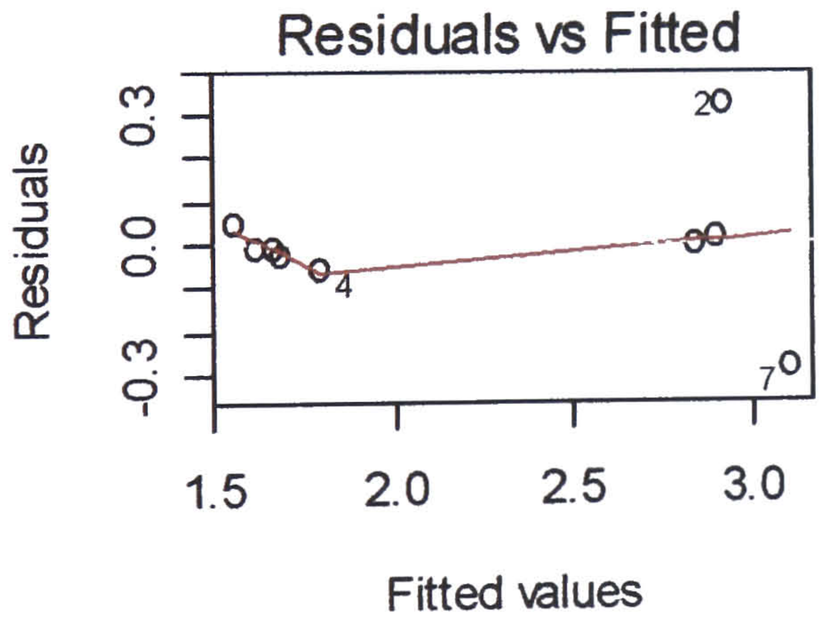


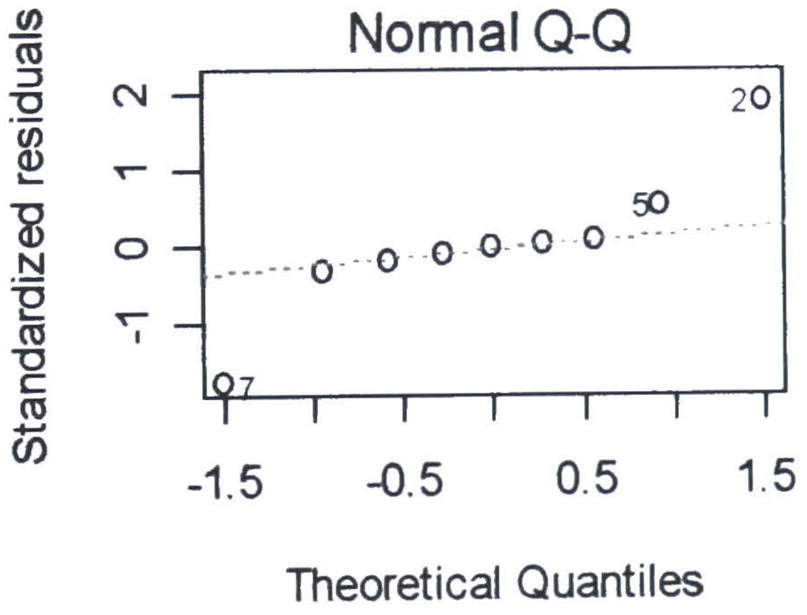


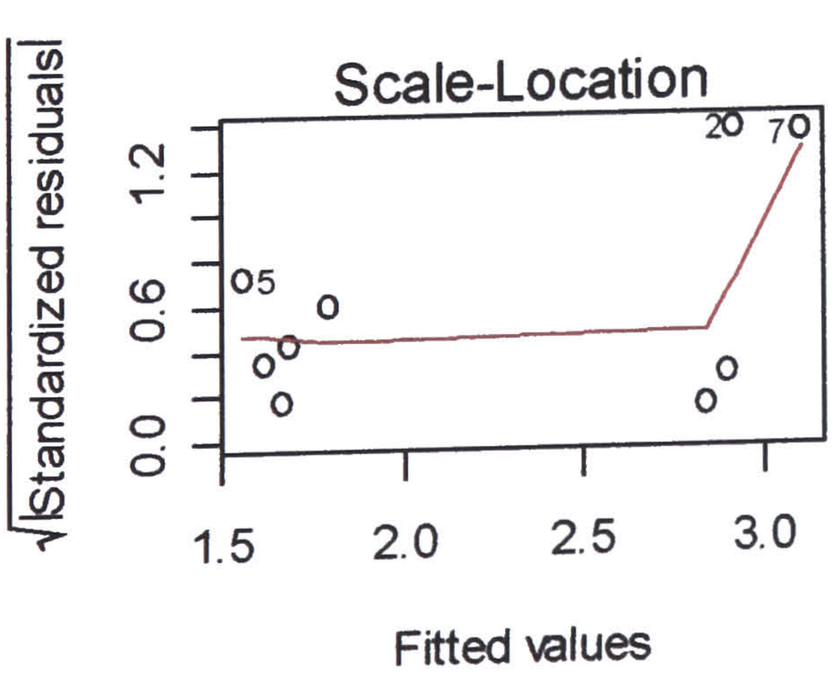


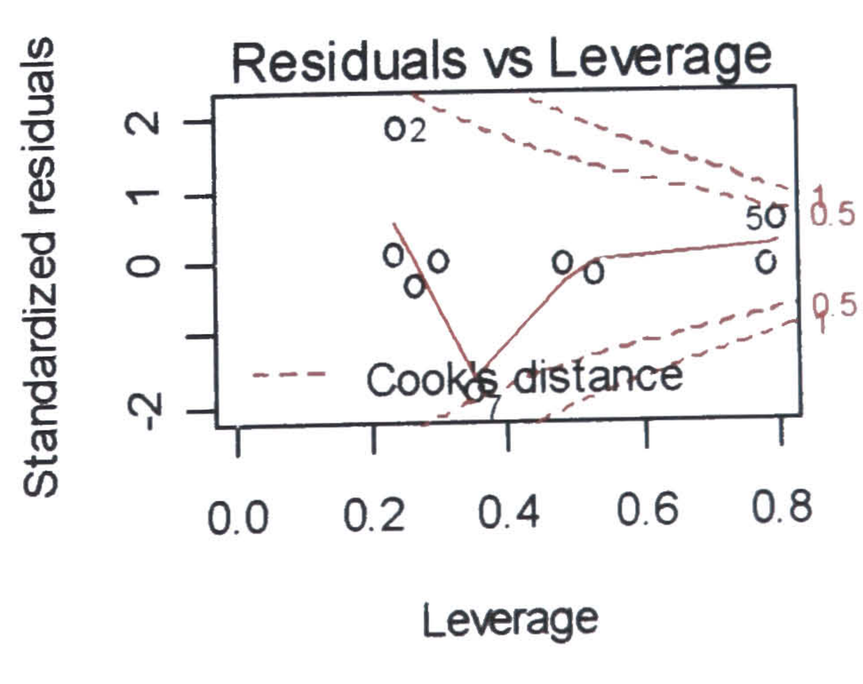
SDE Group "B2" lm Results

```
lmsb2 <- lm(sb2~rate+O7+cur10cm)

### rate=erosion rate, O7= mean burrow depth, cur10cm = current flow at 10cm above
sediment

> summary(lmsb2)

Call:
lm(formula = sb2 ~ rate + O7 + cur10cm)
Residuals:
       1          2          3          4          5          6          7          8
9
-0.024939   0.323296  -0.004489  -0.058714   0.046740  -0.010838  -0.287311   0.013241
0.003015

Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept)  1.832e+00  2.225e-01   8.233 0.000431 ***
rate        -3.026e+02  8.501e+01  -3.559 0.016228 *
O7           9.973e-03  1.689e-03   5.904 0.001984 **
cur10cm     -4.099e+00  6.734e-01  -6.087 0.001731 **

Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
Residual standard error: 0.1968 on 5 degrees of freedom
Multiple R-Squared: 0.9507,     Adjusted R-squared: 0.9211
F-statistic: 32.11 on 3 and 5 DF,  p-value: 0.001082
```



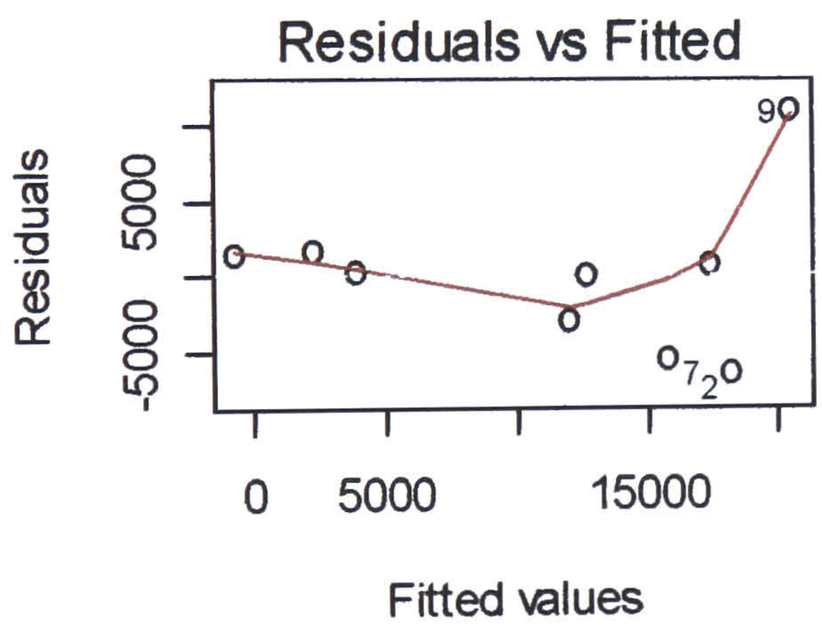


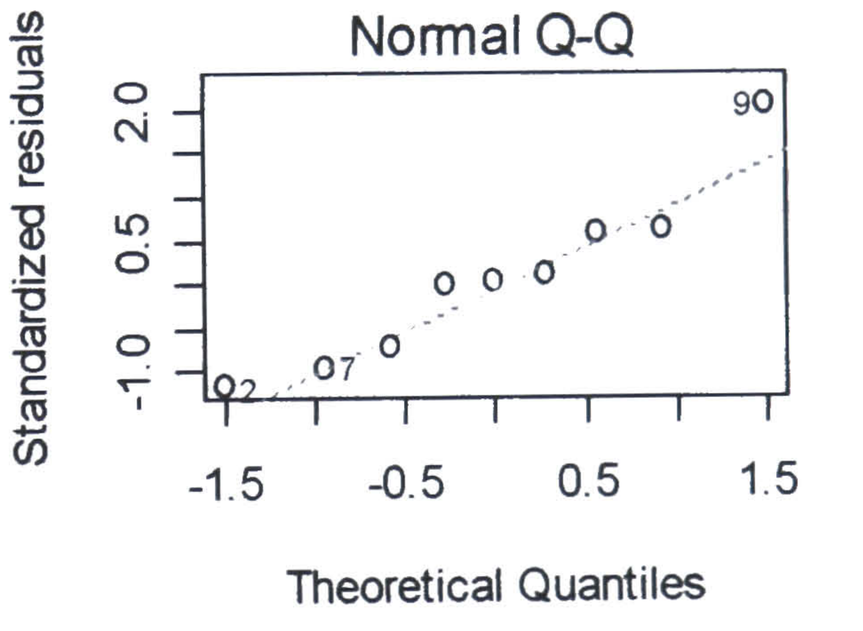


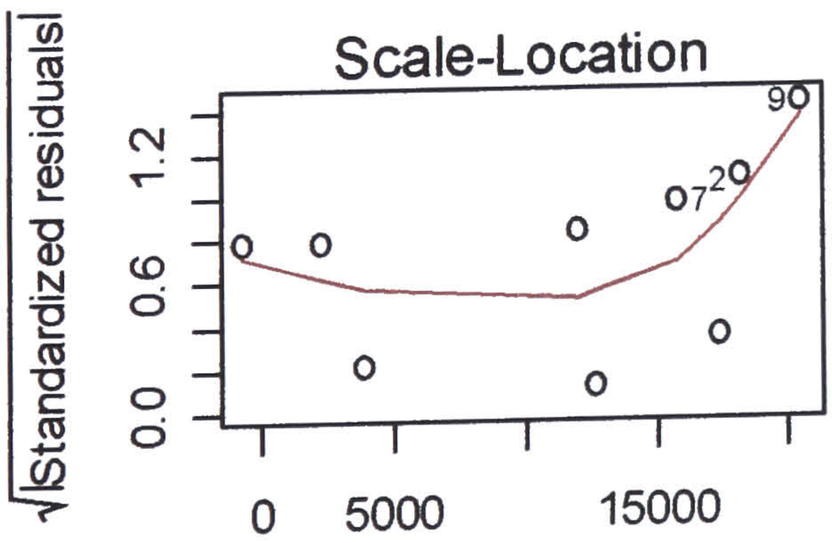


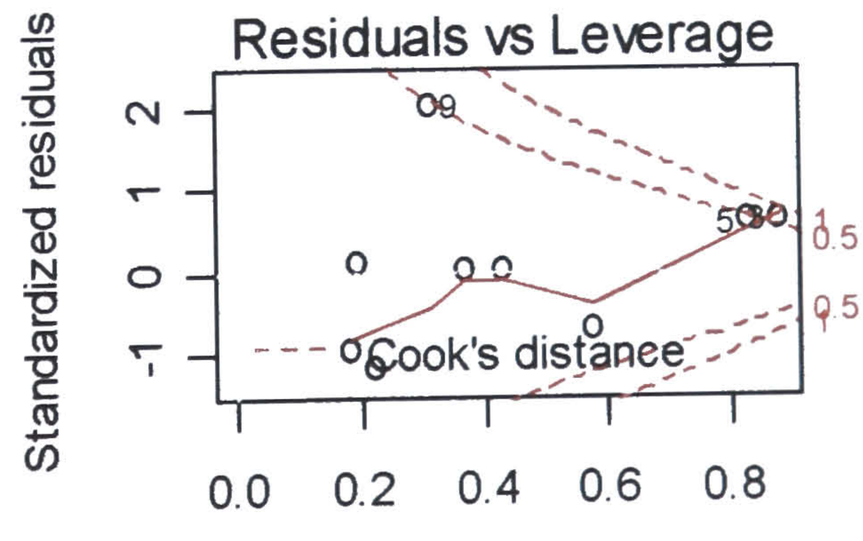
SDE Group Shallow "C1" lm results

```
lm(formula = sc1 ~ cur10cm + Ed + rate)

### cur10cm = current flow at 10cm above sediment, Ed = EPS,  rate=erosion rate

Residuals:
      1       2       3       4       5       6       7       8       9
   63.3 -6592.5  1404.1   223.0  1649.6 -2956.4 -5489.9   680.5 11018.3

Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept)  1.418e+04  5.520e+03   2.569   0.0501 .
cur10cm     -5.408e+04  2.170e+04  -2.493   0.0550 .
Ed           6.373e+01  3.896e+01   1.636   0.1628
rate        -2.829e+06  2.746e+06  -1.030   0.3501

Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
Residual standard error: 6465 on 5 degrees of freedom
Multiple R-Squared: 0.6932,     Adjusted R-squared: 0.5091
F-statistic: 3.766 on 3 and 5 DF,  p-value: 0.09377
```



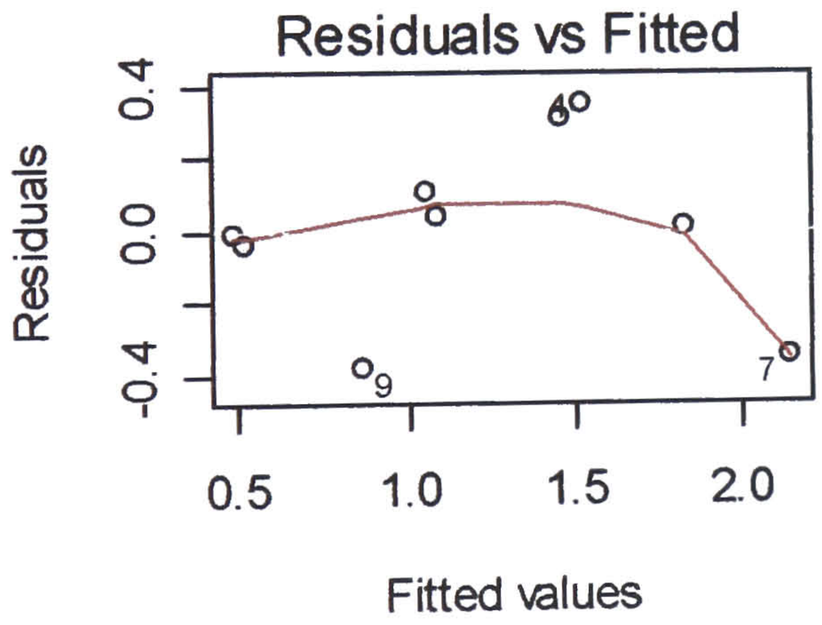


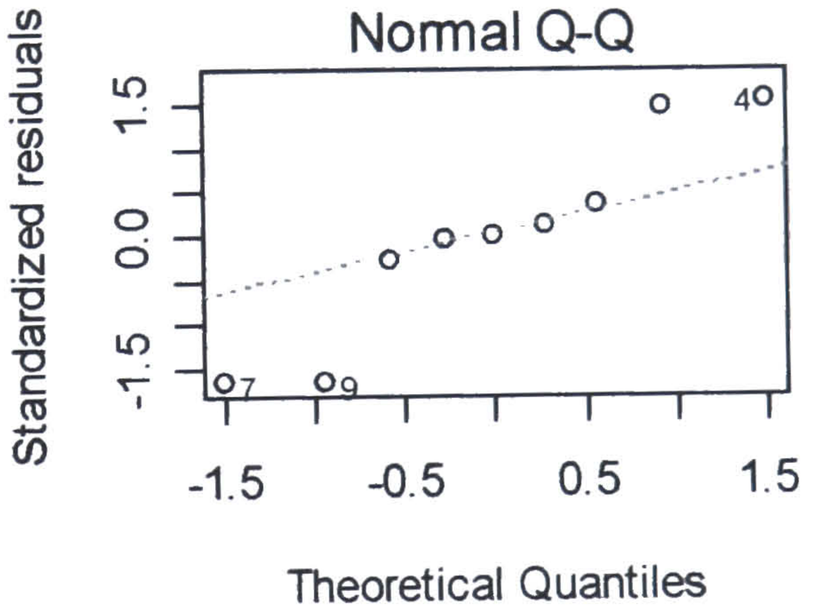


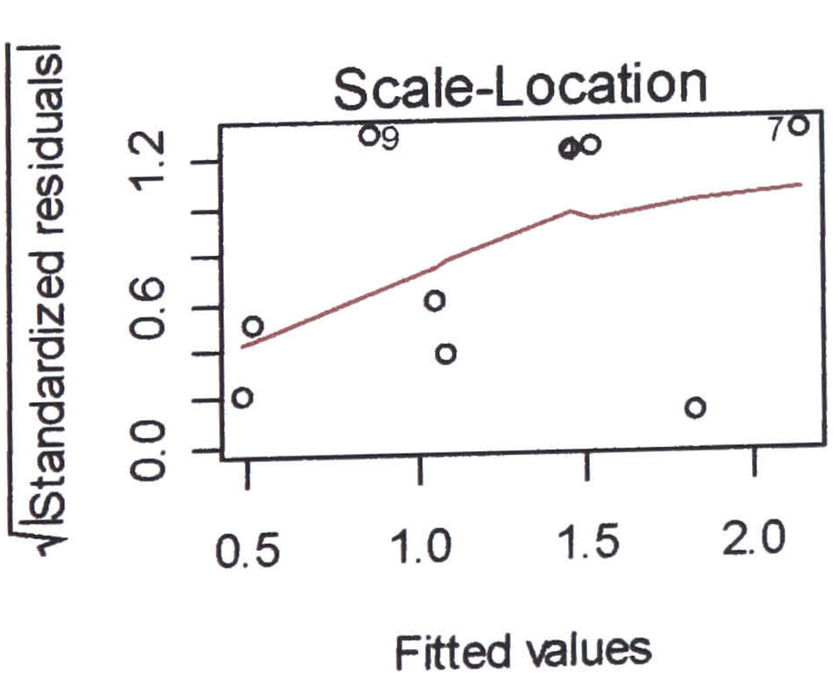


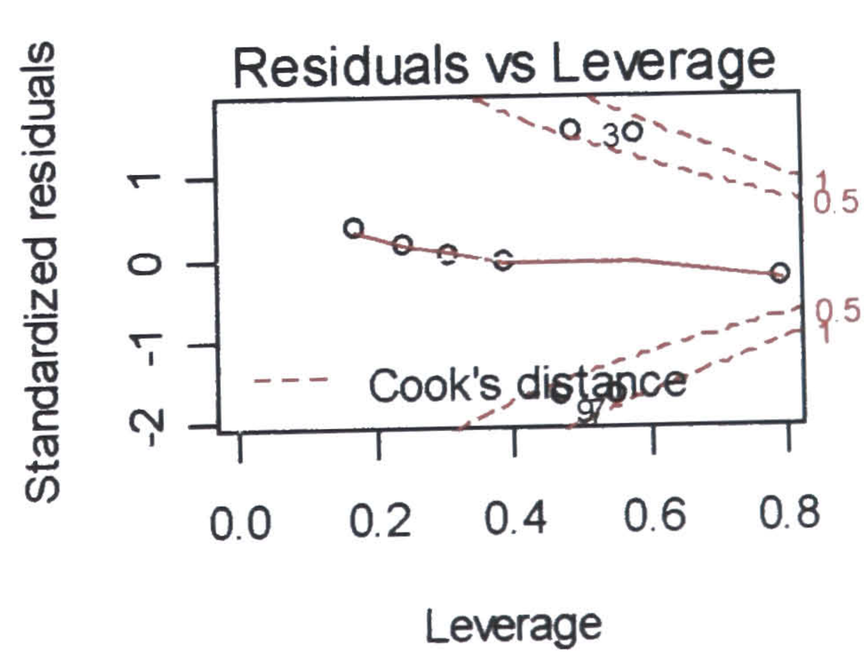
SDE group shallow "C2" lm results

```
lm(formula = sc2 ~ fines + O2 + xsal)

### fines= % sediment particles<63µ, O2= mean depth og RPD, xsal=interstitial salinity.
Residuals:

       1        2        3        4        5        6        7        8

-0.010752 -0.037830  0.304946  0.347352  0.036389  0.003804 -0.357119  0.100294 -

9

0.387082

Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept) -4.768e-01  9.425e-01  -0.506   0.6344
fines       -4.696e-02  1.373e-02  -3.421   0.0188 *
O2           4.468e-01  1.879e-01   2.378   0.0633 .
xsal         7.698e-05  2.070e-05   3.719   0.0137 *

Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
Residual standard error: 0.3175 on 5 degrees of freedom
Multiple R-Squared: 0.8356,     Adjusted R-squared: 0.7369
F-statistic:  8.47 on 3 and 5 DF,  p-value: 0.02097
```



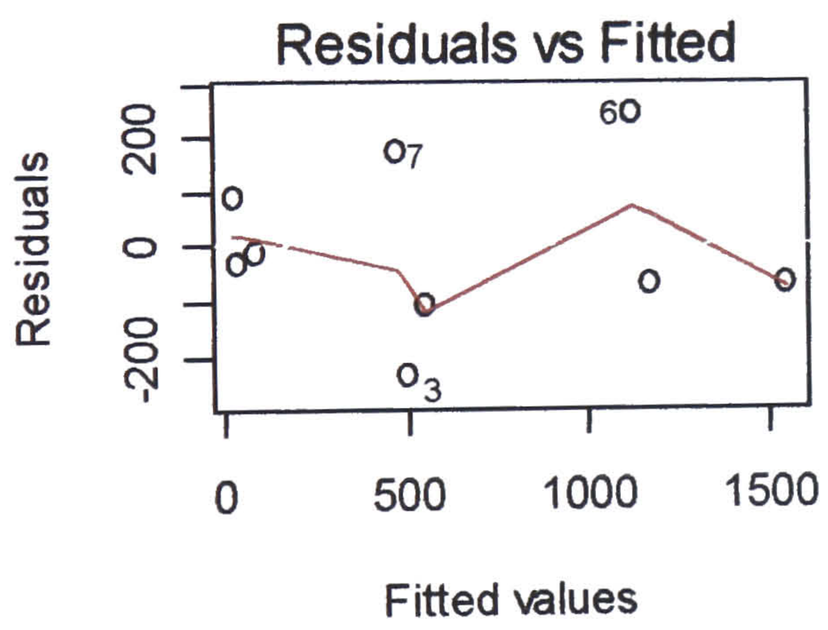


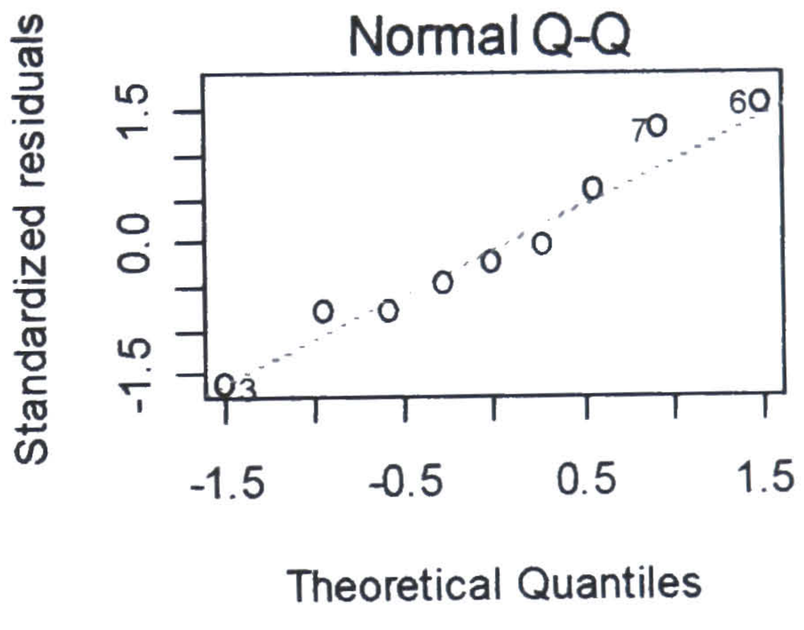


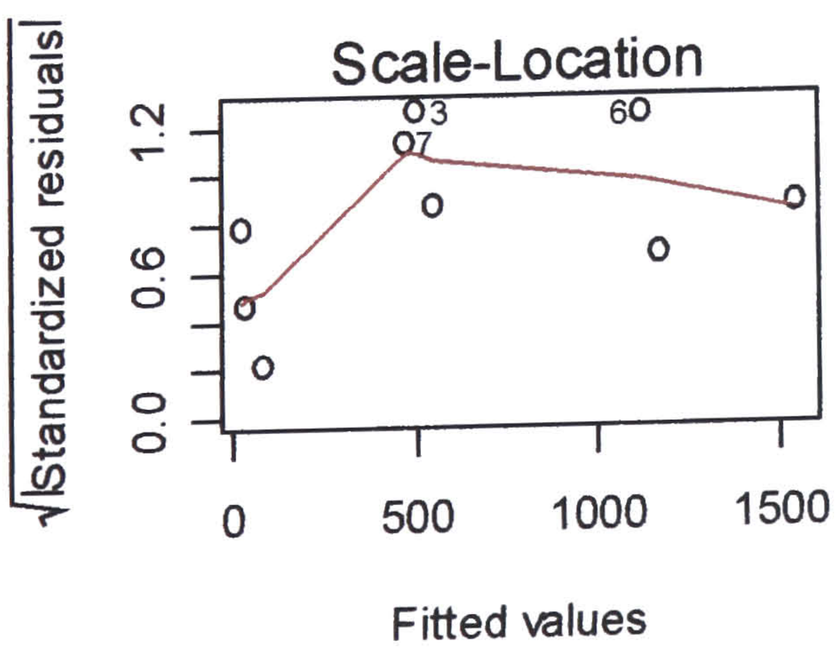


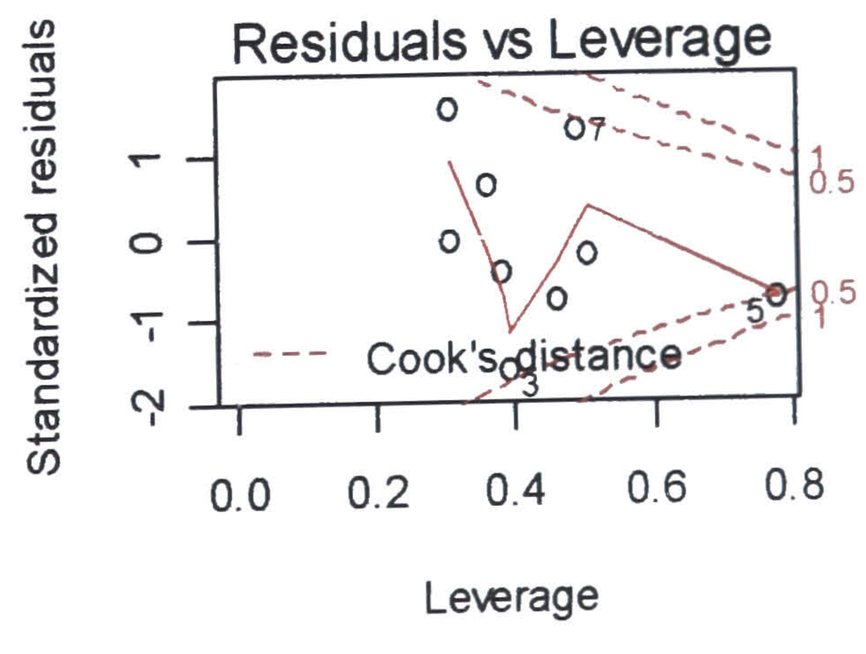
SDE group shallow "C3" lm results

```
lm(formula = sc3 ~ water + rate + Cd)

### water=sediment water content, rate=erosion rate, Cd=Chla concentration

Residuals:
      1       2       3       4       5       6       7       8       9
-104.09  -27.85 -236.23  -66.09  -66.59  245.00  172.60   -7.32   90.57

Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept)    948.19     401.05   2.364 0.064410 .
water          -26.80      10.65  -2.517 0.053398 .
rate        589364.78   75662.12   7.789 0.000558 ***
Cd             37.97      17.29   2.196 0.079452 .

Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
Residual standard error: 186.7 on 5 degrees of freedom
Multiple R-Squared: 0.9335,     Adjusted R-squared: 0.8936
F-statistic:  23.4 on 3 and 5 DF,  p-value: 0.002266
```



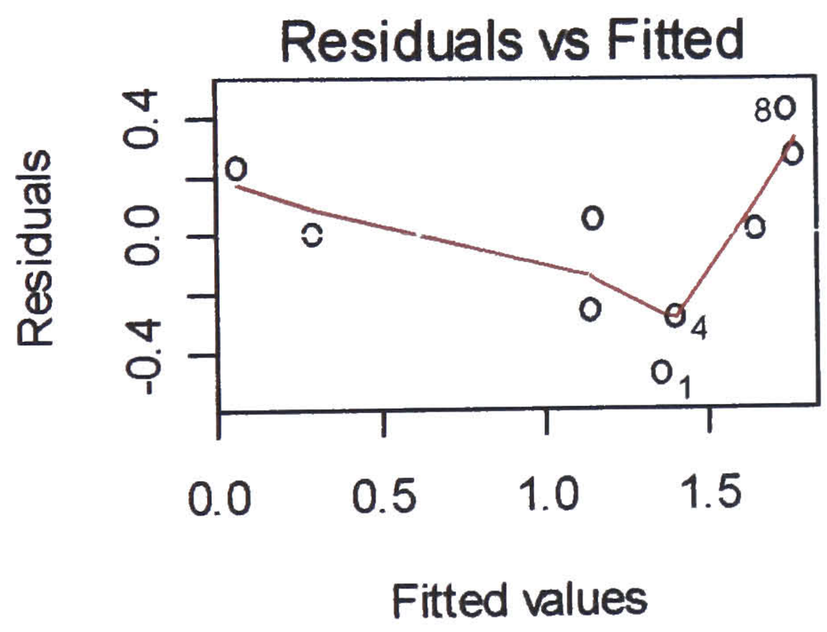


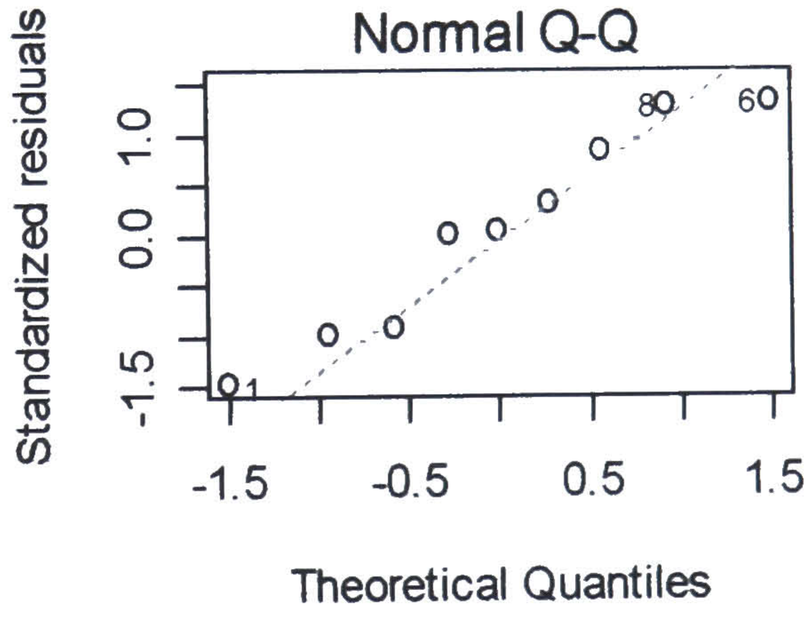


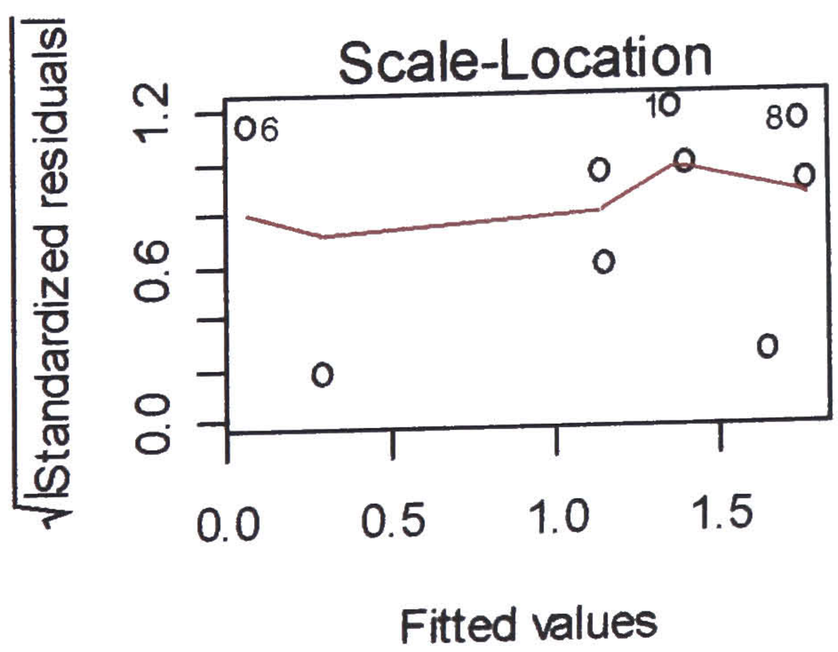


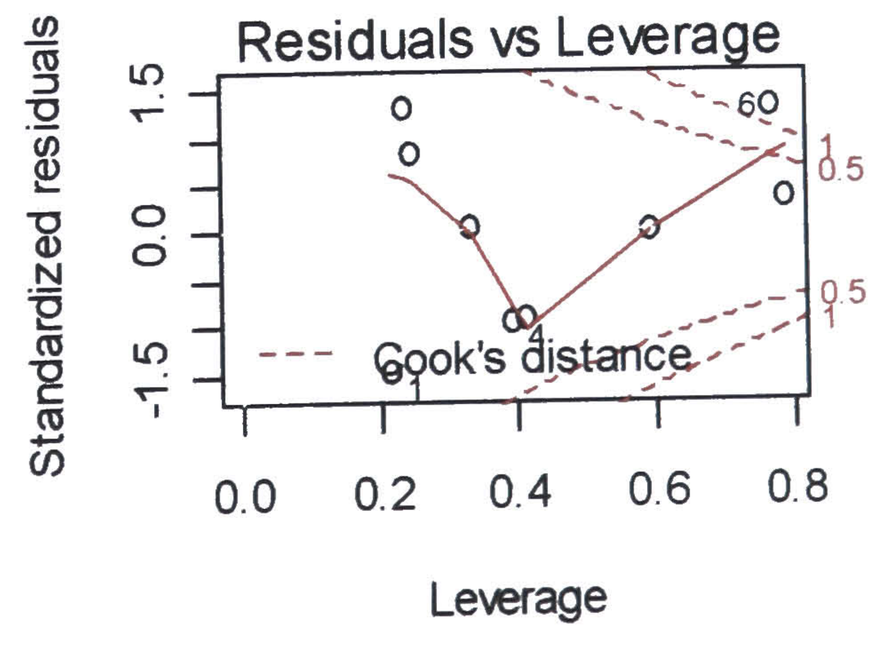
SDE Group "3e" lm Results

```
Call:

lm(formula = X3e ~ fines + rate + O7)

# O7=burrow depth

Residuals:
      1       2       3       4       5       6       7       8       9
-0.47907  0.26868  0.00809 -0.27727  0.05890  0.23440 -0.25668  0.42425  0.01871

Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept) -8.496e-01  5.560e-01  -1.528   0.1870
fines        5.275e-02  1.424e-02   3.704   0.0139 *
rate        -4.042e+02  1.494e+02  -2.705   0.0425 *
O7           2.173e-03  2.955e-03   0.735   0.4951
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.3697 on 5 degrees of freedom
Multiple R-Squared: 0.8151,     Adjusted R-squared: 0.7041
F-statistic: 7.345 on 3 and 5 DF,  p-value: 0.02791
```



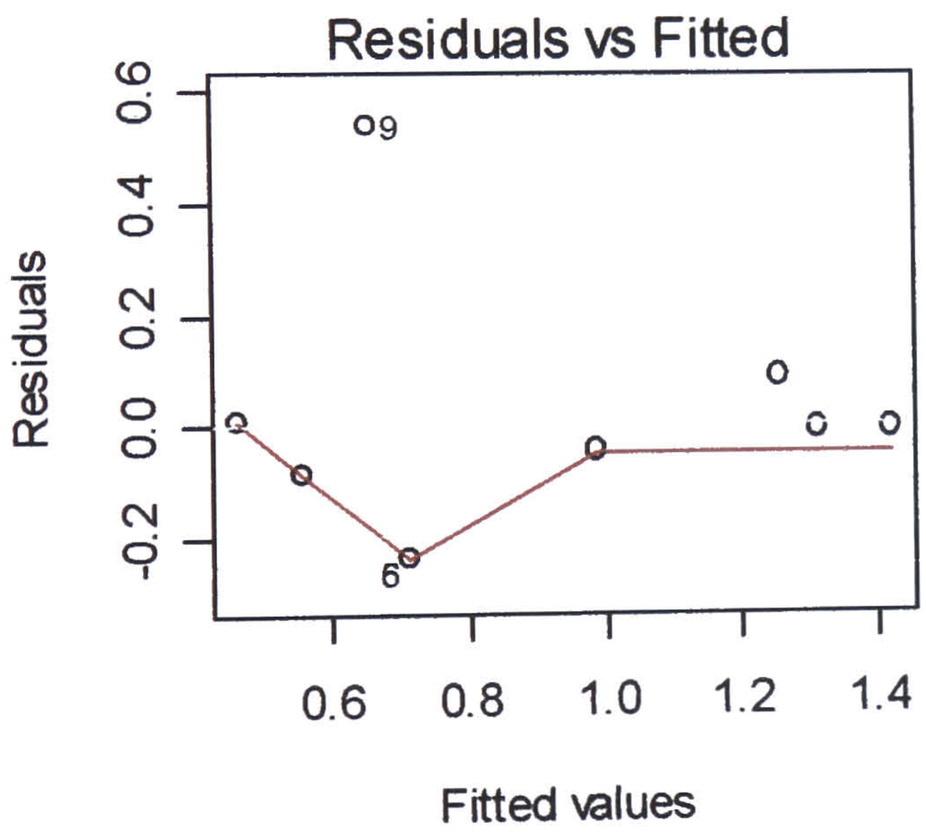


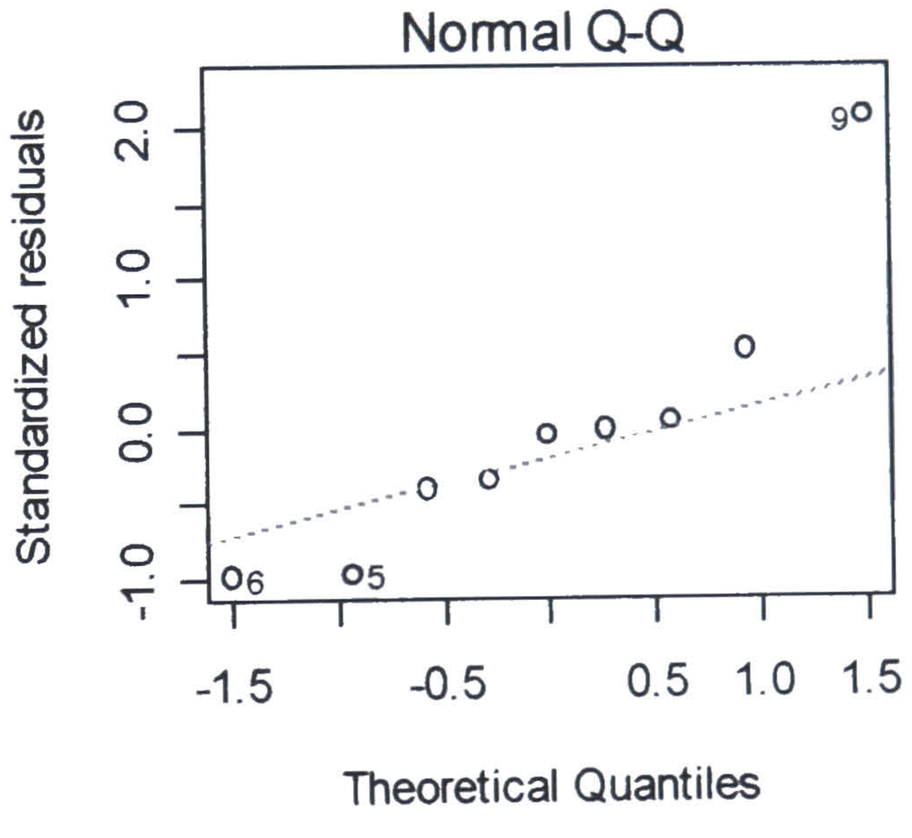


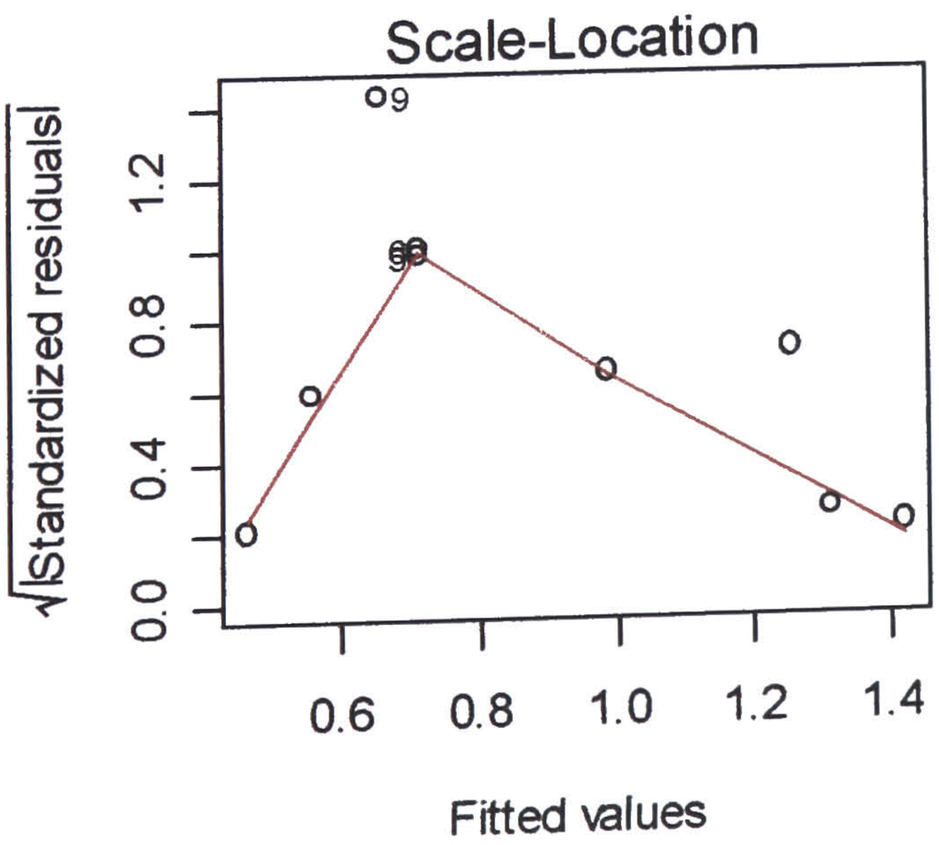


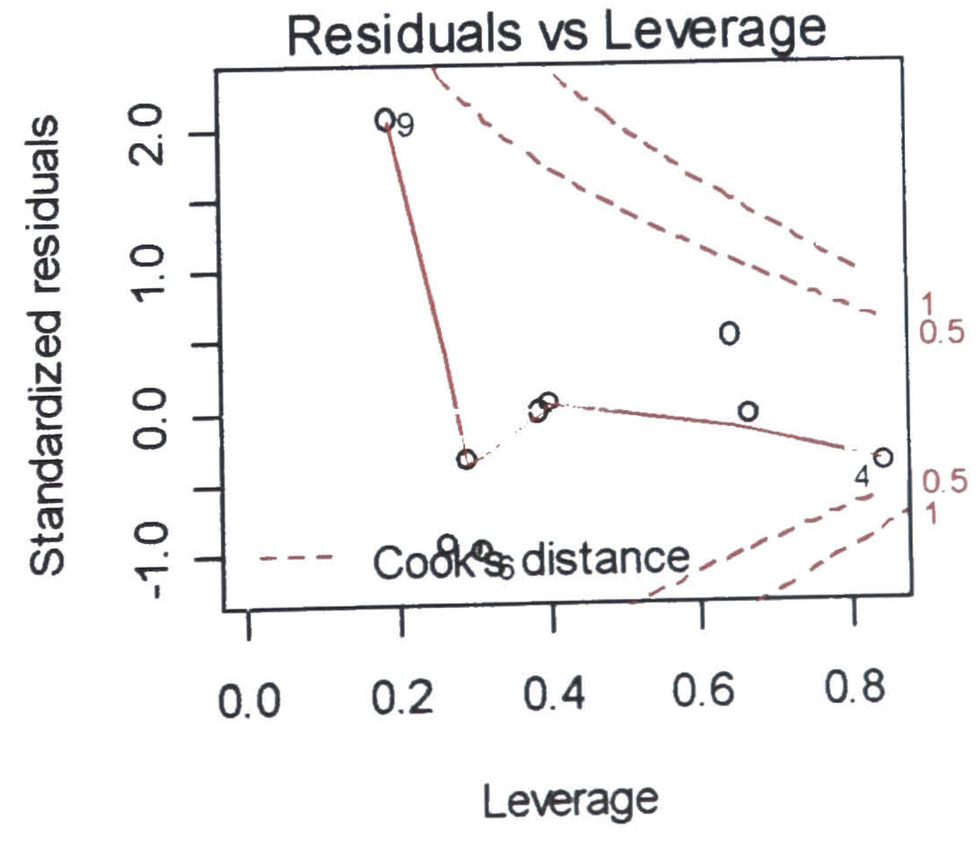
SDE group "5a" lm

```
lm(formula = X5a ~ fines + xsal + water)

Residuals:
       1        2        3        4        5        6        7        8
-0.008517 -0.010524  0.085072 -0.047300 -0.239020 -0.239471  0.008937 -0.084510
       9
 0.535332

Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept)  3.372e+00  8.895e-01   3.791   0.0127 *
fines        2.285e-02  1.446e-02   1.580   0.1750
xsal        -4.096e-05  1.193e-05  -3.433   0.0186 *
water       -4.929e-02  2.034e-02  -2.423   0.0599 .
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
Residual standard error: 0.2891 on 5 degrees of freedom
Multiple R-Squared: 0.7046,     Adjusted R-squared: 0.5274
F-statistic: 3.976 on 3 and 5 DF,  p-value: 0.08575
```



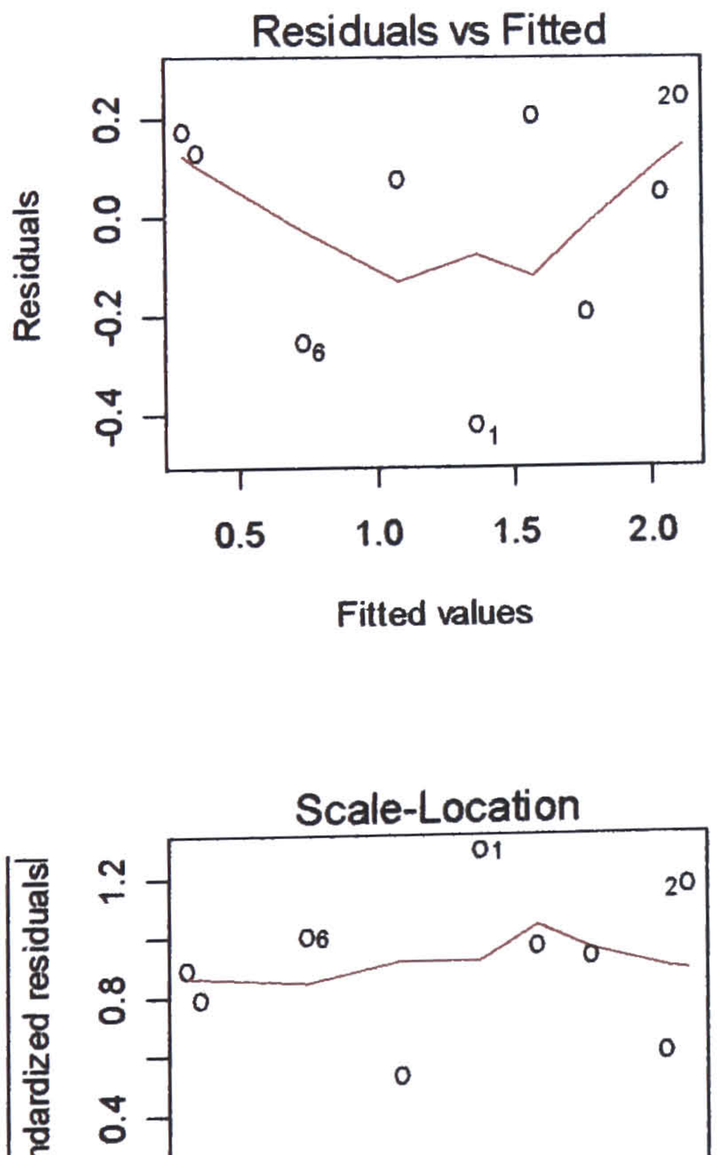


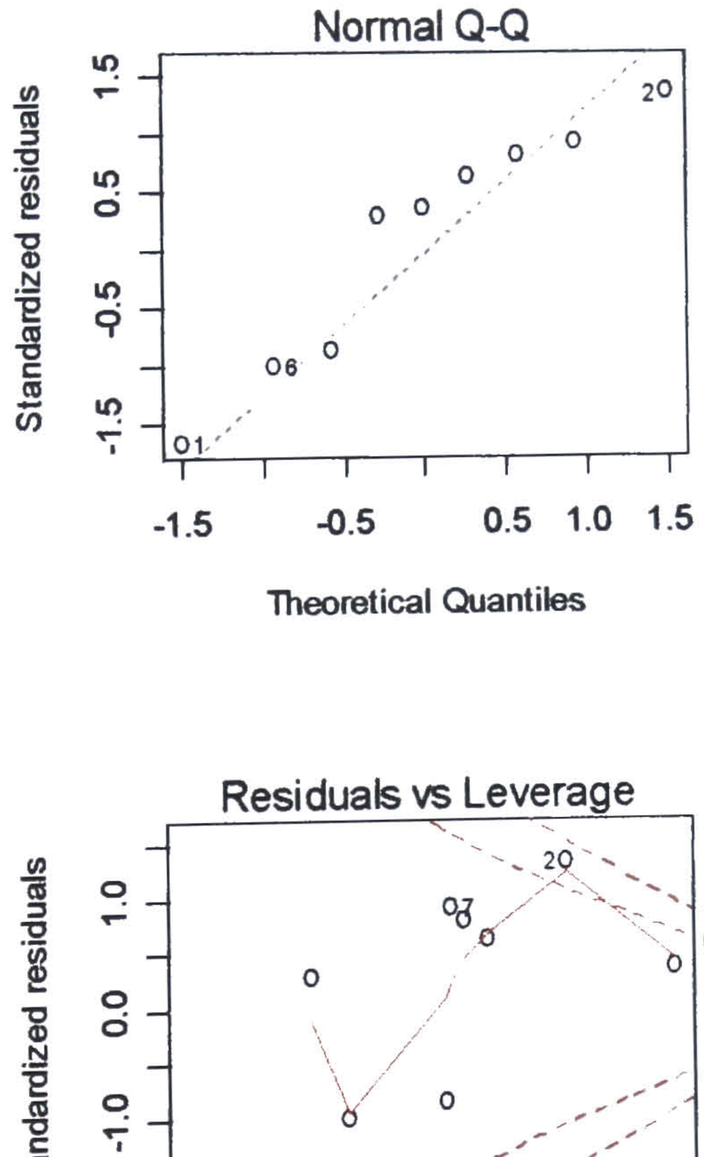




SDE Group "5b" lm

```
Call:
lm(formula = X5b ~ xsal + xTorq + rate)
Residuals:
      1       2       3       4       5       6       7       8
-0.42483  0.24194  0.13054  0.17421  0.04652 -0.25289  0.20410  0.07470
      9
-0.19428

Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept)  1.629e+00  2.440e-01   6.677  0.00114 **
xsal        -6.437e-05  1.105e-05  -5.824  0.00211 **
xTorq       -1.266e+00  2.192e-01  -5.776  0.00219 **
rate         5.774e+02  1.587e+02   3.638  0.01493 *
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.2958 on 5 degrees of freedom
Multiple R-Squared: 0.8963,     Adjusted R-squared: 0.8341
F-statistic: 14.41 on 3 and 5 DF,  p-value: 0.006786
> plot(lmd5b)
```

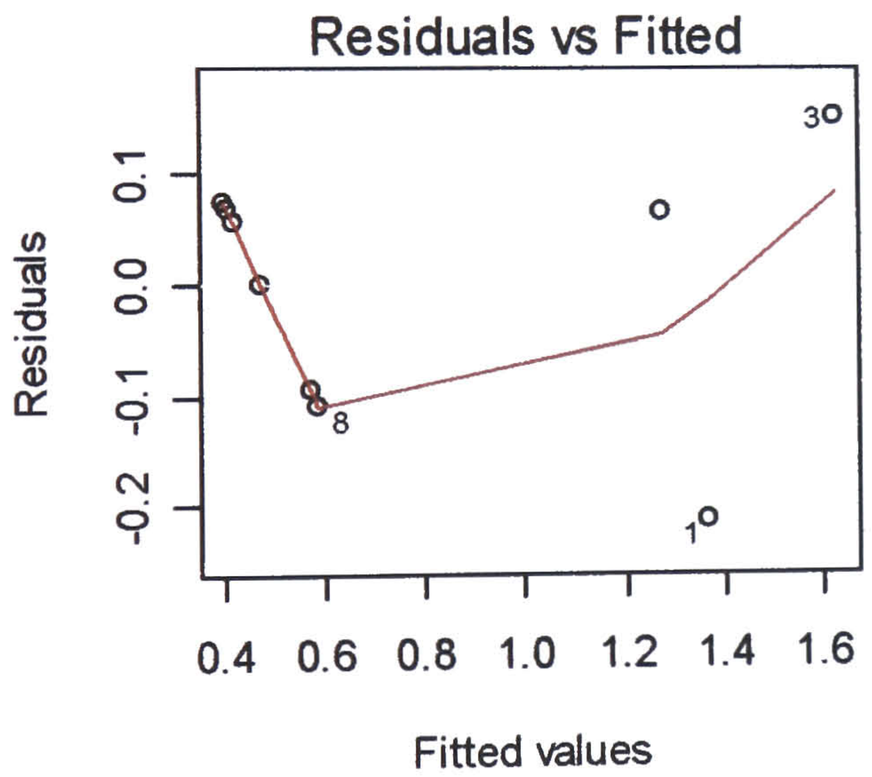


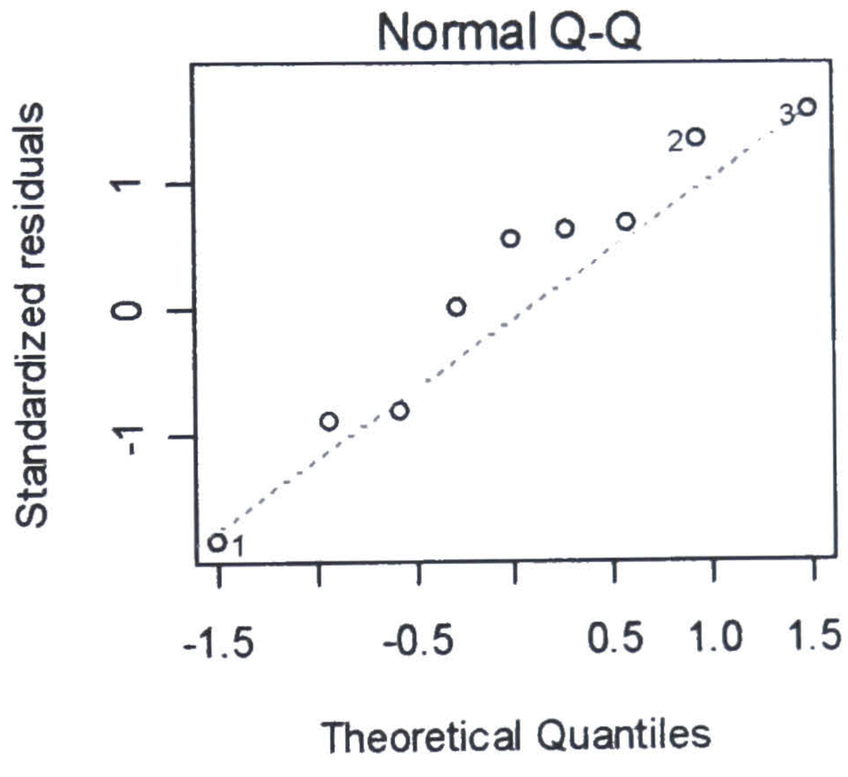


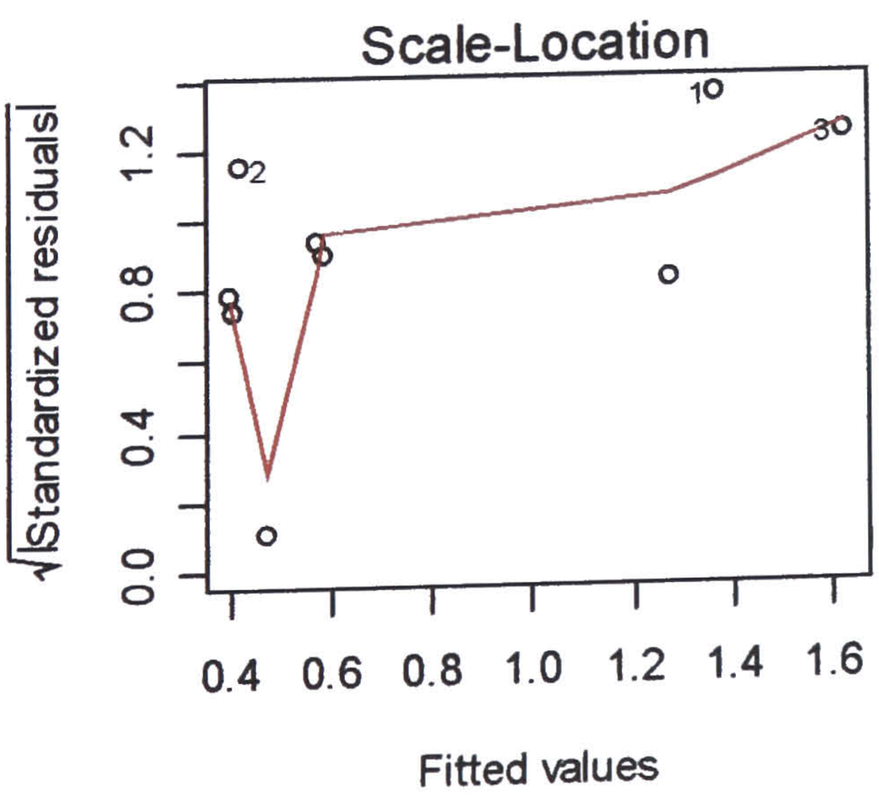
SDE Group "5d" lm

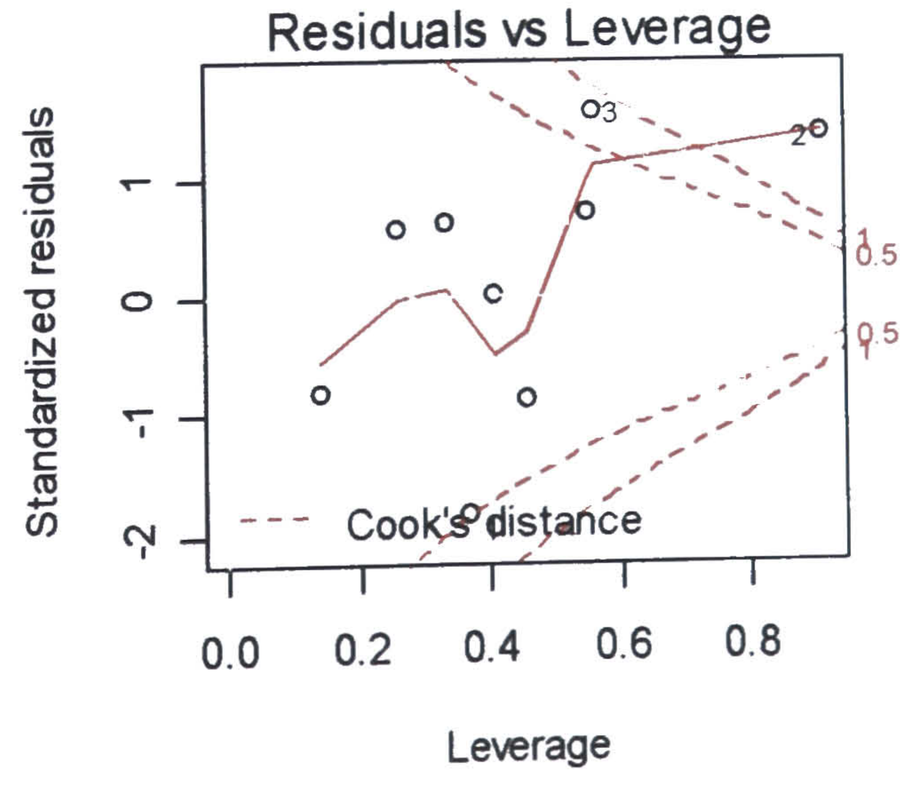
```
Call:
lm(formula = X5d ~ xsal + O2 + cur10cm)

Residuals:
       1        2        3        4        5        6        7        8
-0.214241  0.058145  0.150967 -0.095052  0.066604  0.074341  0.068583 -0.110554
       9
 0.001209

Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept)  2.064e+00  4.401e-01   4.690 0.005385 **
xsal        -3.233e-05  8.007e-06  -4.037 0.009949 **
O2          -2.873e-01  6.918e-02  -4.154 0.008879 **
cur10cm      3.257e+00  4.094e-01   7.955 0.000506 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
Residual standard error: 0.147 on 5 degrees of freedom
Multiple R-Squared: 0.9458,     Adjusted R-squared: 0.9133
F-statistic:  29.1 on 3 and 5 DF,  p-value: 0.001364
```

> **plot(lmd5d)**





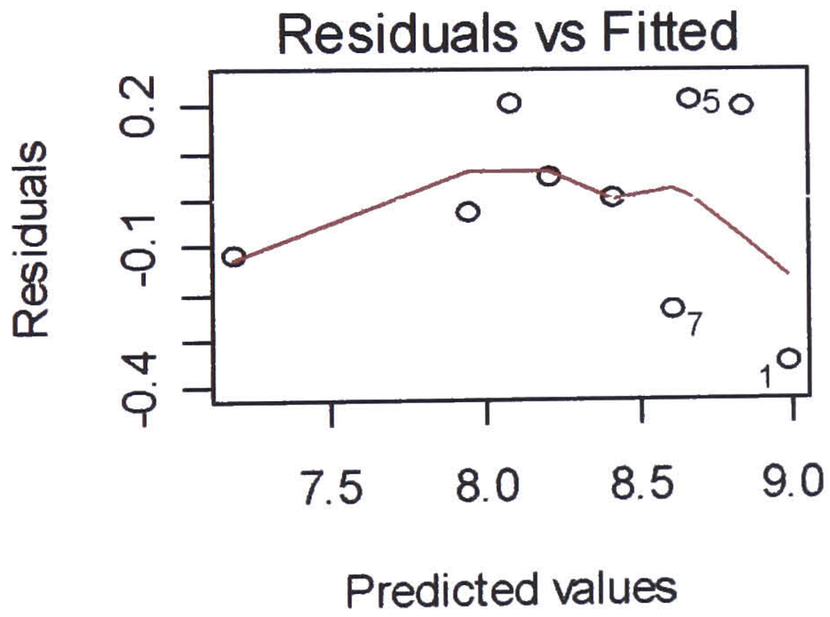


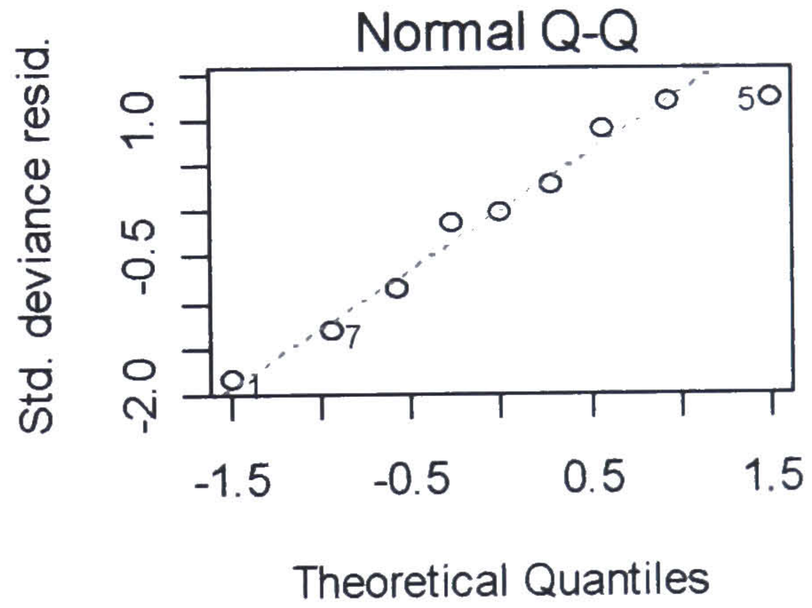


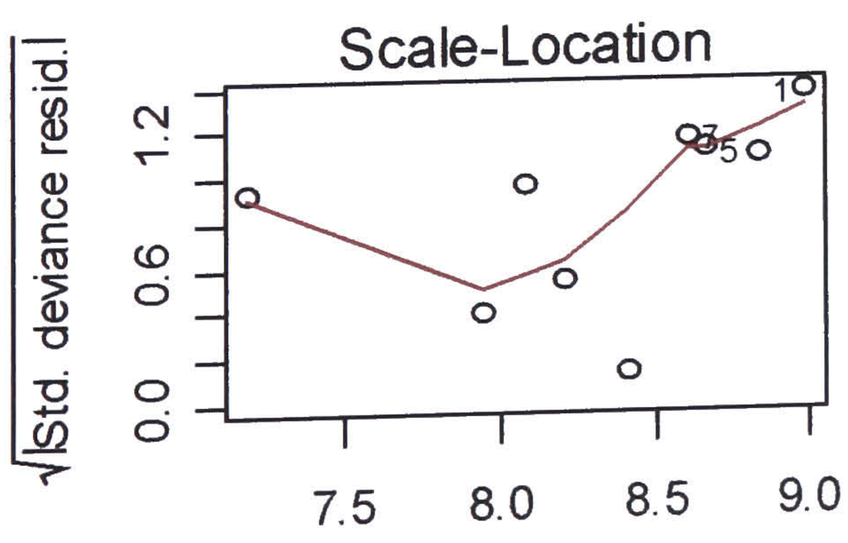
APPENDIX 5

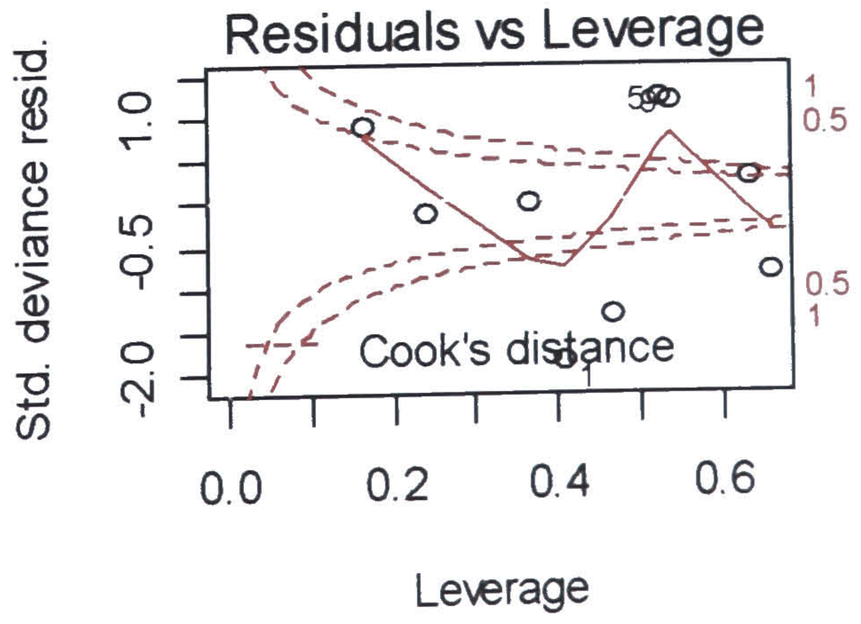
SDE Group "A1" GLM Results

```
glm(formula = a1 ~ sediment shear + current flow at 10cm + mean burrow
depth, family = Gamma(link = log), data = enviro)

Deviance Residuals:
       1         2         3         4         5         6         7         8
-0.356435 -0.123967 -0.002820  0.202852  0.208447  0.041795 -0.242691 -0.031909
       9
 0.196708

Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept)  8.189013   0.267116  30.657 6.93e-07 ***
xTorq       -1.188310   0.206264  -5.761  0.00221 **
cur10cm      6.647870   1.134353   5.860  0.00205 **
O7          -0.013064   0.002696  -4.845  0.00469 **

Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
(Dispersion parameter for Gamma family taken to be 0.06143676)

    Null deviance: 2.21422  on 8  degrees of freedom
Residual deviance: 0.32738  on 5  degrees of freedom
AIC: 155.32
Number of Fisher Scoring iterations: 6
```



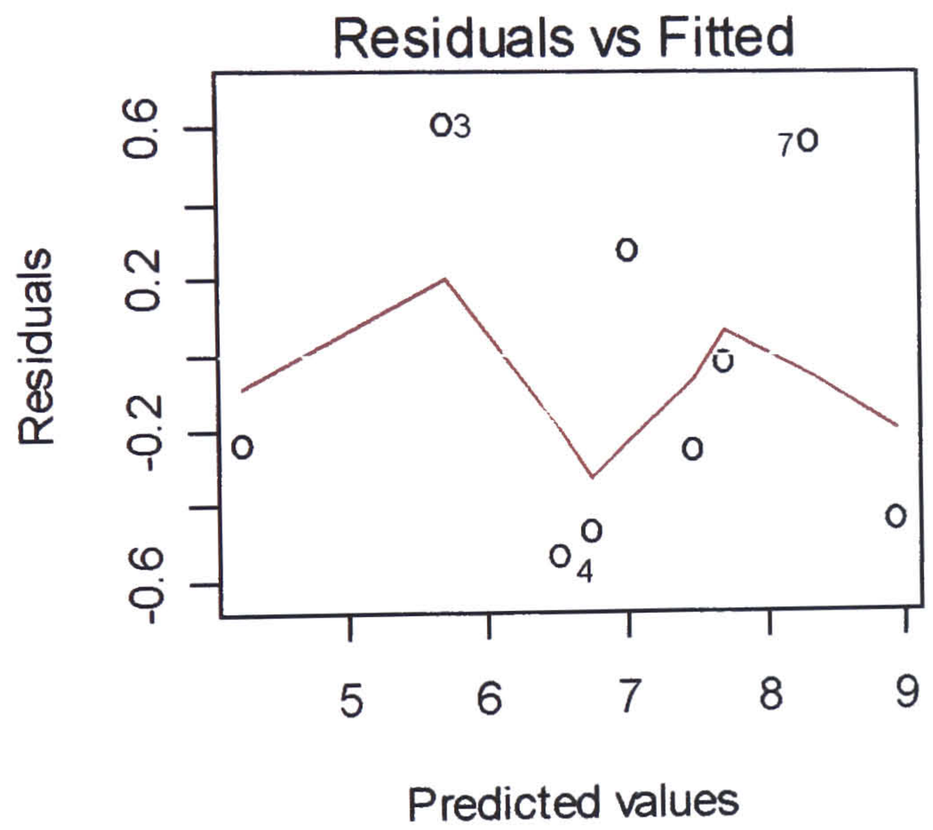


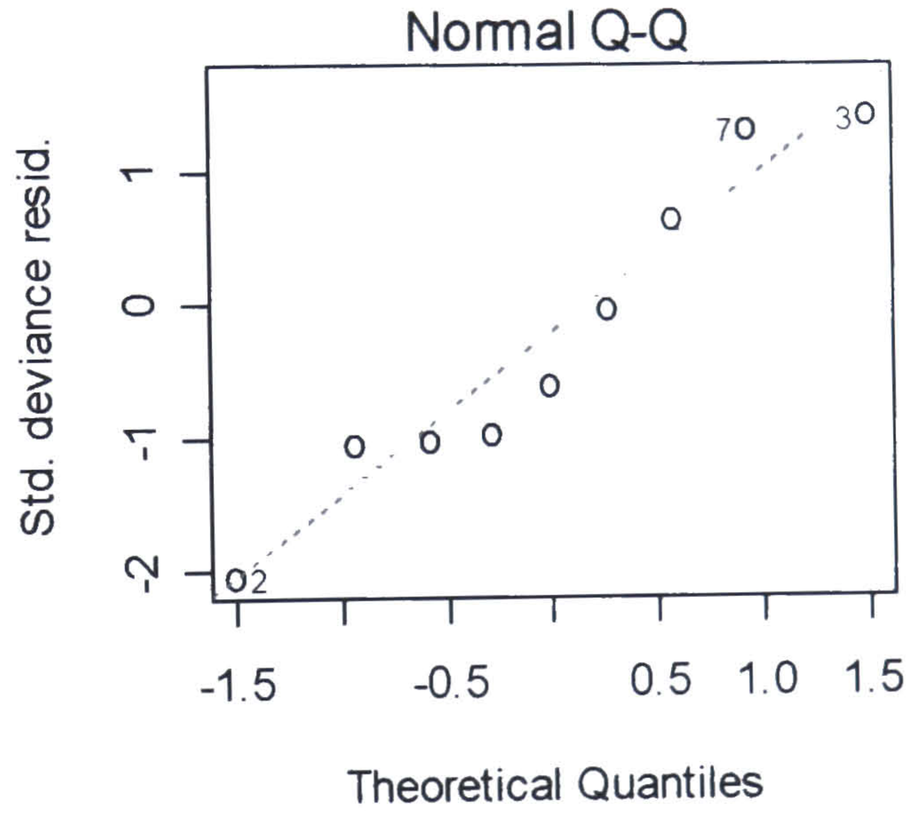


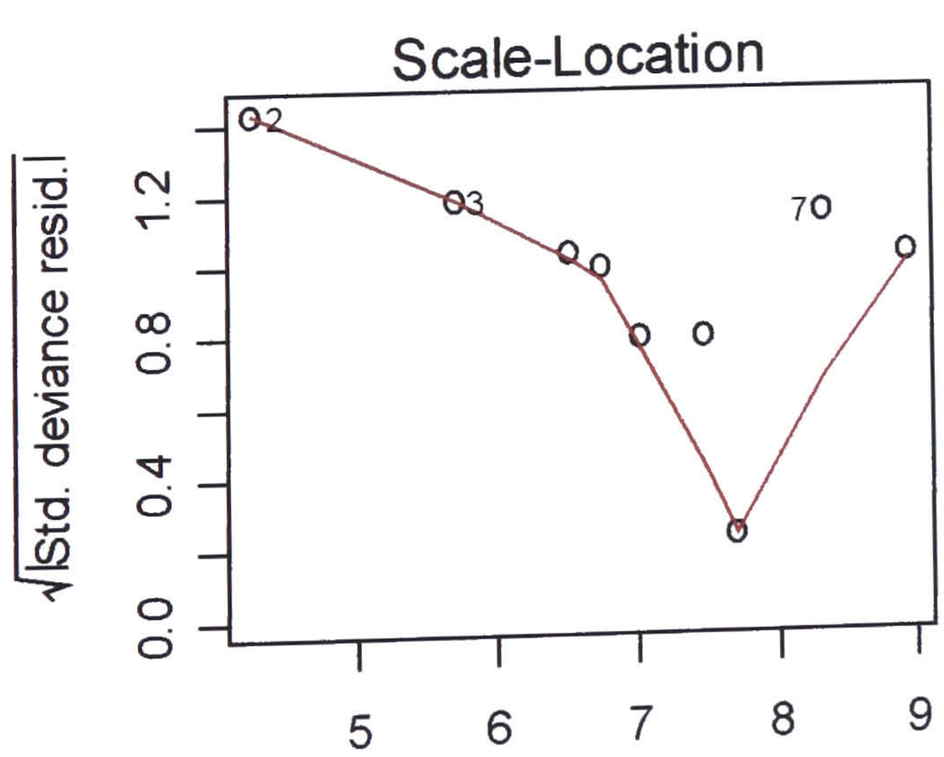


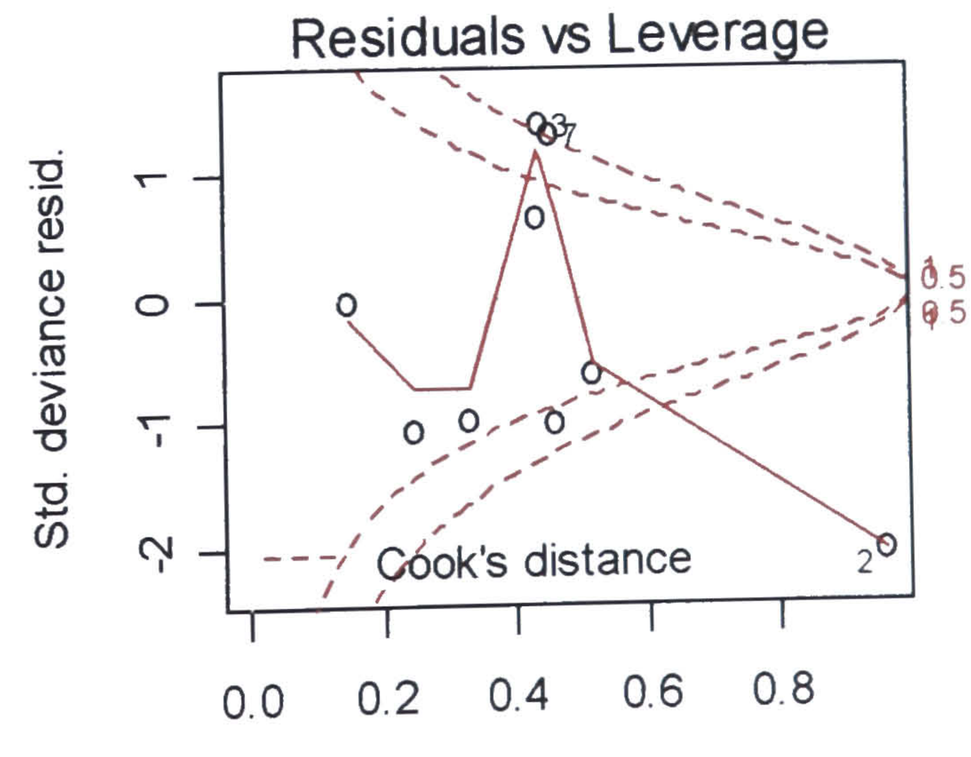
SDE Group "A2" GLM Results

```
glm(formula = sa2 ~ Ed + xTorq + O2, family = Gamma(link = log),

    data = cat)

Deviance Residuals:
      1         2         3         4         5         6         7         8         9
 0.27407  -0.24208   0.60783  -0.53807  -0.25337  -0.46981   0.56097  -0.02761  -0.44081
Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept)  7.173627   0.616236  11.641 8.22e-05 ***
Ed           0.010407   0.003782   2.752   0.0402 *
xTorq       -1.159809   0.340693  -3.404   0.0192 *
O2          -0.724615   0.175023  -4.140   0.0090 **
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
(Dispersion parameter for Gamma family taken to be 0.337674)
    Null deviance: 12.9890  on 8  degrees of freedom
Residual deviance:  1.5874  on 5  degrees of freedom
AIC: 144.13
Number of Fisher Scoring iterations: 7
```



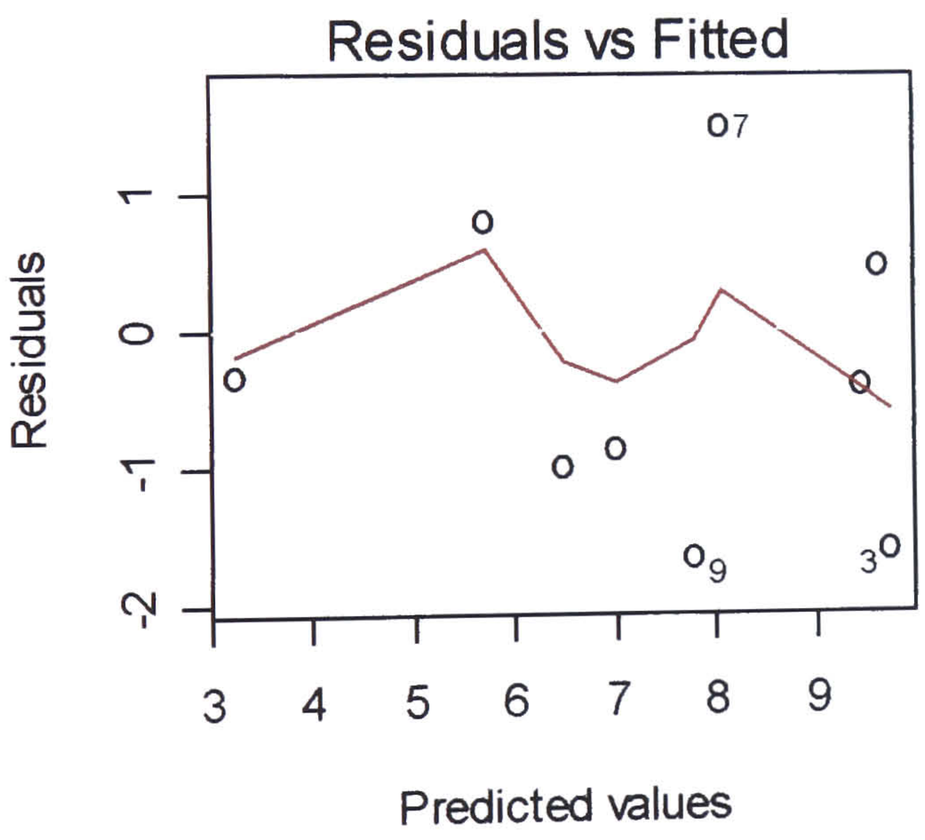


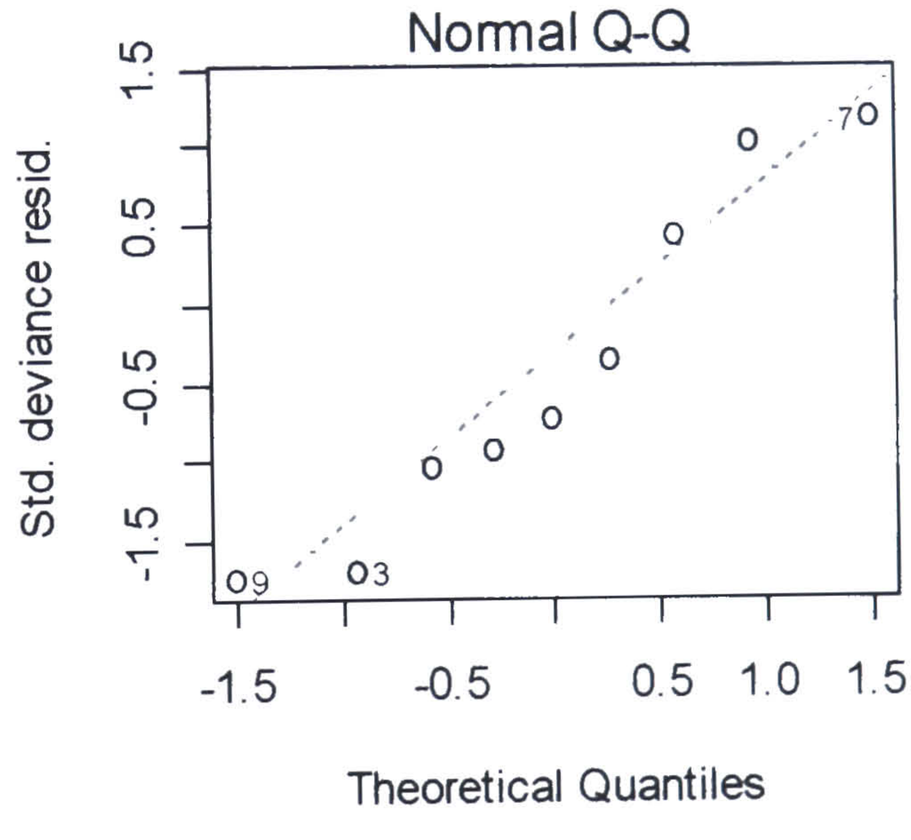


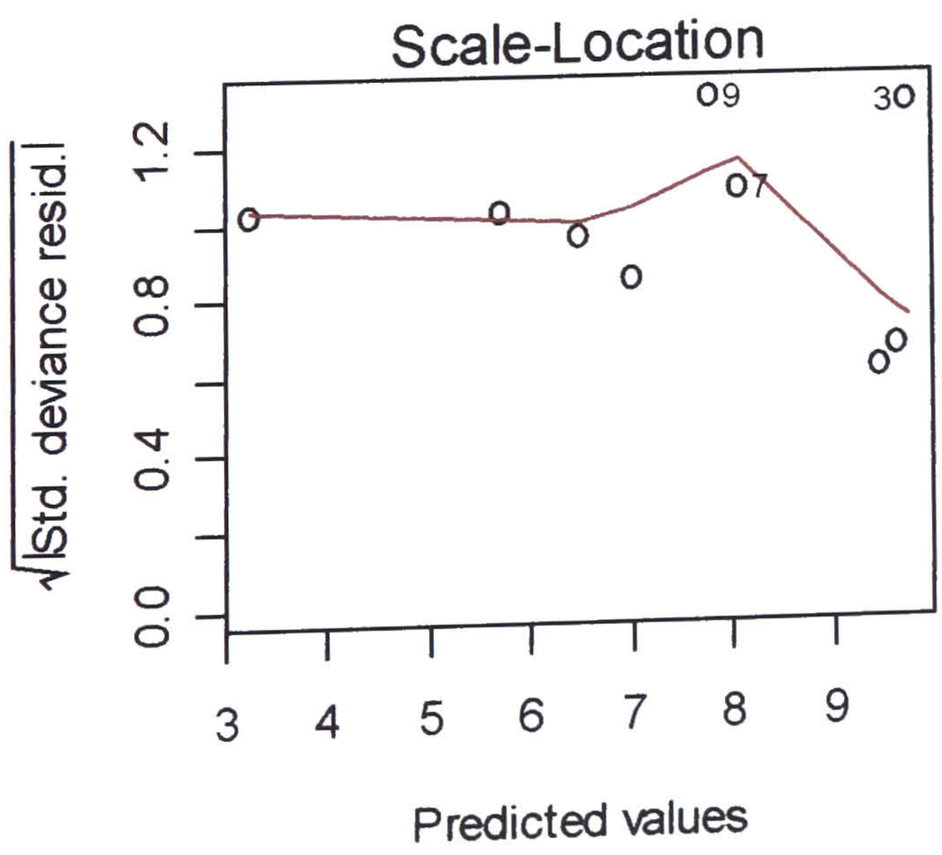


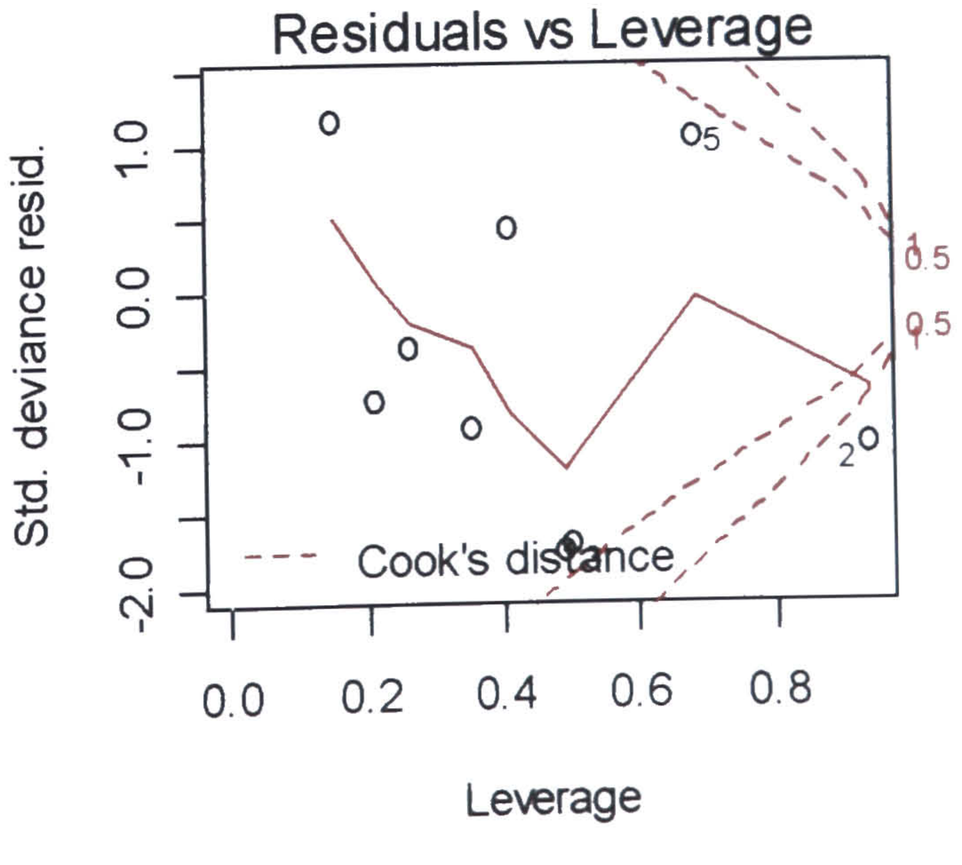
SDE Group "B1" GLM Results

```
glm(formula = B1 ~ sediment water content + mean depth of RPD + current at
10cm, family = Gamma(link = log), data = enviro)

Deviance Residuals:
      1       2       3       4       5       6       7       8
-0.8733 -0.3547 -1.6330 -0.4251  0.7937  0.4618  1.4688 -0.9997
      9
-1.6815
Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept) 16.95918    3.01452   5.626  0.00246 **
water       -0.17152    0.08471  -2.025  0.09877 .
O2          -0.44568    0.53282  -0.836  0.44103
cur10cm     -0.48978    3.99353  -0.123  0.90717

Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
(Dispersion parameter for Gamma family taken to be 1.83351)

    Null deviance: 29.744  on 8  degrees of freedom
Residual deviance: 10.563  on 5  degrees of freedom
AIC: 162.33
```



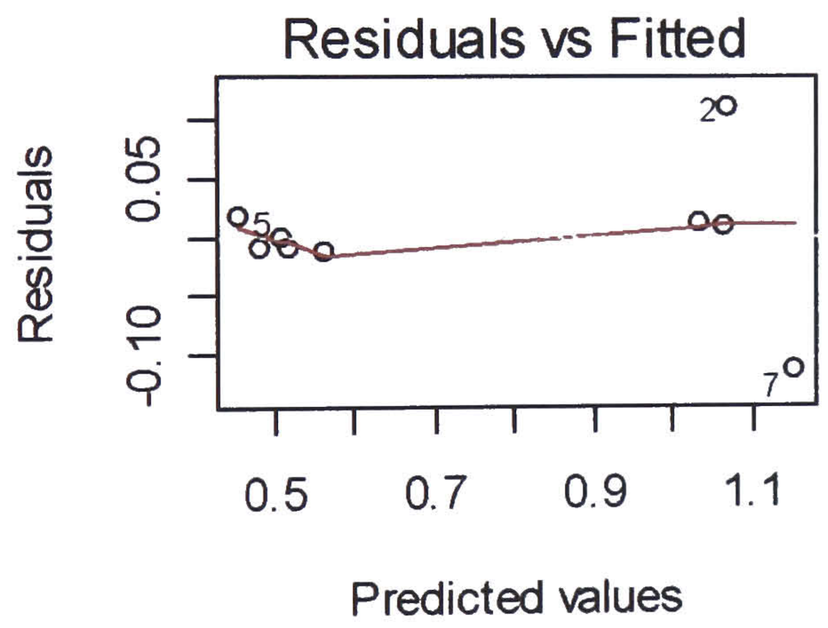


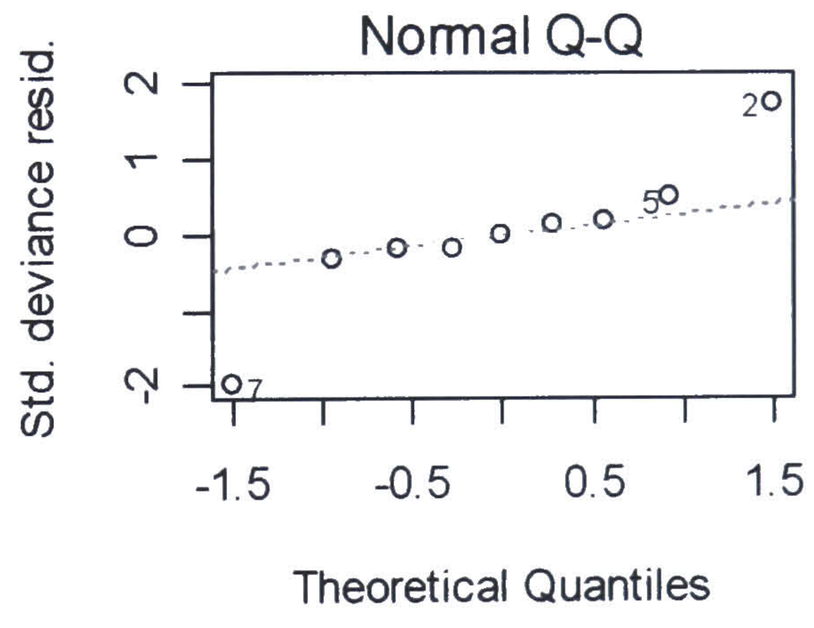


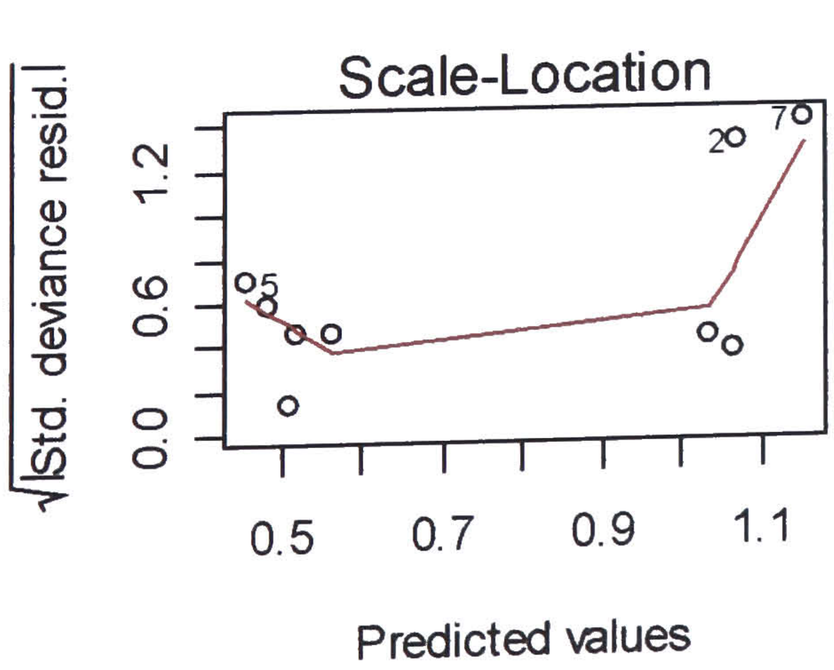


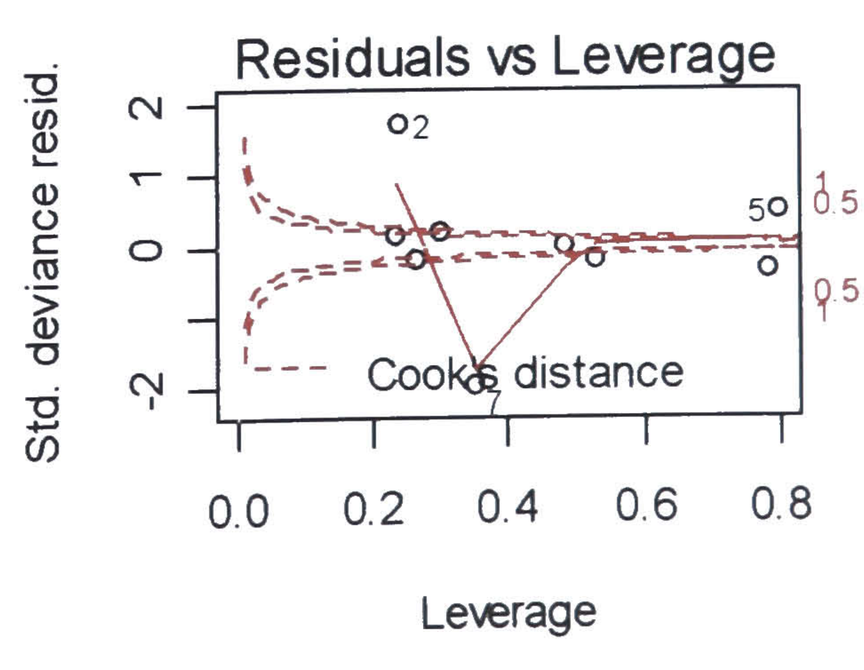
SDE Group "B2" GLM Results

```
glm(formula = sb2 ~ rate + O7 + cur10cm, family = Gamma(link = log))

### rate=erosion rate, O7= mean burrow depth, cur10cm = current flow at 10cm above
sediment

Deviance Residuals:
       1        2        3        4        5        6        7
-0.0102018  0.1076914 -0.0008174 -0.0123801  0.0153216 -0.0113776 -0.1150790
       8        9
 0.0075777  0.0107287

Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept)  5.830e-01  8.074e-02   7.221 0.000795 ***
rate        -1.368e+02  3.085e+01  -4.435 0.006797 **
O7           4.465e-03  6.130e-04   7.284 0.000763 ***
cur10cm     -1.834e+00  2.444e-01  -7.506 0.000664 ***

Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
(Dispersion parameter for Gamma family taken to be 0.00510083)
    Null deviance: 0.777910  on 8  degrees of freedom
Residual deviance: 0.025635  on 5  degrees of freedom
AIC: -3.5246
Number of Fisher Scoring iterations: 4
```



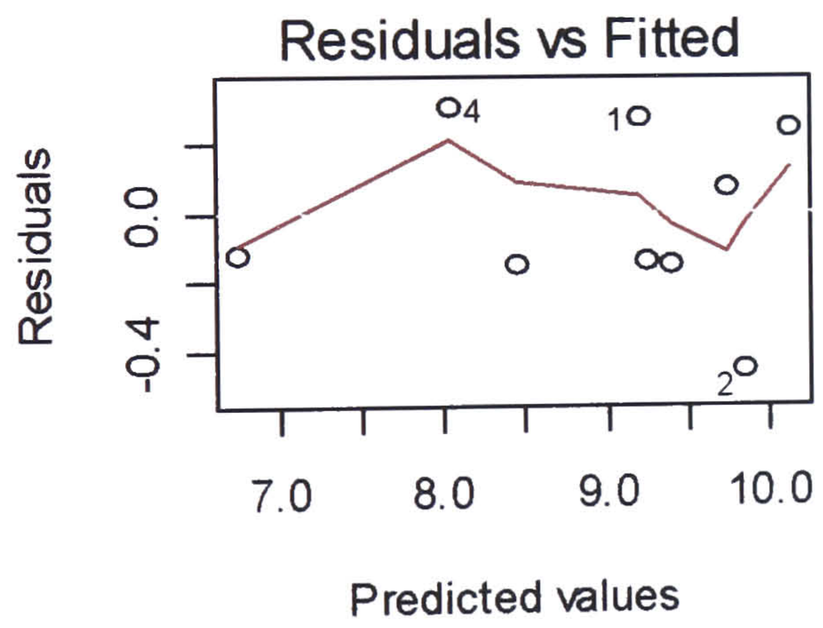


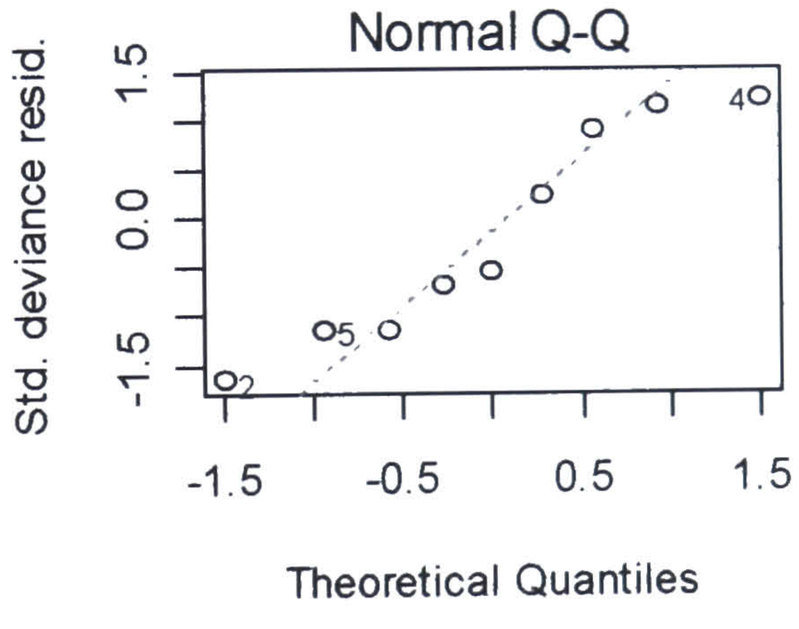


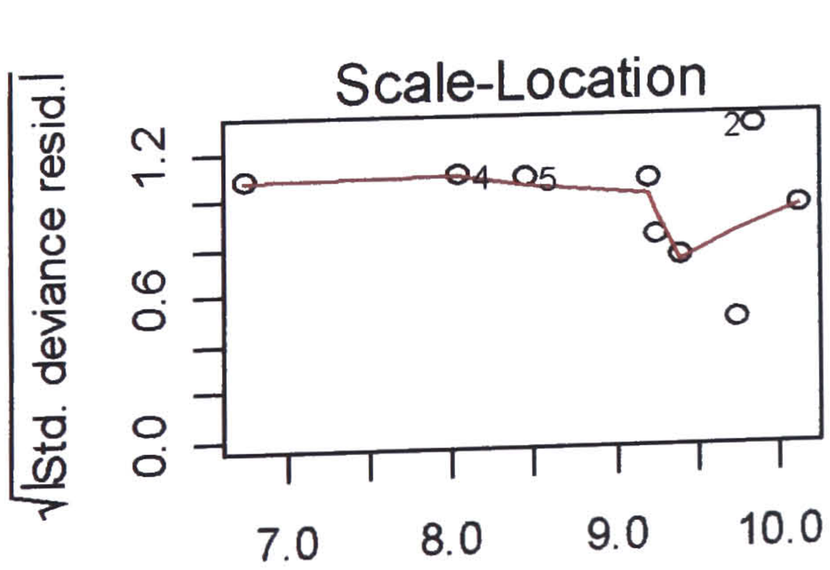


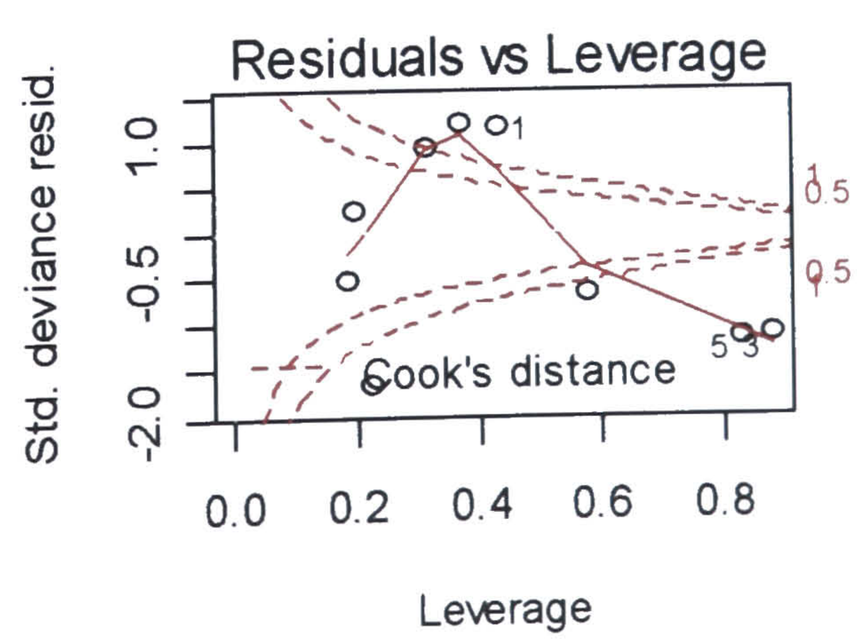
SDE group shallow "C1" GLM results

```
glm(formula = sc1 ~ cur10cm + Ed + rate, family = Gamma(link = log),
    data = enviro)

### cur10cm = current flow at 10cm above sediment, Ed = EPS,  rate=erosion rate


Deviance Residuals:
       1         2         3         4         5         6         7         8
 0.27008  -0.46345  -0.12771   0.29920  -0.15264  -0.14099  -0.15586   0.06293
       9
 0.23649

Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept)   8.76398    0.26921  32.555 5.14e-07 ***
cur10cm      -8.73512    1.05805  -8.256 0.000425 ***
Ed            0.01257    0.00190   6.618 0.001186 **
rate        -52.59653  133.89758  -0.393 0.710647
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for Gamma family taken to be 0.09938091)

    Null deviance: 6.97438  on 8  degrees of freedom
Residual deviance: 0.52092  on 5  degrees of freedom
AIC: 171.12

Number of Fisher Scoring iterations: 5
```



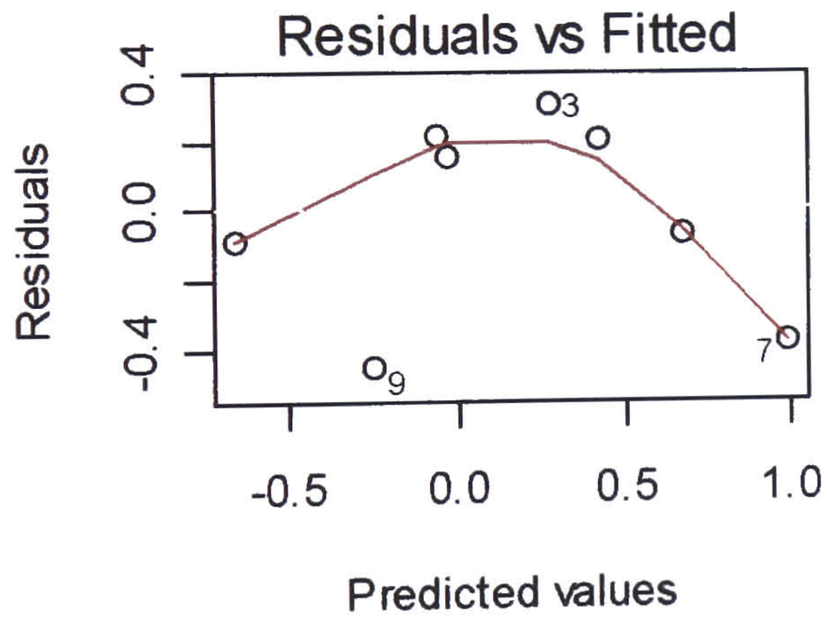


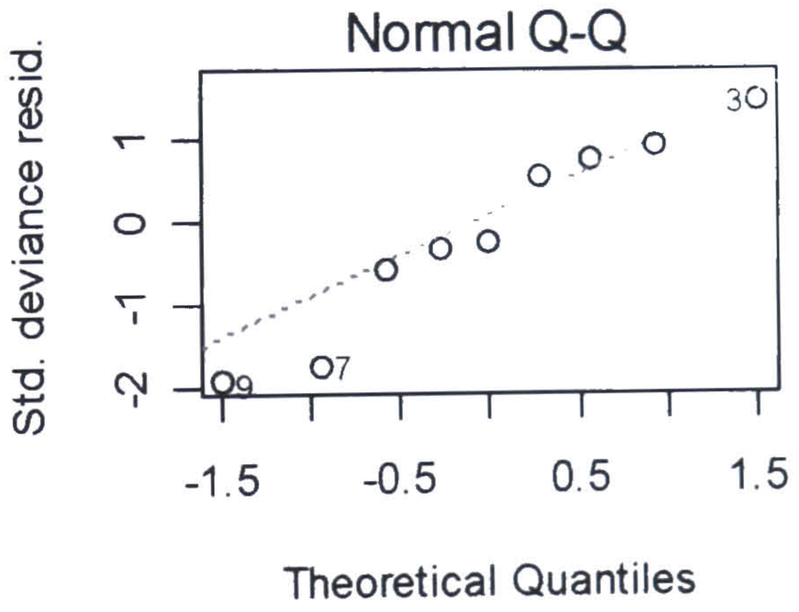


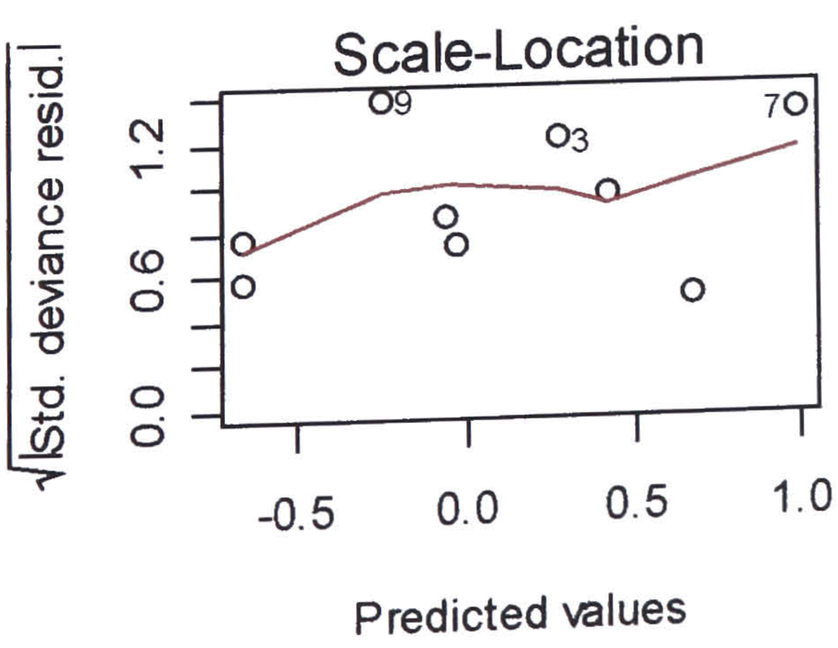


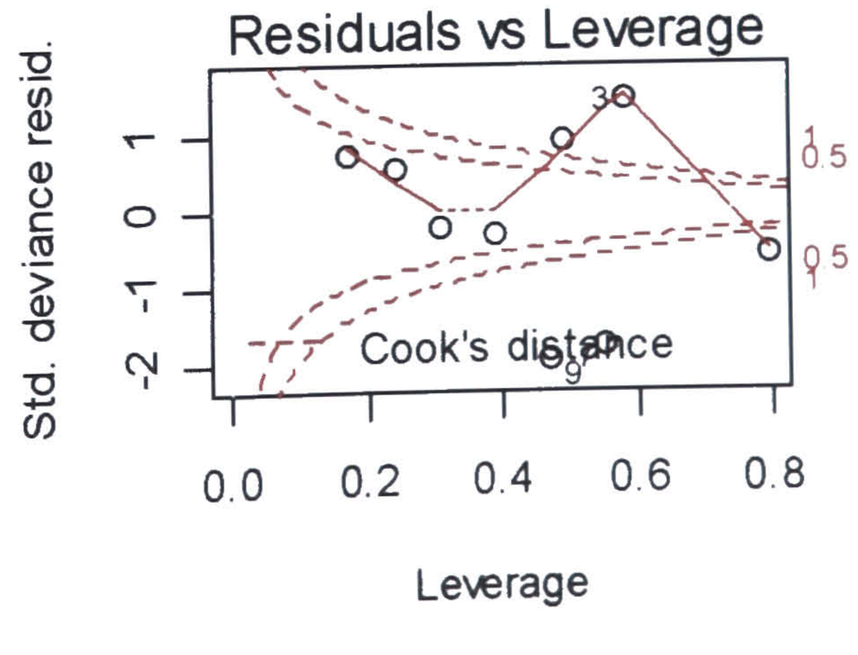
SDE group shallow "C2" GLM results

```
glm(formula = sc2 ~ fines + O2 + xsal, family = Gamma(link = log))

### fines= % sediment particles<63µ, O2= mean depth of RPD, xsal=interstitial salinity.

Residuals:
Deviance Residuals:
      1       2       3       4       5       6       7       8       9
-0.08409 -0.08797  0.30608  0.20926  0.15435 -0.06781 -0.37890  0.21667 -0.45824

Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept) -1.672e+00  9.638e-01  -1.735   0.1433
fines       -4.416e-02  1.404e-02  -3.146   0.0255 *
O2           4.328e-01  1.921e-01   2.253   0.0740 .
xsal         7.672e-05  2.116e-05   3.625   0.0151 *
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for Gamma family taken to be 0.1053899)
    Null deviance: 2.7027  on 8  degrees of freedom
Residual deviance: 0.5812  on 5  degrees of freedom
AIC: 11.806
Number of Fisher Scoring iterations: 6
```



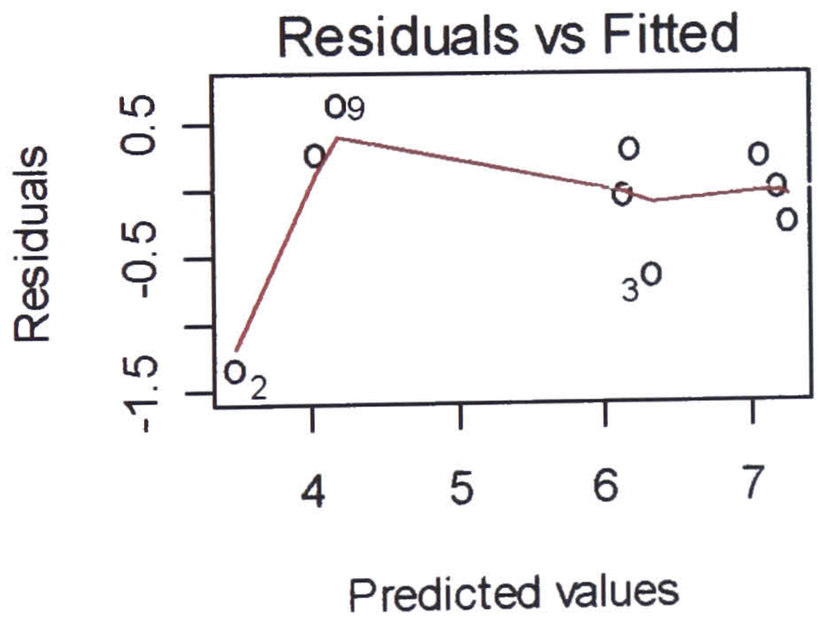


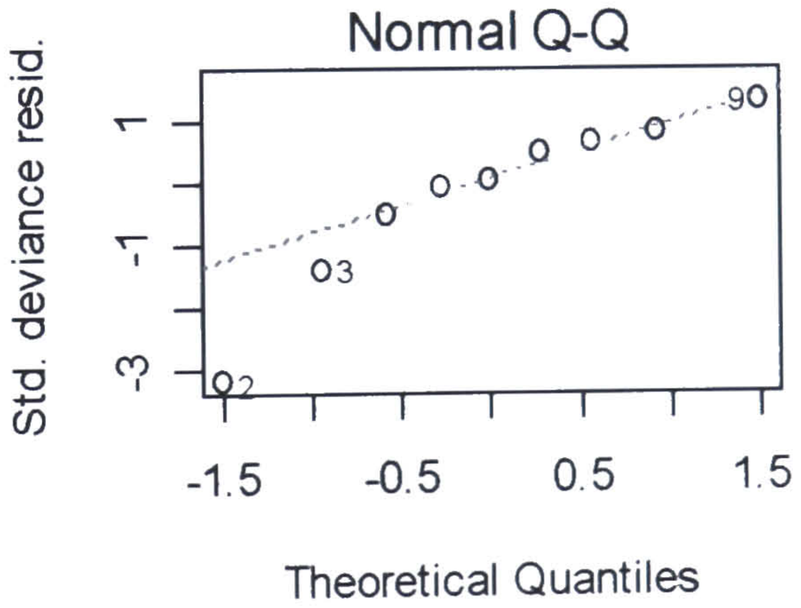


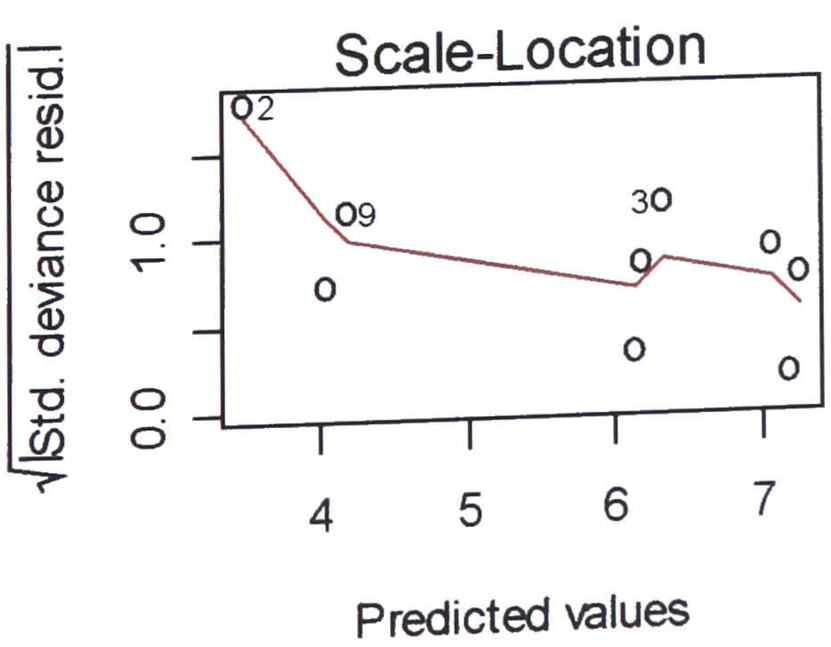


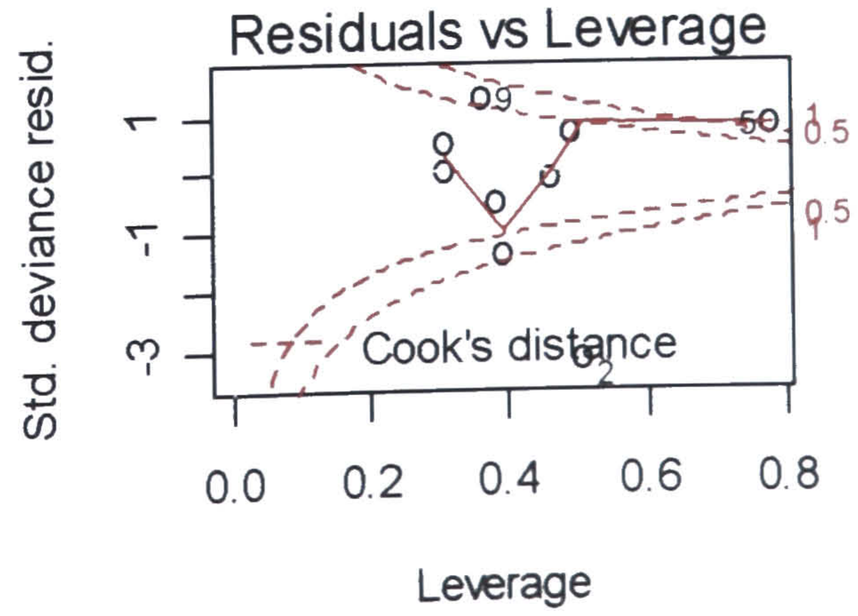
SDE group shallow "C3" GLM results

```
glm(formula = sc3 ~ water + rate + Cd, family = Gamma(link = log),
    data = enviro)

### water=sediment water content, rate=erosion rate, Cd=Chla concentration

Deviance Residuals:
       1         2         3         4         5         6         7         8
-0.04145  -1.36466  -0.65709  -0.25424   0.22970   0.01180   0.28695   0.25288
       9
 0.63398

Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept)  10.51716    1.30640   8.050 0.000479 ***
water        -0.15788    0.03469  -4.551 0.006104 **
rate       1133.16277  246.46502   4.598 0.005853 **
Cd            0.15379    0.05631   2.731 0.041229 *
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for Gamma family taken to be 0.3698793)
    Null deviance: 14.5579  on 8  degrees of freedom
Residual deviance:  2.9616  on 5  degrees of freedom
AIC: 126.96
Number of Fisher Scoring iterations: 11
```



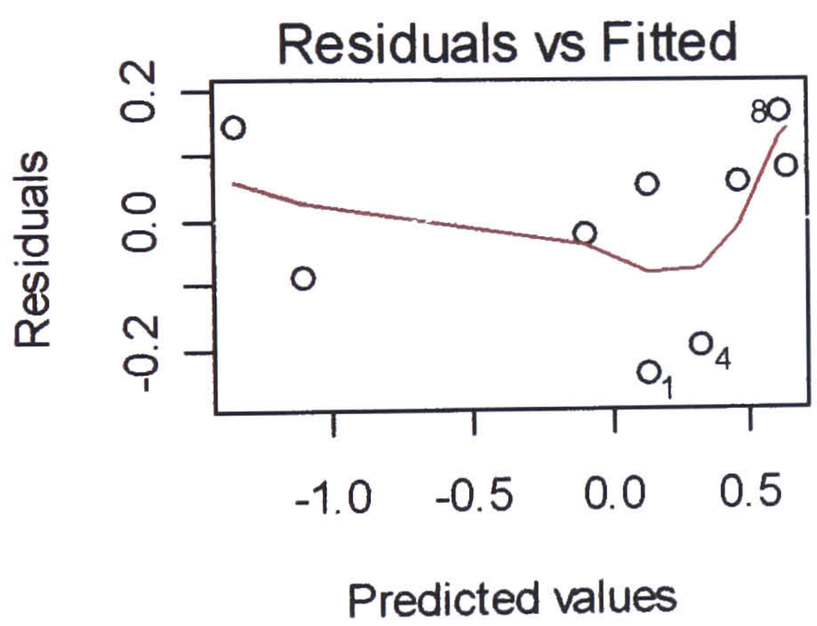


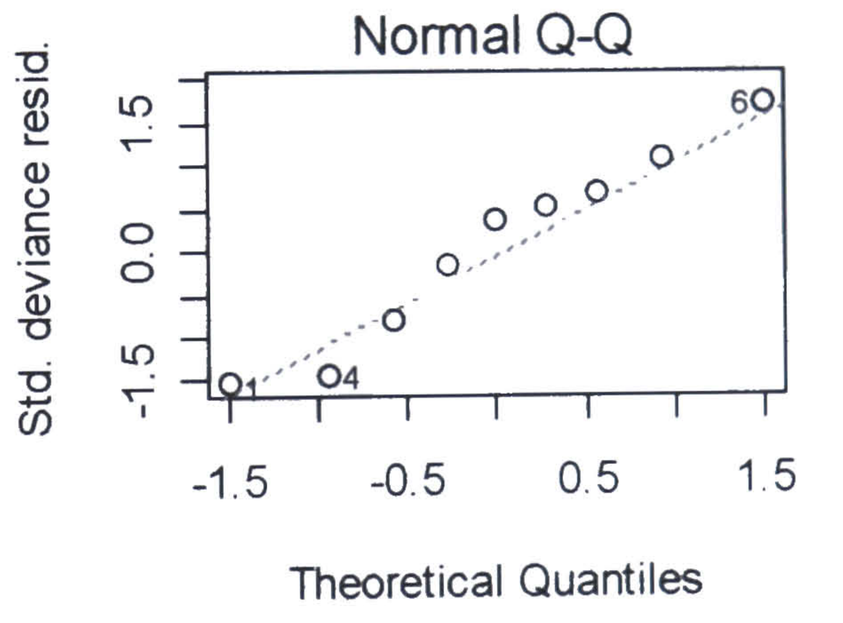


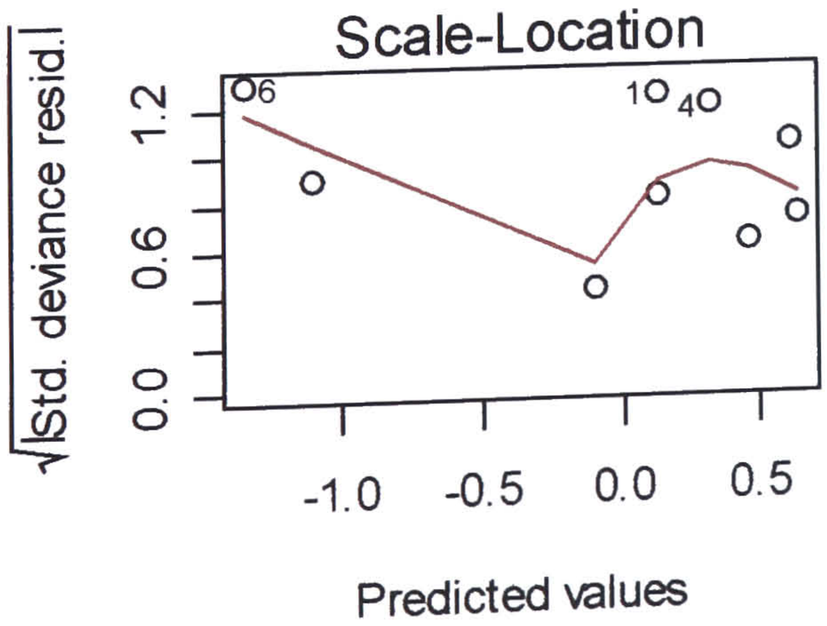


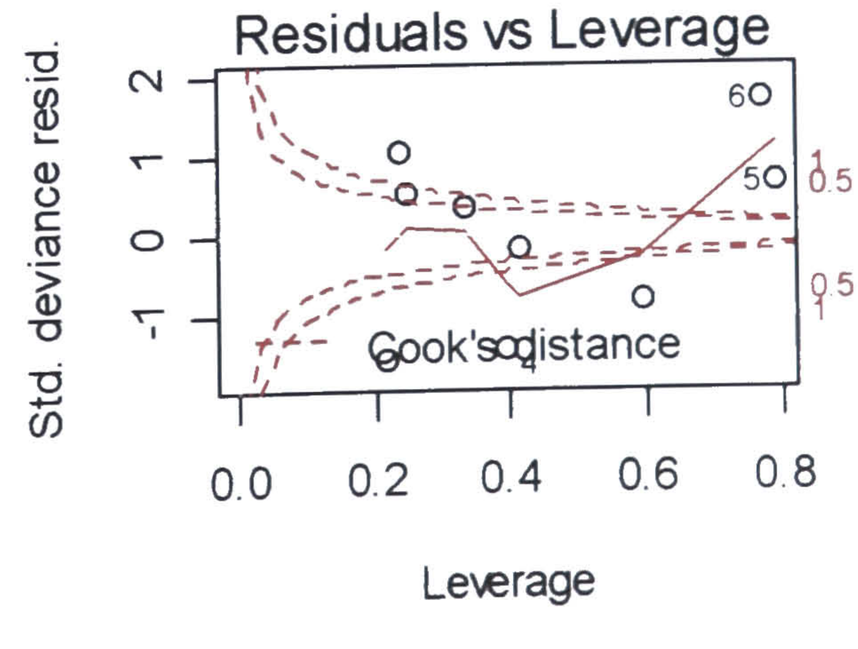
SDE group "3e" GLM results

```
glm(formula = X3e ~ fines + rate + O7, family = Gamma(link = log))

Deviance Residuals:

      1         2         3         4         5         6         7         8         9

-0.24175   0.07897  -0.09074  -0.19653   0.05355   0.14499  -0.02322   0.16482   0.05496

Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept) -2.611e+00  2.671e-01  -9.773 0.000191 ***
fines        6.263e-02  6.843e-03   9.153 0.000261 ***
rate        -3.924e+02  7.180e+01  -5.464 0.002793 **
O7           3.313e-03  1.420e-03   2.333 0.066941 .
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
(Dispersion parameter for Gamma family taken to be 0.03155026)
    Null deviance: 3.60200  on 8  degrees of freedom
Residual deviance: 0.16616  on 5  degrees of freedom
AIC: -1.0326
Number of Fisher Scoring iterations: 5
```



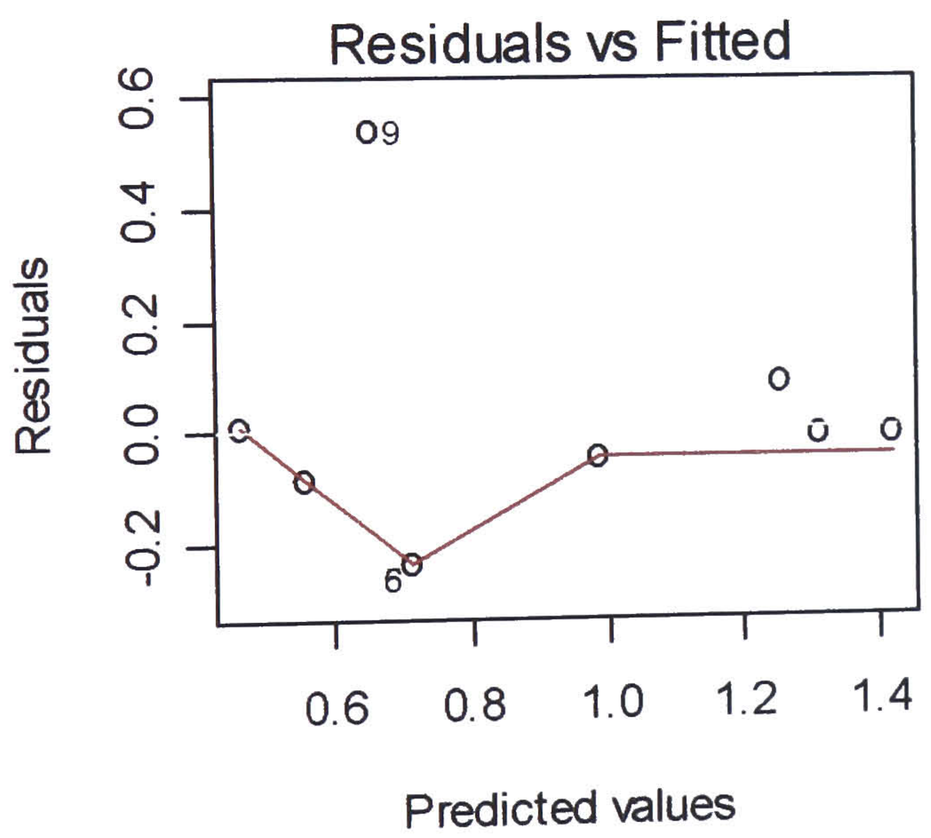


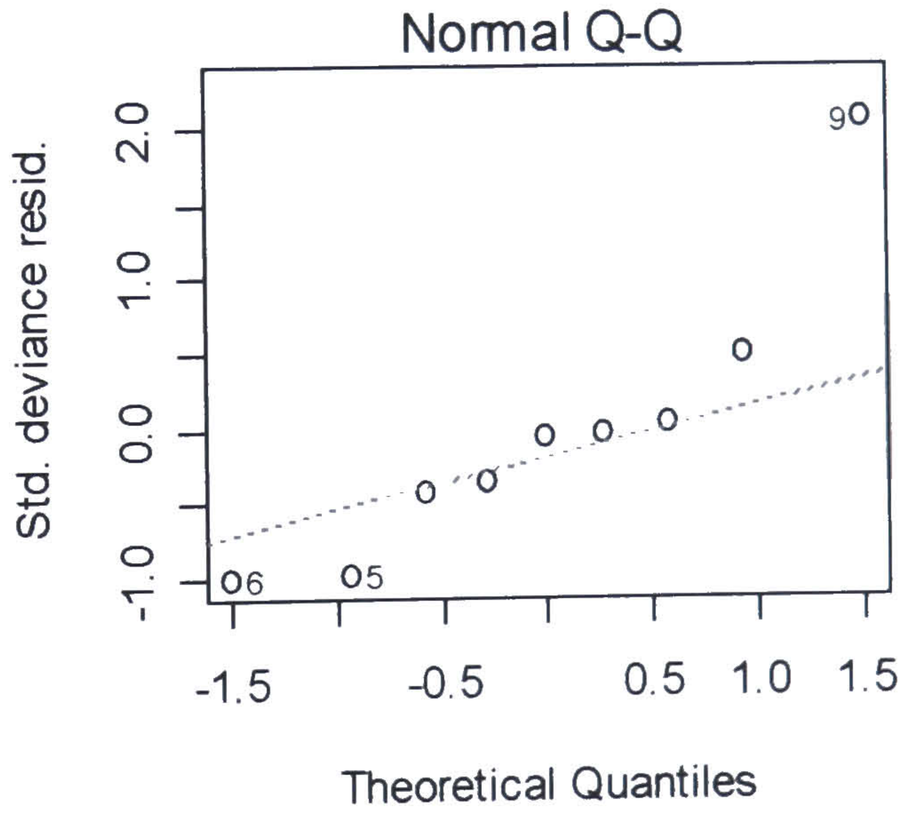


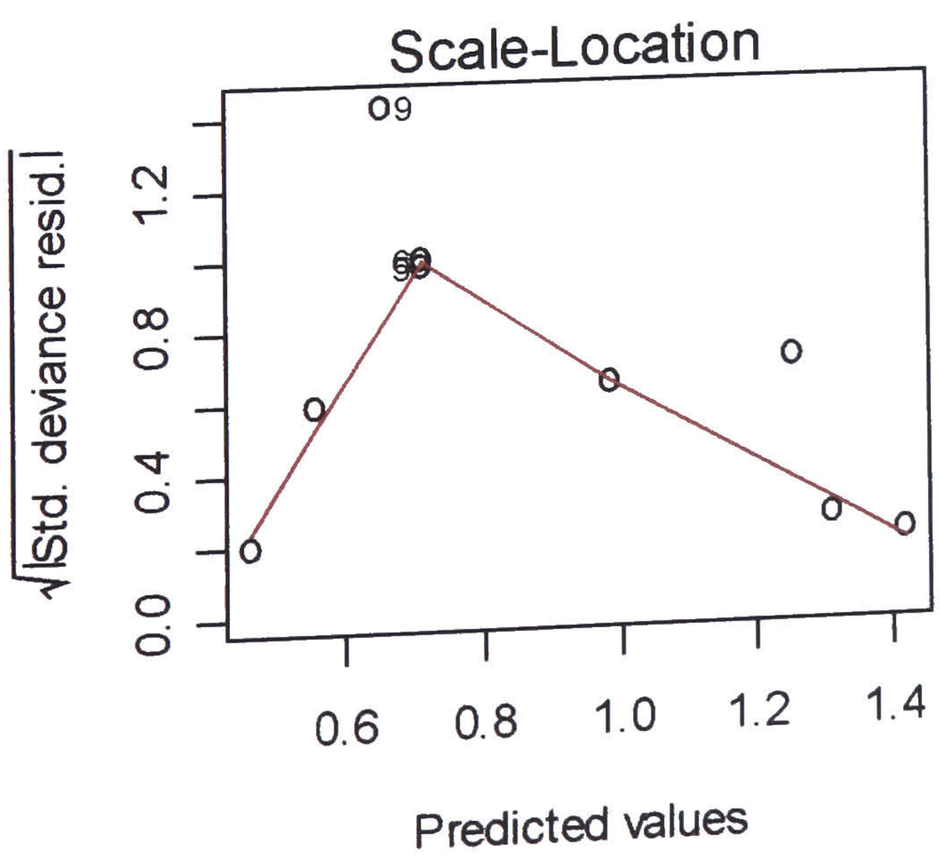


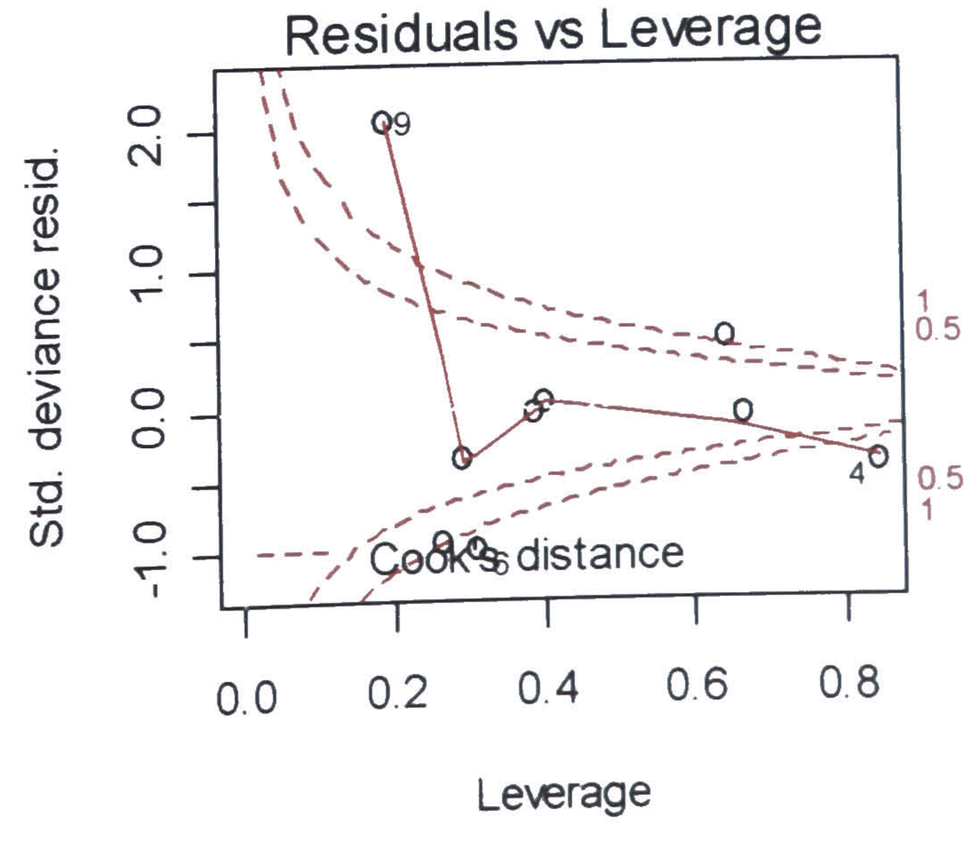
SDE group "5a" GLM results

```
glm(formula = X5a ~ fines + xsal + water)

Deviance Residuals:
       1         2         3         4         5         6         7
-0.008517 -0.010524  0.085072 -0.047300 -0.239020 -0.239471  0.008937
       8         9
-0.084510  0.535332

Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept)  3.372e+00  8.895e-01   3.791   0.0127 *
fines        2.285e-02  1.446e-02   1.580   0.1750
xsal        -4.096e-05  1.193e-05  -3.433   0.0186 *
water       -4.929e-02  2.034e-02  -2.423   0.0599 .
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
(Dispersion parameter for gaussian family taken to be 0.08358746)
    Null deviance: 1.41488  on 8  degrees of freedom
Residual deviance: 0.41794  on 5  degrees of freedom

AIC: 7.914
Number of Fisher Scoring iterations: 2
> plot(glmd5a)
```



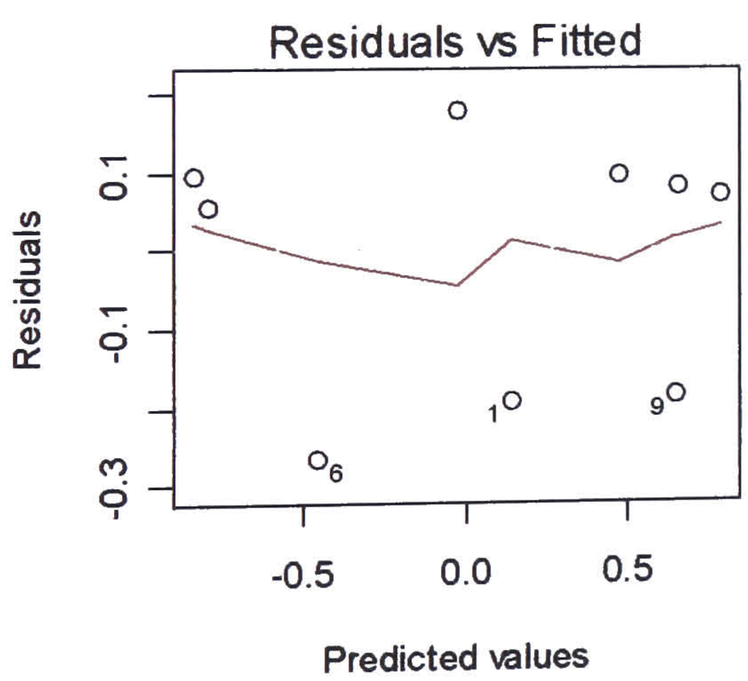


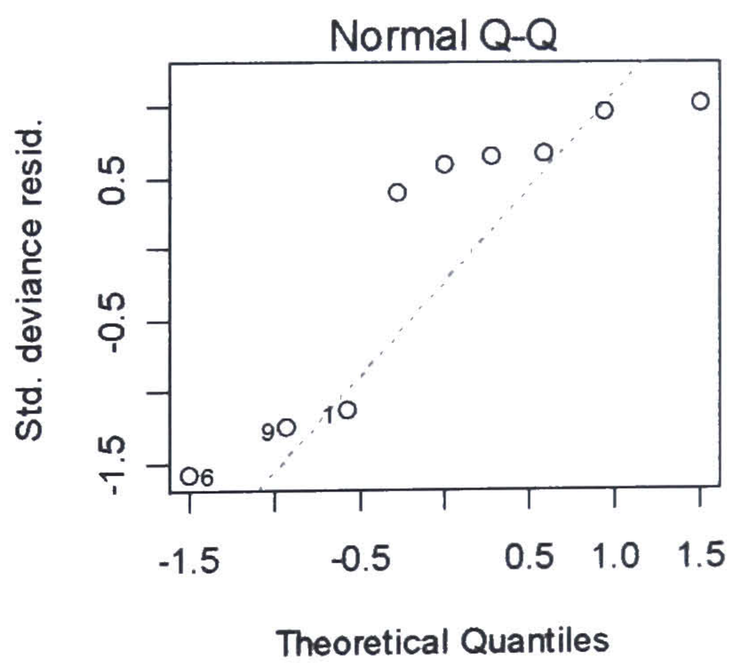


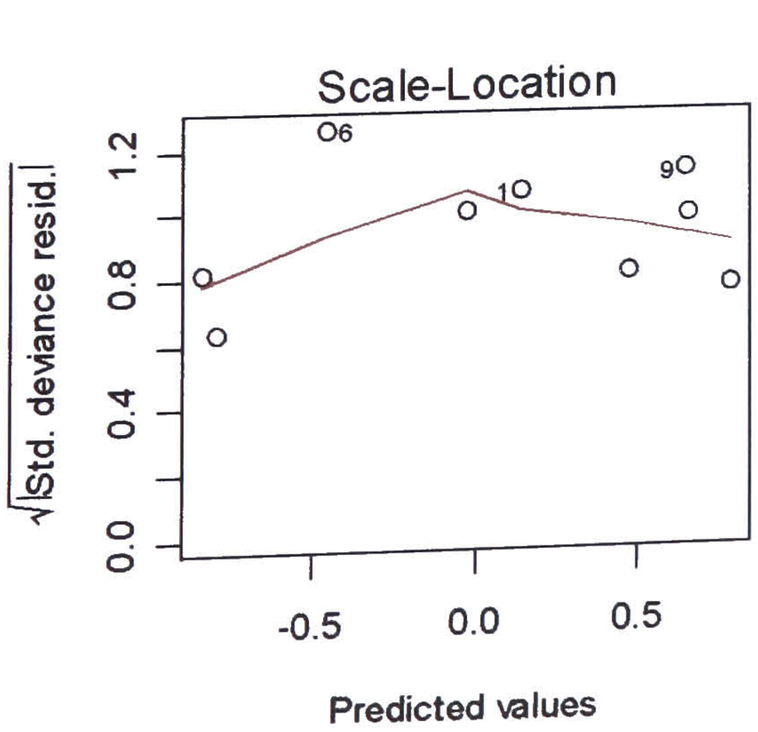


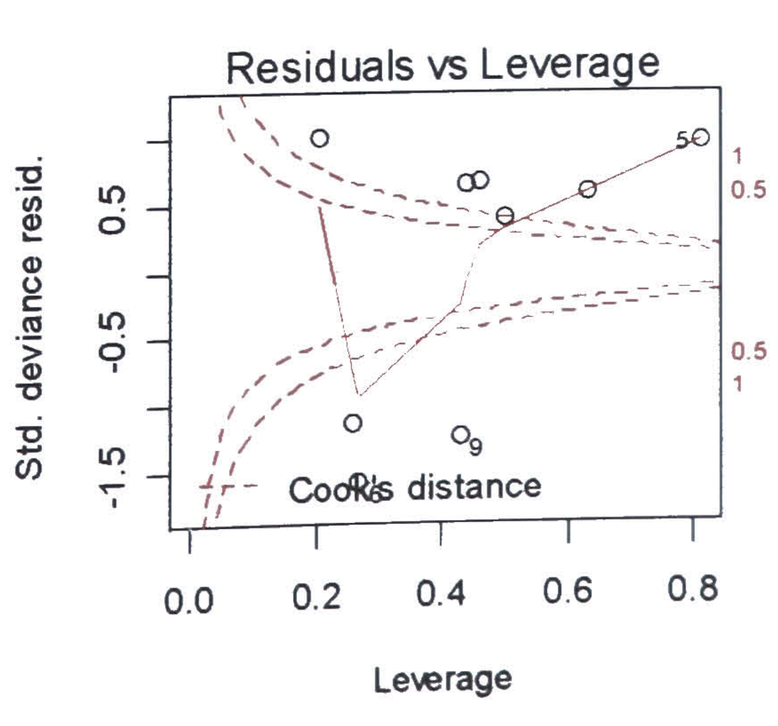
SDE group "5b" GLM results

```
Call:
glm(formula = X5b ~ xsal + xTorq + rate, family = Gamma(link = log))
Deviance Residuals:
       1        2        3        4        5        6        7        8
-0.19426  0.07077  0.05594  0.09642  0.08296 -0.26806  0.09663  0.17848
       9
-0.18835

Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept)  3.412e-01  1.631e-01   2.092 0.090725 .
xsal        -5.505e-05  7.389e-06  -7.449 0.000688 ***
xTorq       -1.197e+00  1.466e-01  -8.168 0.000447 ***
rate         4.538e+02  1.061e+02   4.276 0.007894 **
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for Gamma family taken to be 0.03912305)

    Null deviance: 3.16824  on 8  degrees of freedom
Residual deviance: 0.21057  on 5  degrees of freedom
AIC: 2.7495

Number of Fisher Scoring iterations: 4
```



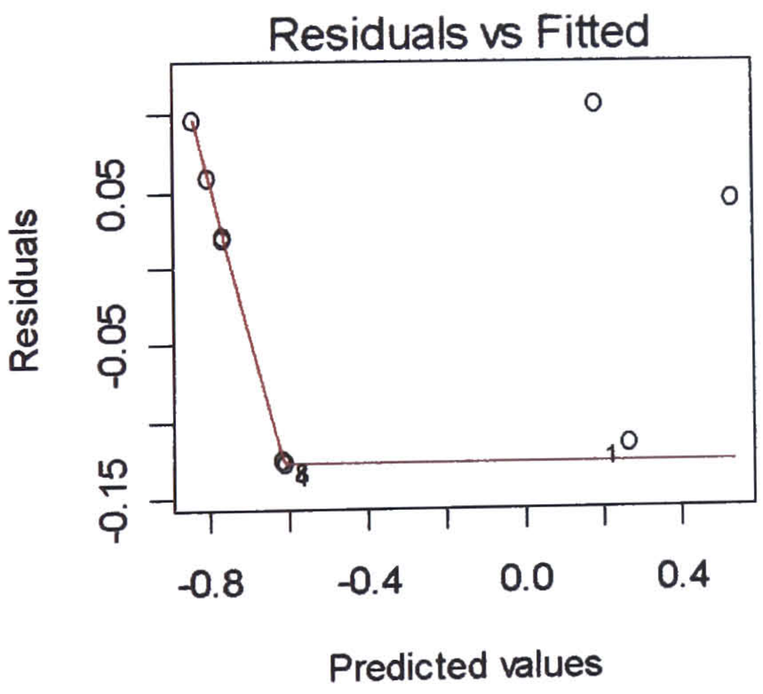


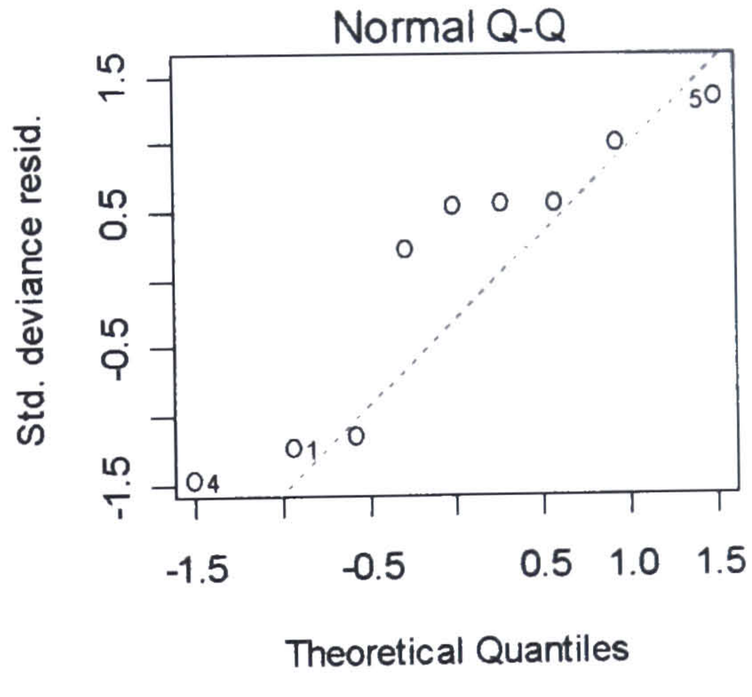


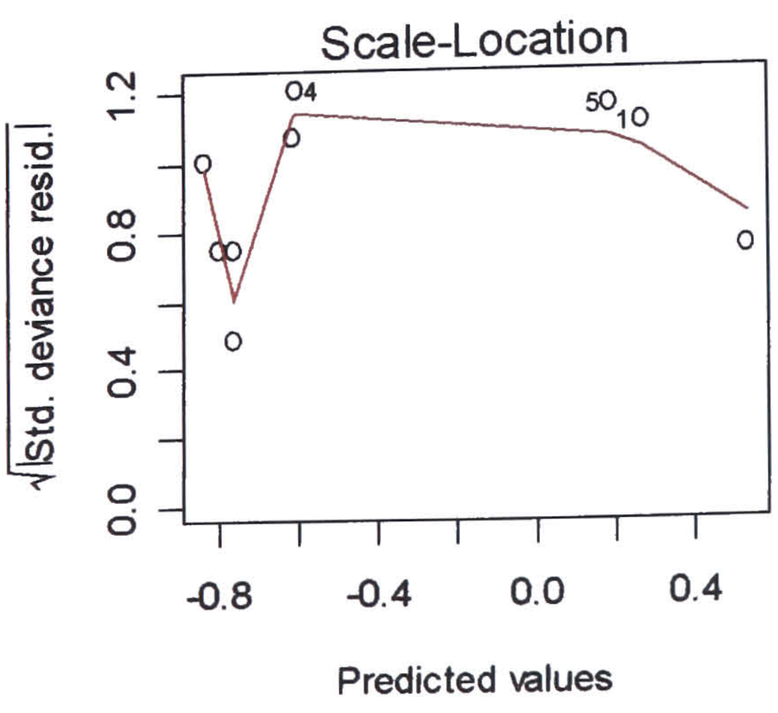


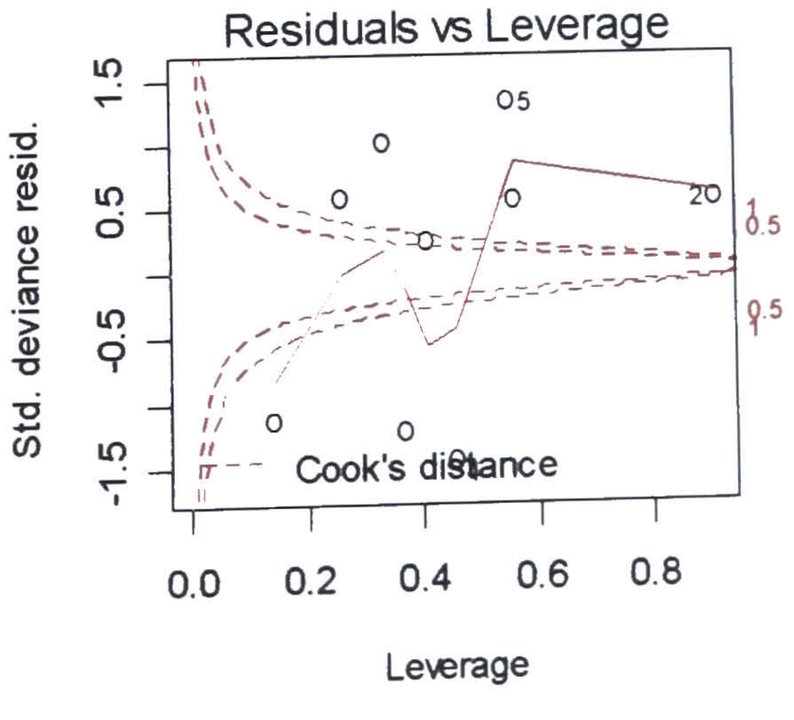
SDE Group "5d" GLM

```
Call:
glm(formula = X5d ~ xsal + O2 + cur10cm, family = Gamma(link = log))

Deviance Residuals:
       1         2         3         4         5         6         7         8
-0.11594   0.01983   0.04296  -0.12752   0.10585   0.09721   0.05816  -0.12601
       9
 0.02144

Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept)  8.855e-01  3.551e-01   2.493 0.054941 .
xsal        -3.391e-05  6.461e-06  -5.249 0.003329 **
O2          -2.936e-01  5.582e-02  -5.259 0.003300 **
cur10cm      3.685e+00  3.303e-01  11.156 0.000101 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for Gamma family taken to be 0.01406297)
    Null deviance: 2.673734  on 8  degrees of freedom
Residual deviance: 0.072317  on 5  degrees of freedom
AIC: -14.720
Number of Fisher Scoring iterations: 4
```









Hydrobiologia (2007) 588:45–58
DOI 10.1007/s10750-007-0651-4

ECSA38

Can functional groups be used to indicate estuarine ecological status?

Jeanette L. Sanders · Mike A. Kendall · Anthony J. S. Hawkins · John I. Spicer

Abstract International legislation demands that statutory bodies report on the health of aquatic ecosystems. Traditionally, ecosystem components have been characterised according to species assemblages but with limited success in predicting health. On the other hand, many studies based upon functional groupings that include trophic relationships and bioturbation potential have shown response to pollution. However, these and other functional group responses have not yet been linked to broad scale physical variables. To date this has hindered the development of a predictive model of function based on abiotic factors. In addition, most functional studies ignore any potential role of body size when assessing the importance of each species to overall functional group measures. By weighting all species that belong to the same guild equally, the investigator risks overestimating the true importance of any one guild to the environment. This study compared the ability of different functional group approaches to discriminate between separate estuarine sites, whilst linking biotic data with abiotic factors. Using data for the Tamar Estuary, we show that no two methods of classifying the biotic data, according to function, produce the same groupings of sites; nor did any method produce groupings that matched clusters based on abiotic factors alone. Instead, results show that not only can choice of functional method alter our perception of site associations but also, can influence the strength of similarity relationships between abiotic and biotic datasets. Both the use of bioturbation measures and weighting species abundance data by body size provided better relationships between biotic and abiotic data than the use of trophic groups. Thus both methods merit further research to produce algorithms for modelling studies.

Keywords Function · Macrobenthos · Bioturbation · Body size · Tamar

Guest editors: R. Lafite, J. Garnier & V. De Jonge
Consequences of estuarine management on hydrodynamics and ecological functioning

J. L. Sanders (✉) · M. A. Kendall · A. J. S. Hawkins
Plymouth Marine Laboratory, Prospect Place, The Hoe, Plymouth PL1 3DH, UK
e-mail: jesa@pml.ac.uk

J. L. Sanders · J. I. Spicer
Department of Biological Sciences, The University of Plymouth, Drake Circus, Plymouth PL4 8AA, UK

Introduction

There is increasing awareness that anthropogenic effects can have lasting impacts upon our environment (Carson, 1962; Wiesner, 1995; Wright, 2000; Levin et al., 2001). This has led to various

initiatives to develop ways of quantifying impacts of human activities upon ecosystem status (Gergel et al., 2002). There have been studies on the use of sentinel species (the "bioindicator" approach of Hilty & Merenlender, 2000), attempts to measure water and air quality to determine their suitability for sustaining life (Mattiessen & Law, 2002), as well as modelling studies that attempt to predict species assemblages (Emlen, 2003).

Environmental managers seek methods, which are not specific to one location or time and which are cheap and easy to both apply and interpret. This has often led to a search for a set of broad scale physical parameters that will predict an expected community assemblage in the absence of anthropogenic influences (Wright, 2000; Skriver, 2001; Austin, 2002). Theoretically, this would then allow interpretation of the presence or absence of community members in terms of ecosystem health. Many countries and international bodies are introducing legislation that places a legal requirement upon signatories to define such "reference conditions" (Simboura & Zenetos, 2002). One example is the European Water Framework Directive (Directive 2000/60/EC), which stipulates that ecological quality will be decided according to the relationship between observed biological parameters and the relevant reference conditions.

Definition of reference conditions for estuarine waters is proving problematic, as is the prediction of the associated macrobenthic assemblages (A. Prior, Personal Communication). Estuaries are naturally stressful environments for organisms to inhabit, due to the range of hydrodynamic and chemical conditions that can prevail (Ysebaert et al., 2002). Approaches based upon predictive modelling often fail at the initial attempt to predict the community assemblage (Hols, 1996). One principal reason for this failure is insufficiently robust relationships between broad-scale, physical parameters and species distributions (Attrill et al., 1999; Austen, 2002; Emlen et al., 2003). For example, the lack of a mathematical, hydrodynamic model prevented Warwick et al. (1991) from making specific predictions of species distributions in response to proposed changes to the physical environment of the Severn Estuary. Failure to develop models may also be due to the large range of biotic variation found, both spatially and temporally, within and between estuaries (Platell & Potter, 1996; Hagberg et al., 2003).

There have been some successful attempts to model estuarine species distribution patterns, as predicted by abiotic variables (Ysebaert et al., 2002; Attrill, 2002). The most notable feature of such attempts is the vast amount of fine-scale biotic and abiotic data that are required to produce predictions. For example, Attrill (2002) successfully used "mean salinity range" as a predictor of alpha diversity in the Thames estuary, but the salinity values were predictions from an estuary-specific model of salinity. In a similar way, the logistic regression employed by Ysebaert et al. (2000) also had input from estuary-specific models capable of fine-scale predictions for salinity and tidal currents. The time and effort frequently required to produce detailed hydrodynamic models deter attempts to apply this approach elsewhere (Attrill et al., 1999). Thus, although there is often general consensus as to which abiotic factors are most influential, algorithms that truly represent the relationships across all estuaries are still not available.

In an attempt to reduce the effects of variability within the biological data, some researchers have considered grouping species into functional groups, rather than analysing simple species abundance (Pianka, 1978; Pearson, 2001). This appeals to environmental managers since, from their perspective, it is not the species that is important, but the overall "status" of the ecosystem. The presence or absence of a species may not be as easy to interpret as changes in occurrence of functional groups (Pearson, 2001). However, Snelgrove and Butman (1994) stress the need to choose functional definitions with care to avoid loss of information when applying a reductionist approach.

Within the coastal and estuarine environments, examinations employing functional groups have mainly focussed on the traditional areas of trophic or bioturbatory activities (Dauwe et al., 1998). Early work by Pearson and Rosenberg (1978) demonstrated changes in trophic diversity and in the identity of the predominant group (based upon feeding and motility attributes)

along a depth gradient, as organic enrichment increased. To differentiate between coastal sites according their bioturbation "potential", Swift (1993) proposed a system of scoring species. Muzik & Elliott (2000) combined both of these approaches with work by Gerino et al. (1993), Wheatcroft et al. (1994) and Dauwe et al. (1998), to examine relationships between functional groups and sediment dynamics, along a pollution gradient. They successfully demonstrated changes in function with distance from a pollution source. None of these studies set out to quantify the relationships between changes in functional groups and either the physical environment or ecological status. Thus, whilst such studies advance our conceptual understanding of ecosystem function, they have not addressed the need for a predictive management tool to aid in the determination of "ecological status". To date, none have investigated which method provides the best match to a given set of environmental variables. Until this has been addressed, interpretation of the changes between relative abundances of each functional group remains qualitative rather than quantitative.

This present study seeks to redress this shortfall by examining how two functional groups may be linked to the physical environment. We assess how changing the way in which the biota are classified alters the match of biological and abiotic data, and the implication this has for our understanding of ecosystem health. Muzik & Elliott (2000) demonstrated that the bioturbation potential scores of Swift (1993) and trophic groups both altered with increasing pollution levels. We extend their work by examining how well each category differentiates sites along natural environmental gradients and how easily the results can be interpreted.

However, the presence or absence of a functional group may be too coarse a measure upon which to base ecosystem management decisions. We propose a more sensitive approach, measuring variation in amount of "function" to help identify more subtle fluctuations and act as an early warning indicator of change to status. Swift's method (1993) went some way to differentiating between the contributions of component species, awarding a score to each species, according to that species' ability to promote bioturbation. The score was the sum of values allocated according to three activities: burrowing, motility and feeding. This was a real attempt to place relative numeric values on bioturbatory activity, and which highlighted coastal site associations according to values of bioturbation potential. However, the system assumes that any two species with the same potential score are active at the same scale and level of intensity, i.e., they have equal potential to cause displacement of sediment particles, but no consideration is taken of how far those particles might be moved or how often. Muzik & Elliott (2000) point out that bioturbation scores could have greater ecological significance if biomass, abundance and body size were also considered.

Each species will contribute to any given function on the scale at which its activities occur (Peterson et al., 1998). Thus consideration must be given to assessing which species do in fact contribute at the scale at which the manager wishes to investigate and predict. Thayer (1983) proposed ways to calculate individual sediment disturbance rates, but in general, there is insufficient knowledge of each species' activities to apply this measure (Snelgrove & Butman, 1994). Whilst sediment turnover rates have in the past been described (Hall, 1994) no attempt has been made to use these to apportion species contribution to bioturbation. Hall (1994) showed that turnover rates do not vary greatly according to trophic group, reworking mode or sediment type classifications, and concluded that characteristics, which are specific to a species, for example body size and burrowing depth, did merit consideration.

We expand on Swift's (1993) work by weighting the relative contribution of each species to its functional group according to its body size. We apply the same approach to trophic groups and abundance data, thereby turning theoretical grouping according to function into a more integrated measure of functional performance. Under such a scheme, where two species contribute to a single function at similar levels of activity, then greater ecological importance would be accorded to the larger species.

Thus, in this study, our aim has been to determine which functional group approach

provides the best correlations with abiotic data, and how such relationships are influenced by introducing body size weightings to the calculations of overall function.

The null hypotheses are:

(1) The way in which the biological data are classified will not alter the way in which the estuary sites are grouped by multi-dimensional scaling (MDS) and cluster analysis;
(2) Weighting the biological datasets, according to the body size of component species will not alter the way in which the estuary sites are grouped by MDS and cluster analysis; and
(3) Weighting the biological data classification methods, according to the body size of component species, will not alter the relationships between the biological classifications and the abiotic data.

Methods

Biological dataset

To test the hypotheses, data were obtained from the JNCC Marine Recorder Database, for a survey carried out on the Tamar Estuary in Devon, UK in 1992 (1992 SWW Tamar Estuary and Sublittoral Sediment Survey). The data used were derived from Day grab samples collected at 17 locations along the main channel of the River Tamar into Plymouth Sound (Fig. 1). Each sample was sieved (mesh size = 0.5 mm) and the number of individuals and the number of species were recorded together with the sediment particle size analysis (fractions retained on sieve meshes of 8 mm, 4 mm, 2 mm, 1 mm, 500 μm, 250 μm, 125 μm, and 63 μm).

The biotic data were then transformed to produce functional group datasets based on the bioturbation score proposed by Swift (1993) and trophic feeding guilds (Fauchald & Jumars, 1979; Barnes, 1987), with species being assigned to one of five trophic categories: omnivores, surface deposit feeders, sub-surface deposit feeders, suspension feeders and generalists/carnivores.

A literature search was undertaken to obtain sufficient information for each species to be allocated into the appropriate functional categories and for maximum adult body size (length) to be estimated for most species. All of this information was then combined to produce six separate classifications of the biotic data to be used in analyses, these being

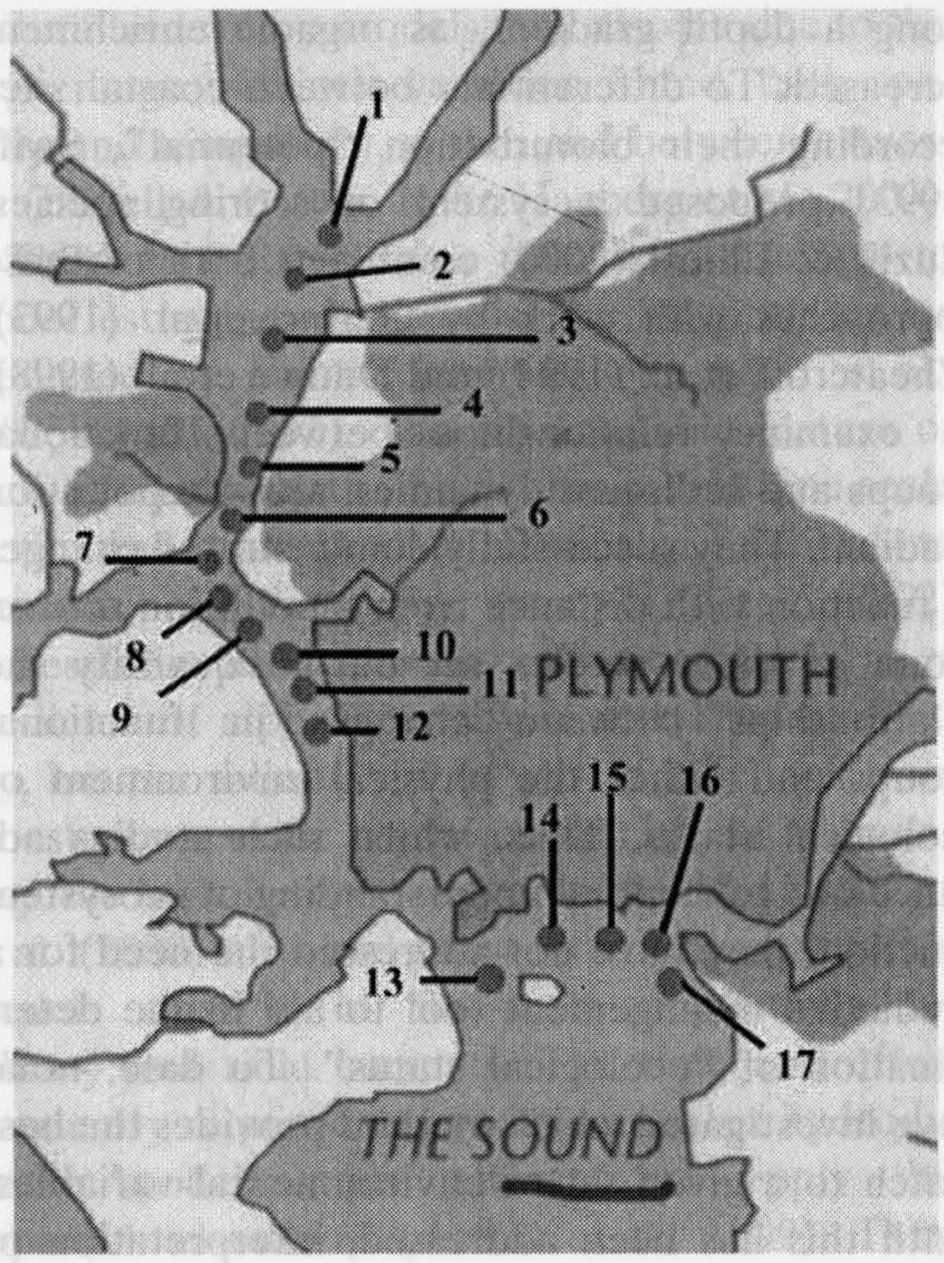


Fig. 1 Location of sample sites for 1992 SWW Tamar Estuary and Sublittoral Sediment Survey

(1) "Abundance" dataset: raw species abundance data.
(2) "Bioturbation" dataset: each species was allocated a score using the method of Swift (1993) and this score was multiplied by the number of individuals for each site.
(3) "Trophic Group" dataset: the total number of individuals in each trophic group.
(4) "Weighted Abundance" dataset: each species' abundance multiplied by body size for that species.
(5) "Weighted Bioturbation" dataset: each individual species' value in the "Bioturbation" dataset value multiplied by its body size.
(6) "Weighted Trophic Group" dataset: each species' abundance multiplied by its body

size and values summed into respective trophic groups.

All statistical procedures and analyses were performed using PRIMER 6 software (Plymouth Routines in Multivariate Ecological Research).

For each dataset non-metric, multi-dimensional scaling (MDS) plots, based on Bray-Curtis similarity (Field et al., 1982), were produced over which results of cluster analysis (hierarchical agglomerative method with group-average linkage) were overlaid, to aid visualisation of the ordination.

For sites that changed their association according to classification method, a SIMPER test was used to investigate which species were driving the dissimilarity between clusters. For each species, this test calculates its overall percentage contribution to the average dissimilarity between two groups, which enables species to be listed in order of importance (Clarke & Gorley, 2001).

Physical data

Sediment particle size analysis data were available for all sites and were used to calculate four parameters: median grain size, sorting, skewness, and kurtosis (Folk & Ward, 1957).

Since no other physical data were available from the 1992 SWW survey, interpolation from other sources was necessary. Another set of survey data was obtained from the JNCC Marine Recorder database: the "1986 OPRU HRE Plymouth Harbour and Yealm Estuary Survey". This 1986 OPRU study contained categorical data, based upon methodology from the MNCR monitoring programme (Connor, 1999), for salinity, wave exposure and tidal currents for many sites along the estuary. To check the validity of interpolation from the 1986 OPRU data, salinity profiles were also obtained from the UK Environment Agency (EA) for stations along the estuary. For each point the maximum salinity range was calculated from the EA data and compared to categorical interpolations based upon the OPRU dataset. These two datasets concurred for similar sites and hence were used to estimate categorical salinity values for the sites from the SWW Tamar survey. Data from the Tidal Stream Atlas for Plymouth Harbour and Approaches (1991) were used in a similar way, to validate interpolations based upon tidal current categories in the "OPRU" dataset. Wave exposure was based purely on interpolation of the OPRU dataset, whilst depth was estimated from Plymouth Harbour and Rivers Chart (Imray Chart C14) (Table 1).

This dataset was normalised, an MDS plot (based on the Euclidian distance similarity matrix) was produced and cluster analysis was again superimposed on the ordination to aid interpretation. A comparison of the underlying similarity matrices (used in the production of the MDS plots) was then undertaken to determine which, if any, of the biological datasets provided the best match to the environmental data. The comparison was based upon Spearman Rank Correlation and all abiotic variables were included (RELATE test, Clarke & Gorley, 2001). Subsequently, a BIOENV test (based again on Spearman rank correlation, but between the biotic similarity matrix and matrices derived from each of the various possible combinations of abiotic variables, Clarke & Gorley, 2001) was used to investigate which of the combined environmental variables contributed most to the match between abiotic and biotic datasets. Finally a second stage MDS plot of the similarity (based on Spearman Rank Correlations) between the abiotic and all six biotic datasets was produced, to aid visualisation of the relationships between the various methods employed.

Results

As shown in Fig. 2 neither "Trophic Group" nor "Bioturbation" classifications produced the same cluster patterns as using "Abundance" data.

Table 2 shows the SIMPER results, for clusters with more than one site, for the "Abundance" and "Bioturbation Potential" datasets, detailing those species with the greatest percentage contribution to overall within-cluster similarity.

For "Bioturbation", dissimilarity between Sites 6, 7, 9, 10, 11 and 12 (hereafter referred to as Cluster 2) and Site 8 was characterised by Site 8 having lower abundance of *Aphelochaeta marioni* and *Cauleriella* sp. (by more than a factor of 10) and greater abundance of *Corophium sextonae*.

Table 1 Environmental values used (Rank and actual as appropriate), for each survey site

SWW site	Salinity rank code	Exposure rank code	Tidal streams rank code	Median phi	Sorting rank code	Skew rank code	Kurtois rank code	Depth
1	2	2	3	2.14	5	4	3	1
2	2	2	3	3.13	5	5	4	1
3	2	2	3	3.37	4	5	4	1
4	2	2	3	3.42	5	4	4	1
5	2	2	3	3.82	4	4	4	1
6	2	2	3	–0.3	6	1	2	3
7	2	3	3	3.27	5	5	5	2
8	2	3	3	2.25	6	5	1	2
9	2	3	3	4.1	6	5	1	3
10	2	3	3	1.1	5	3	2	3
11	2	3	3	2.7	6	5	1	3
12	3	3	3	1.4	6	5	1	3
13	3	3	3	–2.13	5	1	4	4
14	3	3	3	0.36	5	3	4	4
15	3	4	3	0.31	5	3	4	4
16	3	4	2	3.4	4	5	5	4
17	3	4	2	2.8	6	5	4	4

Rank codes as follows: Salinity 2 = reduced/low (0.5–30 ppt), 3 = variable (18–35 ppt), Exposure 2 = extremely sheltered, 3 = very sheltered, 4 = sheltered, Tidal stream 2 = <1 knot, 3 = 1–3 knots, Sorting 4 = moderately sorted, 5 = poorly sorted, 6 = very poorly sorted, Skewness 1 = very finely skewed, 3 = symmetrical, 4 = coarse skewed, 5 = very coarse skewed, Kurtosis 1 = very platykurtic, 2 = platykurtic, 3 = mesokurtic, 4 = leptokurtic, 5 = very leptokurtic, Depth 1 = <5 m, 2 = <10 m, 3 = <15 m and 4 = ≥15 m

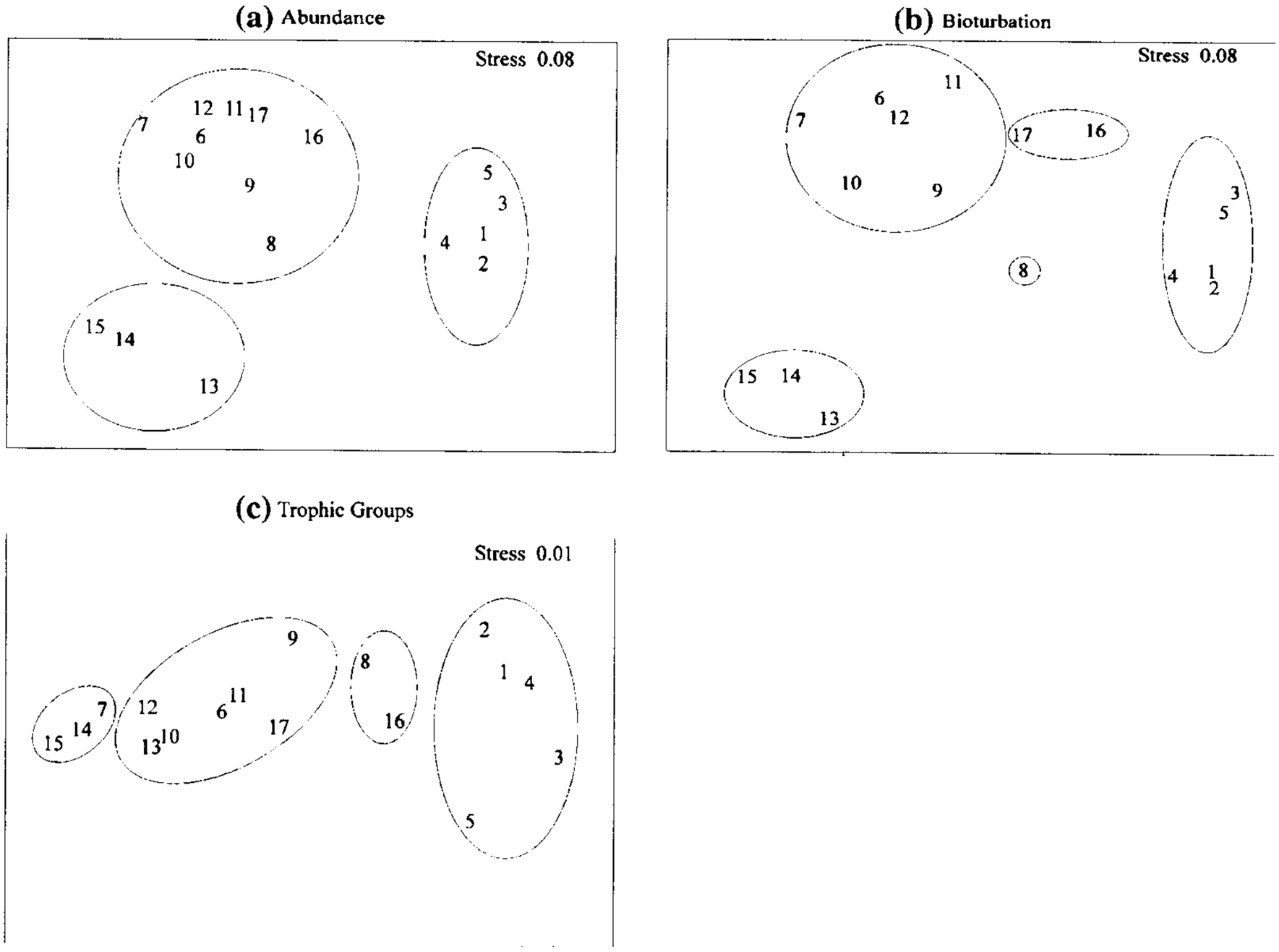


Fig. 2 MDS plots, with clusters overlain for (**a**) abundance data, (**b**) bioturbation potential, (**c**) trophic groups

Table 2 Percentage contribution to the within cluster similarity (Four largest contributions shown in bold and underlined), survey sites falling within each cluster are listed below corresponding "cluster number"

	"Abundance" dataset			"Bioturbation" dataset			
Cluster number	1	2	3	1	2	4	5
Sites within cluster	1–5	6–12,16–17	13–15	1–5	6,7,9–12	13–15	16,17
Species name							
Nephtys hombergii	68.38	5.88		70.6			6.2
Streblospio shrubsolii	15.15	0		11.23			
Aphelochaeta marioni	3.00	45.77	1.01	4.19	72.97	1.75	
Melinna palmata		7.98			2.27		17.78
Corophium sextonae	2.51	3.79	18.78	3.92		36.03	
Caulleriella sp.	3.03	14.44	1.22	3.74	12.44	1.83	6.16
Tubificoides benedii		10.97	8.05		3.62	9.37	26.2
Apseudes latreillii			26.52			18.71	
Gammarella fucicola			13.22			6.1	
Nemertea			434			4.88	
Myriochele heeri							16.06
Heteromastus filiformis		2.07				7.48	14.72

Table 3 Percentage contribution to cluster similarity, of major trophic groups characterising each cluster

Cluster number	1	2	3	4
Sites within cluster	1–5	6, 9–13,17	8,16	14,15,7
Trophic groups				
Generalists	57.51	7.73	16.17	5.76
SDF	38.57	87.27	77.14	89.51

SIMPER analysis applied to the "Trophic Group" clusters revealed a gradient of decreasing abundance of generalists and increasing surface deposit feeders across the plot, from upstream areas (right on the plot) to downstream sites. The results are summarised in Table 3.

The MDS plots for the weighted groupings are shown in Fig. 3. These plots also show different cluster patterns to the original raw abundance. "Weighted Abundance" and "Weighted Bioturbation" produced almost identical MDS plots and only differed in cluster analysis, when Site 13 and 15, respectively, separated out as individual clusters. A RELATE test revealed significant similarity between the two datasets ($\rho = 0.966$, $P = 0.1\%$). In addition, the original "Bioturbation" MDS plot was significantly similar to both the "Weighted Abundance" (RELATE $\rho = 0.901$, 0.1%) and "Weighted Bioturbation" (RELATE $\rho = 0.908$, $P = 0.1\%$), but placed both Sites 13 and 15 in one cluster with Site 14.

SIMPER analysis reveals that Site 8 is differentiated from sites in Cluster 2 (6, 7, 9, 10, 11 and 12), for both "Weighted Abundance" and "Weighted Bioturbation", by a strong signal from *A. marioni* (70.8% dissimilarity for "Weighted Abundance", 77.89% for "Weighted Bioturbation") and, to a lesser extent, by *Nephtys hombergii* (4.03% dissimilarity for "Weighted Abundance", 3.38% for "Weighted Bioturbation") and *Tubificoides benedii* (9.05% for "Weighted Abundance", 6.41% for "Weighted Bioturbation"). Each of these species had a greater contribution to sites within Cluster 2 than to Site 8.

The same species also separated Site 8 from Sites 16 and 17 (Cluster 6) in the "Weighted Abundance" analysis with *A. marioni* providing a far greater contribution to Site 8, but *T. benedii* and *N. hombergii* being more important to Sites 16 and 17. For "Weighted Bioturbation", again *A. marioni* also played a major role with *N. hombergii* but *Heteromastus filiformis* provided a similar strength contribution to *T. benedii*.

Site 13 was also isolated when the "Weighted Abundance" classification was employed. This separated from Sites 14 and 15, due to *T. benedii* (21.36% contribution), *H. filiformis* (16.03%) and Nemertea (12.81%), all of which had greater contributions to Sites 14 and 15.

This contrasts with "Weighted Bioturbation", where Sites 13 and 14 clustered together and Site

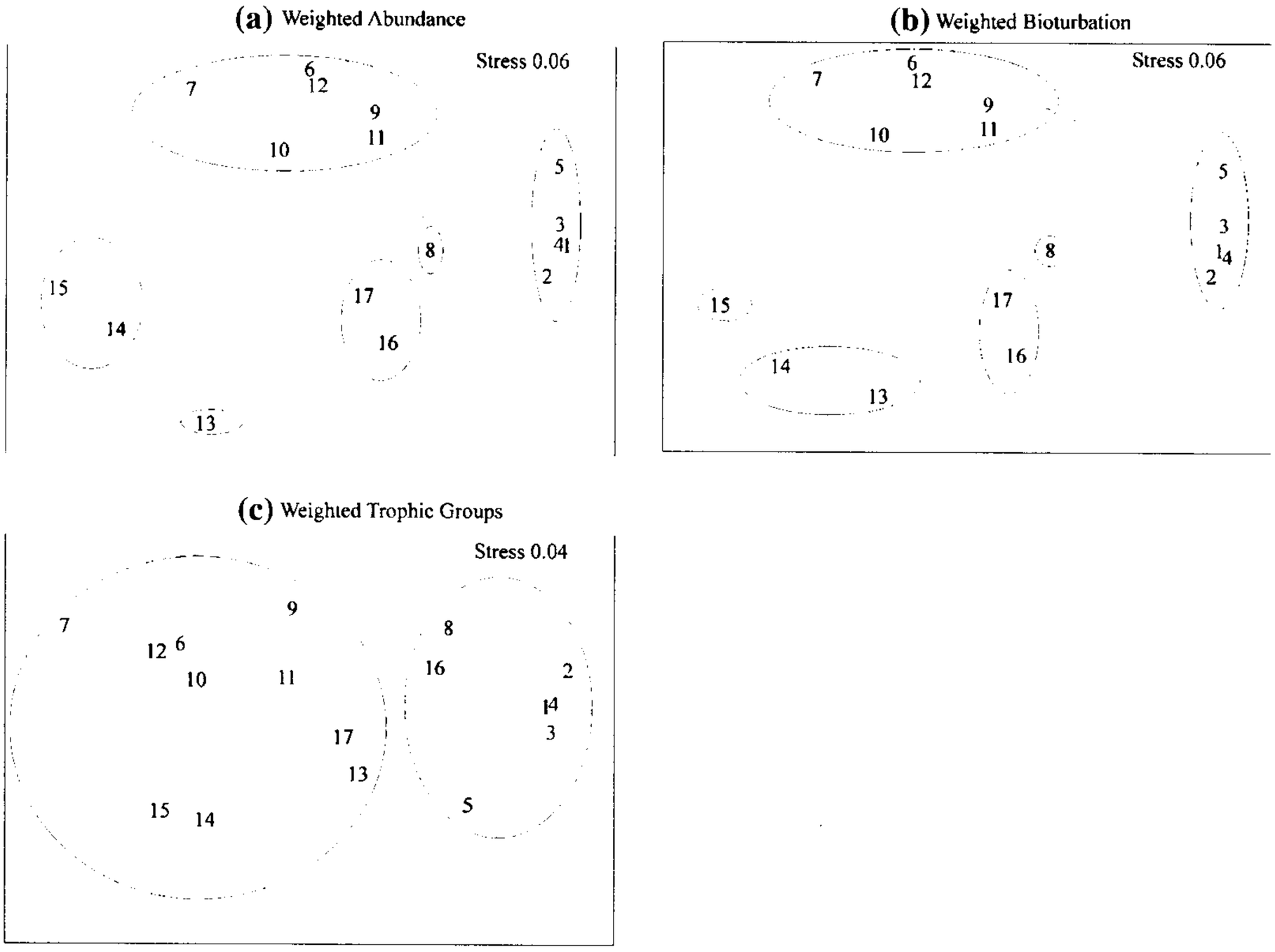


Fig. 3 MDS plots with clusters overlain for (**a**) Weighted Abundance, (**b**) Weighted Bioturbation, (**c**) Weighted Trophic Group

15 separated out. *Heteromastus filiformis* contributed most to the dissimilarity (25.48%) with much greater importance to Sites 13 and 14 than 15. *Capitella capitata* and *Platynereis dumerilii* also contributed over 16% each to the dissimilarity but with far greater contributions to Site 15.

Characterising species for clusters are summarised in Table 4 for clusters containing greater than one site.

For the "Weighted Trophic Group" only two clusters emerged, the first characterised by generalists (83.51%) (Sites 1–5, 8 and 16) and a low contribution from surface deposit feeders (11.52%). The second cluster had a much-reduced contribution from generalists (19.89%), a small level of contribution from sub-surface deposit feeders (9.94%) and a dominance of surface deposit feeders (69.2%).

Linking abiotic and biotic datasets

The MDS plot for the physical data is shown in Fig. 4. The four clusters did not form the same site associations as any of the biotic classifications. The results of RELATE tests (Table 5) revealed that similarity between abiotic (using all variables) and biotic matrices was greatest when abundances were weighted according to body size. The use of trophic groupings decreased the association between the environmental variables and biological dataset.

A BIOENV test revealed that, for all datasets, the match between abiotic and biotic variables was due to either depth alone, or to a combination of depth, median phi and wave exposure. The correlations were greatest for abiotic data matched to "Bioturbation Potential" using depth alone (0.649) and slightly reduced for "Abundance" data (0.639), with other classifications showing correlations in the range 0.543–0.593.

A second stage MDS plot, of the similarity matrices for abiotic and all six biotic datasets (Fig. 5), shows that the trophic groupings are less similar to the abiotic data than any of the other classification methods. The "Weighted Abundance" and "Weighted Bioturbation" are so similar

Table 4 Percentage contribution of major species driving within-cluster similarity

	Weighted abundance				Weighted bioturbation potential			
Cluster names	1	2	5	6	1	2	4	6
Sites	1–5	6,7,9–12	14–15	16–17	1–5	6,7,9–12	13–14	16–17
Species names								
N. hombergii	**93.09**	**1.45**		**18.22**	**93.26**	**5.36**		**19.18**
S. shrubsolii								
A. marioni		**81.22**				**85.62**	**5.28**	
C. sextone							**5.76**	
Caulleriella sp.								
T. benedii	**1.06**	**31.85**	**25.42**			3.23		**22.31**
A. latreillii		**14.44**						
G. fucicola		**8.75**						
Nemertea		**22.3**				**8.19**		
M. heeri								**7.46**
H. filiformis			**11.81**			**60.0**		**22.8**
A. mucosa			**12.14**					

Contribution of four largest contributors are shown in bold and underlined

that one overlies the other in this plot. Although "Bioturbation" produced similar MDS plots to, and was shown to correlate significantly with, both "Weighted Abundance" and "Weighted Bioturbation" methods, this second stage MDS plots only the two weighted datasets at the same location, with "Bioturbation" lying next to "Abundance". This suggests that body size imposed a stronger signal than the application of a bioturbation score.

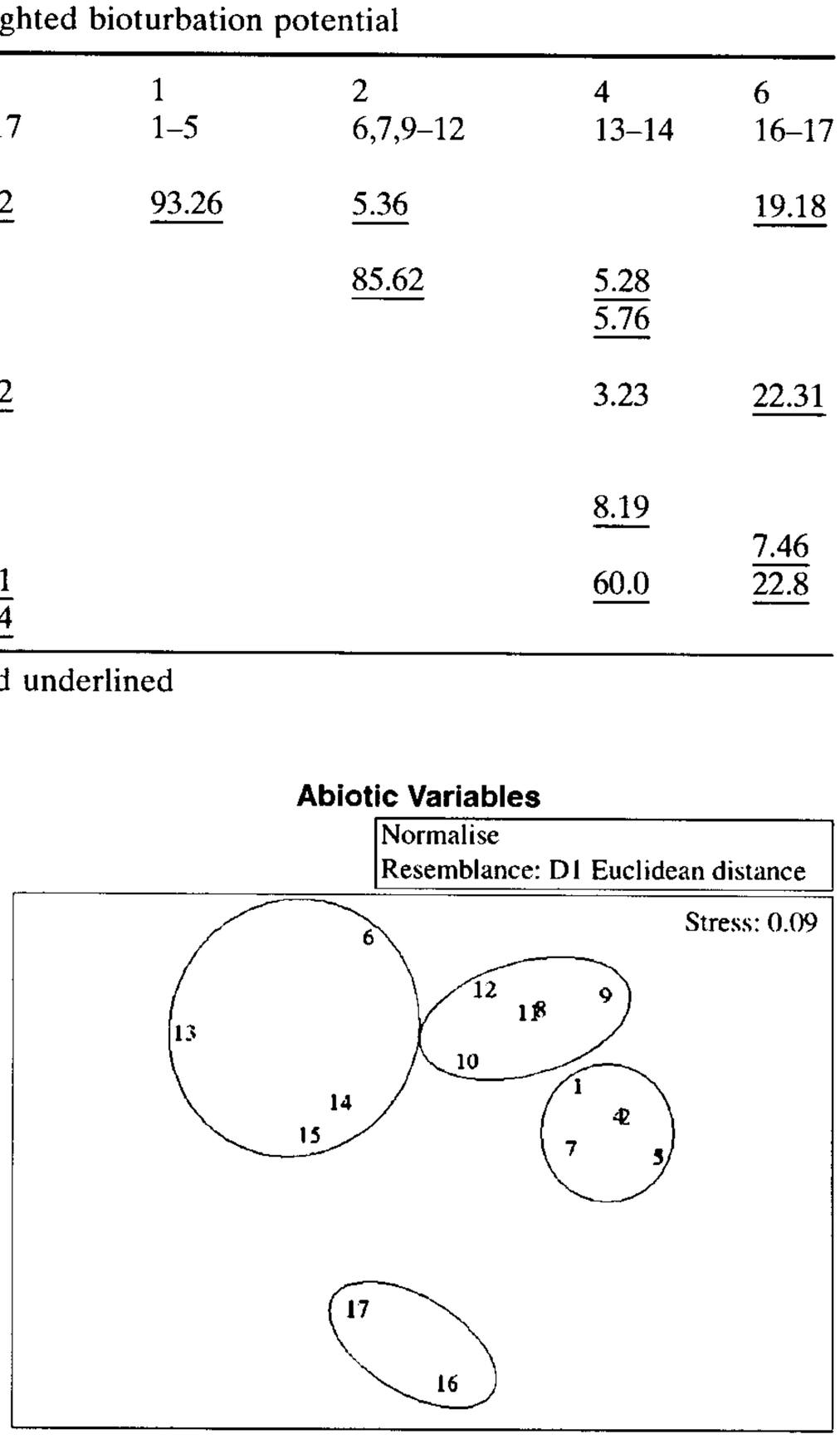


Fig. 4 MDS plot of the environmental variables with clusters overlain

Discussion

Influence of functional group classifications

MDS plots and cluster analyses, using different methods of classifying the biotic data, show that associations between sites vary according to the method employed. There was an overall consensus that sites 1–5 constituted a cluster, but sites 8, 16 and 17 separated from the others on the basis of "Bioturbation" whereas the use of "Trophic Groups" produced visibly dissimilar plots.

The difference between results of "Abundance" and "Bioturbation" classification methods is the association of sites 16 and 17, and the isolation of site 8 in the "Bioturbation" plot. Consideration of bioturbation potential scores has selectively magnified the contribution of certain species, and hence separated out the clusters. In this case, three infaunal surface deposit feeders, each with similar bioturbation potential scores (8 for *A. marioni*, 7 for *Caulleriella* and 9 for *C. sextonae)*, have transformed an initial similarity on species abundance into a difference, due to bioturbation potential. These species are apparently doing similar things, but the overall potential for bioturbatory activity varies between clusters. Whether the perceived difference in bioturbation between these sites accurately mimics the true picture cannot be ascertained on the basis of these clusters alone.

The "Trophic Group" dataset shows a different pattern to both "Abundance" and "Bioturbation". There is a clear decrease in the

Table 5 RELATE test results

Biological classification	RELATE results	
	ρ	Significance %
Abundance	0.37	0.3
Bioturbation potential	0.369	0.2
Trophic group	0.215	2.9
Weighted abundance	0.386	0.1
Weighted bioturbation potential	0.371	0.4
Weighted trophic group	0.15	5.5

A significant value indicates that similarity between the two matrices being compared is significant

importance of generalists from upstream areas on the River Tamar, to the higher salinity areas in Plymouth Sound, with a corresponding increase in abundance of surface deposit feeders. Again, it is not possible to interpret the relevance of this gradient without reference to the physical environment at those sites. Does the pattern truly reflect a change in overall function? The pattern was similar to that found by Bonsdorff and Pearson (1999) in the Baltic Sea, but they too were unable to conclusively and quantitatively link changes in trophic guilds to abiotic data.

Nevertheless, from this present work, it does seem that when attempting to interpret the biological significance of clusters, in relation to ecosystem status, different functional groups may not be interchangeable. Each group provides different information about the area surveyed. This means that interpretation may be difficult for environmental managers who would prefer an indication of "health status" rather than function. Close attention needs to be paid to choosing the correct "functional group" with relevant links to the appropriate conditions of environmental health (Snelgrove & Butman, 1994; Gerino et al., 2003). The appropriate functional group will change according to the questions posed by environmental managers.

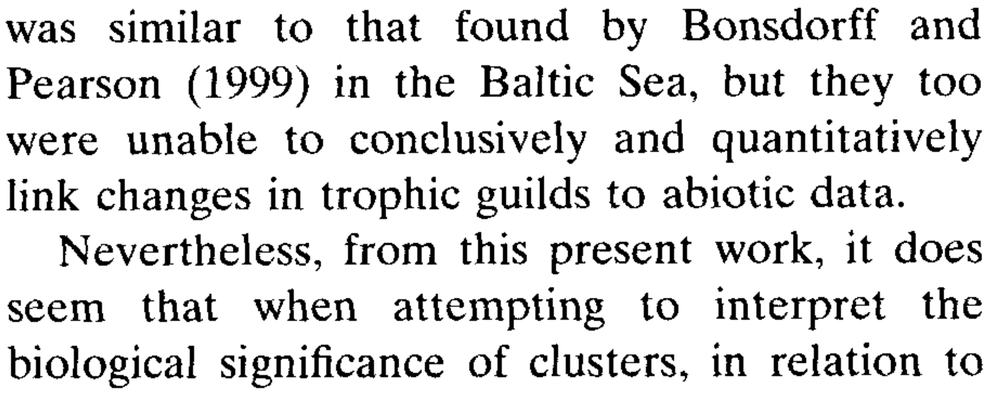


Fig. 5 Second stage MDS plot using the similarity matrices of each dataset and displaying graphically the correlations between them. (1 = abundance, 2 = bioturbation, 3 = trophic groups, 4 = weighted abundance, 5 = weighted bioturbation, 6 = weighted trophic groups)

Influence of body size as a method of weighting function contribution

We hypothesised that weighting the contribution of individual species to functions according to their body size may affect the site association patterns. In this study, weighting by body size did alter the site ordinations, but there appeared to be a general pattern emerging, with broad consensus between "Bioturbation", "Weighted Bioturbation" and "Weighted Abundance". The "Trophic Group" pattern of clustering was more affected by the weighting and clusters were very different to those obtained by the other methods.

SIMPER analysis revealed that, for "Weighted Abundance" data, Site 8 was isolated due a change from an emphasis on abundance to an emphasis on size. Therefore, less abundant but relatively larger species were now playing a role in cluster differentiation. The same estuarine site was also isolated by the "Weighted Bioturbation" classification, but with slight changes in the species driving the dissimilarity between sites.

An initial cluster of Sites 13, 14 and 15 arose using "Abundance" data. This changed when using data weighted for body size. Either Site 13 or 15 became isolated, according to either an emphasis on larger species or a combination of larger size and greater bioturbation potential of species.

Since actual values of bioturbation occurring at each site are not known it is not possible to test the accuracy of apparent patterns in reflecting field-levels of bioturbation. Thus, although there was a convergence in pattern on MDS plots for "Bioturbation", "Weighted Abundance" and "Weighted Bioturbation" there were subtle dif-

ferences, driven by the change of emphasis from abundance to a size and effect weighting. This is not evident from the MDS plots alone, which suggests that these changes are subtle and need a combination of methods for detection.

Linking biological patterns to environmental variables

The question remains: "are observed patterns biologically relevant and can they be linked to the physical environment?" To help answer this question the biotic MDS plots were compared to the plots derived from the abiotic data alone. The latter produced four clusters. However, the resulting pattern was different from those produced using any of the six ways of classifying the biota.

The RELATE tests revealed that the relationships between abiotic and biotic datasets were greatest if the species abundances were weighted for body size. Excluding the trophic group methods, which produced very different plots, the differences between the biota and environmental variables appeared to be driven by the way in which sites 6, 7 and 8 clustered. Unlike biological data, the abiotic variables did not isolate Site 8, rather placed it in a cluster with neighbouring estuarine sites, whilst Sites 6 and 7 were separated from each other.

Thus the site ordination, according to the physical attributes, is not mirrored in any of the biological datasets, although a minimal improvement in the match could be achieved by the application of weighting according to body length. This lack of concordance between the abiotic and biotic data could be due to either insufficient sensitivity in the abiotic information, leading to inability to differentiate sites, or a choice of functional grouping methods that are not truly influenced by the physical attributes selected. Although several factors were included in the abiotic data used, the small number of sample sites has greatly reduced variability for each parameter. For example, only two categories of salinity could be applied. In addition, only the granulometry was expressed as actual values. All other data were ranked. This will have masked some of the more subtle variations that may occur and indeed, the ranks were often based upon interpolation from the nearest known data values, again introducing errors of estimation of unknown size.

Although weighting the biotic dataset by body size may improve the level of correlation with the environmental data, the 2nd stage MDS plot indicates that further improvements could be made. The "Trophic Group" and "Weighted Trophic Group" are placed much further away from the abiotic site. This may suggest that altering the "function" element of the weighting system moves resultant groups either towards or away from the abiotic data, and that links can be improved by refining the functional classification schemes.

Our ability to place species into appropriate functional groups and apply a weighting, also influences the usefulness of the resultant functional groups (Snelgrove & Butman, 1994; Pearson, 2001; Gerino et al., 2003). For example, the method proposed by Swift (1993) requires several aspects of each species' motility, feeding and burrowing behaviours to be categorised. Often such information is not available and must be inferred from similar species. This lack of information has started to be addressed by recent studies, such as the work by Mermillod-Blondin et al. (2003, 2005), in which activity rates of dominant species in assemblages are estimated. Also, new definitions of bioturbatory functional groups, e.g., gallery diffusers, erratic movers etc. are being proposed (François et al., 2002; Gerino et al., 2003; Ouellette et al., 2004) which may be more useful than the schemes employed above.

Within the context of macrobenthic assemblages, linking bioturbation to abiotic variables holds more promise for developing predictive relationships, than does the use of trophic groupings. In this study, both weighted and unweighted trophic groupings were less related to the selected abiotic variables than were the other methods. This may partly be due to the nature of environmental parameters chosen. For example, no information was available for turbidity levels, suspended particulate matter or similar variables that might impact directly upon trophic function. This is supported by the work of Hall (1994), who was unable to relate trophic groups to sediment

turnover, and Dauwe et al. (1998) who found links between groupings, based on combinations of trophic and bioturbatory activities, and the quality of organic matter. This present study did indeed demonstrate changes in trophic functioning along the surveyed area. However, our inability to link this information to environmental factors limits its usefulness. To assess the relevance of changes in function, managers need to link such changes to the expected "normal" range of "function amount" for a "healthy" location. Historically, for most estuarine locations, and indeed many ecosystems, only a limited suite of environmental variables is available upon which predictions can be based without needing to implement new sampling strategies. Further, physical data are more prevalent than are chemical surveys. This present study implies that correlations based upon the physical interplay, between species and the environment, will be easier to detect than those based upon trophic interplay.

The weighting of the datasets for body size did subtly alter some of the cluster patterns. This has a number of important implications. Environmental managers seek methods that are based on grouping species without losing information (Snelgrove & Butman, 1994). Thus, this present study provides evidence that functional groups can be used to provide more information about estuarine sites than the underlying abundance alone. Classifications according to bioturbation potential and body size each produced similar patterns but with different driving species. The relative merits of either method are not clear and require further investigation. Nevertheless, it did appear that body size had a more dominant effect than bioturbation potential, driving convergence of "Weighted Abundance" and "Weighted Bioturbation" datasets. This needs further investigation to determine whether the influence of body size should be scaled in some way. For example, instead of using body length, the surface area that a species presents to the sediment, as it goes about its activities, may be a more appropriate measure.

This present study was limited to a very small area of one estuarine system. Its application to a broader range of estuary types, covering a wider range for each environmental variable, might improve some of the correlations and make patterns of associations clearer.

Conclusions

This study clearly demonstrated that functional classifications of biotic data could alter our perception of site-to-site relationships. In addition, we showed that weighting those groups, according to the relative strength of component species, could change the links between the physical environment and biota, and may help to interpret changes in patterns of site associations.

Functional bioturbation score proved almost as useful as weighting by mean body size. The benefits of one classification over the other are difficult to disentangle. There was no apparent loss of information when using these two classifications, rather an improvement in our ability to interpret how changes in the biology reflect physical changes in the site. If such links can consistently be made, then functional groups promise to improve our ability to link biotic and abiotic variables in a consistent and predictive way. If we can link site differentiation patterns to measurable, broad-scale, physical parameters, then these patterns can form the basis for future predictions of "expected function level", based upon knowledge of the physical environment alone.

Future work is needed to replace Swift's scoring system with more relevant bioturbatory categories, such as those proposed by Mermillod-Blondin et al. (2003), and François et al. (2002), which are based on measured activity levels. Attention also needs to be given to determining which measures of "body size" are most appropriate and for which species. By combining these foci we can produce quantitative values of bioturbatory contribution. These can be used to investigate links to the physical and chemical environment with greater confidence in the ecological significance of resultant patterns.

Acknowledgements We would like to thank D. J. Swift, JNCC and the UK Environment Agency for the provision

of data, Alison Miles and Amanda Prior for constructive discussions and two anonymous reviewers for their helpful comments. This work was supported financially by the Natural Environment Research Council.

References

Attrill, M. J., M. Power & R. M. Thomas, 1999. Modelling estuarine Crustacea population fluctuations in response to physico-chemical trends. Marine Ecology Progress Series 178: 89–99.

Attrill, M. J., 2002. A testable linear model for diversity trends in estuaries. Journal of Animal Ecology 71: 262–269.

Austin, M. P., 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. Ecological Modelling 157: 101–118.

Barnes, R. D., 1987. Invertebrate Zoology, 5th ed. Saunders College Publishing.

Bonsdorff, E. & T. H. Pearson, 1999. Variation in the sublittoral macrozoobenthos of the Baltic Sea along environmental gradients: a functional group approach. Australian Journal of Ecology 24: 312–326.

Carson, R., 1962. Silent Spring. Houghton Mifflin.

Clarke, K. R. & R. N. Gorley, 2001. Primer v5: User Manual/tutorial. Primer-E Ltd, Plymouth.

Connor, D., 1999. Marine Nature Conservation Review Guidance Notes for completion of recording forms. JNCC, UK.

Dauwe, B., P. M. J. Herman & C. H. R. Heip, 1998. Community structure and bioturbation potential of macrofauna at four North Sea stations with contrasting food supply. Marine Ecology Progress Series 173: 67–83.

Emlen, J. M., D. C. Freeman, M. D. Kirchhoff, C. L. Alados, J. Escos & J. J. Duda, 2003. Fitting population models from field data. Ecological Modelling 162: 119–143.

Fauchald, K. & P. A. Jumars, 1979. The diet of worms: a study of polychaete feeding guilds. Oceanography and Marine Biology. An Annual Review 17: 193–284.

Field, J. G., K. R. Clarke & R. M. Warwick, 1982. A practical strategy for analysing multi-species distribution patterns. Marine Ecology Progress Series 8: 37–52.

Folk, R. L. & W. C. Ward, 1957. Brazos River bar, a study in the significance of grain-size parameters. Journal of Sedimentary Petrology 27: 3–27.

François, F., M. Gerino, G. Stora, J.-P. Durbec & J.-C. Poggiale, 2002. Functional approach to sediment reworking by gallery-forming macrobenthic organisms: modelling and application with the polychaete Nereis diversicolor. Marine Ecology Progress Series 229: 127–136.

Gergel, S. E., M. G. Turner, J. R. Mille, J. M. Melack & E. H. Stanley, 2002. Landscape indicators of human impacts to riverine systems. Aquatic Sciences 64: 118–128.

Gerino, M., G. Stora, G. Gontier & O. Weber, 1993. Quantitative approach of bioturbation on continental margins. Annales de l'Institut Oceanographique 63: 177–181.

Gerino, M., G. Stora, F. François-Carcaillet, F. Gilbert, J.-C. Poggiale, F. Mermillod-Blondin, G. Desrosiers & P. Vervier, 2003. Macro-invertebrate functional groups in freshwater and marine sediments: A common mechanistic classification. Vie Milieu 53: 221–231.

Hagberg, J., N. Jonzen, P. Lundberg & J. Ripa, 2003. Uncertain biotic and abiotic interactions in benthic communities. OIKOS 100: 353–361.

Hall, S. J., 1994. Physical disturbance and marine benthic communities: Life in unconsolidated sediments. Oceanography and Marine Biology. An Annual Review 32: 179–239.

Hilty, J., A. Merenlender, 2000. Faunal indicator taxa selection for monitoring ecosystem health. Biological Conservation 92: 185–197.

Hols, D. R., 1996. National biomonitoring programme for riverine ecosystems. Framework document for the programme. NBP Report Series No 1. Institute for Water Quality Studies, Department of Water Affairs and Forestry, Pretoria, South Africa.

Levin, L. A., F. F. Boesch, A. Covich, C. Dahm, C. Erseus, K. C. Ewel, R. T. Kneib, A. Moldenke, M. A. Palmer, P. Snelgrove, D. Strayer & J. M. Weslawski, 2001. The function of marine critical transition zones and the importance of sediment biodiversity. Ecosystems 4: 430–451.

Mattiessen, P. & R. J. Law, 2002. Contaminants and their effects on estuarine and coastal organisms in the United Kingdom in the late twentieth century. Environmental Pollution 120: 739–757.

Mermillod-Blondin, F., S. Marie, G. Desrosiers, B. Long, L. de Montety, E. Michaud & G. Stora, 2003. Assessmant of the spatial variability of intertidal benthic communities by axial tomodensitometry: Importance of fine-scale heterogeneity. Journal of Experimental Marine Biology and Ecology 287: 193–208.

Mermillod-Blondin, F., F. François-Carcaillet & R. Rosenberg, 2005. Biodiversity of benthic invertebrates and organic matter processing in shallow marine sediments: an experimental study. Journal of Experimental Marine Biology and Ecology 315: 187–209.

Muzik, K. & M. Elliott, 2000. The effects of chemical pollution on the bioturbation potential off estuarine intertidal mudflats. Helgolaender Marine Research 54: 99–109.

Ouellette, D., G. Desrosiers, J.-P. Gagne, F. Gilbert, J.-C. Poggiale, P. U. Blier & G. Stora, 2004. Effects of temperature on in vitro sediment reworking processes by a gallery biodiffsor, the polychaete Neanthes virens. Marine Ecology Progress Series 266: 185–193.

Pearson, T. H., R. Rosenberg, 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanography and Marine Biology. An Annual Review 16: 229–311.

Pearson, T. H., 2001 Functional Group Ecology in soft sediment marine benthos: The role of bioturbation.

Oceanography and Marine Biology: an Annual Review 39: 233–267.
Peterson, G., C. R. Allen & C. S. Holling, 1998. Ecological Resilience, Biodiverstiy and Scale. Ecosystems 1: 6–18.
Pianka, E. R., 1978. Evolutionary Ecology. Harper and Row, New York.
Platell, M. E. & I. C. Potter, 1996. Influence of water depth, season, habitat and estuary location on the macrobenthic fauna of a seasonally closed estuary. Journal of the Marine Biological Association of the United Kingdom 76: 1–21.
Simboura, N. & A. Zenetos, 2002. Benthic indicators to use in Ecological Quality classification of Mediterranean soft bottom marine ecosystems, including a new Biotic Index. Mediterranean Marine Science 3/2: 1–35.
Skriver, J., 2001. Biological Monitoring in Nordic Rivers and Lakes. Report to Nordic Council of Ministers, National Environment Research Institute Report 2001: 513, Denmark.
Snelgrove, P. V. R. & C. Butman, 1994. Animal-sediment relationships revisited: cause versus effect. Oceanography and Marine Biology. An Annual Review 32: 111–177.
Swift, D. J., 1993. The macrobenthic infauna off Sellafield (north-eastern Irish Sea) with special reference to bioturbation. Journal of the Marine Biological Association of the United Kingdom 73: 143–162.
Thayer, C. W., 1983. Sediment-mediated biological disturbance and the evolution of marine benthos. In Tevesz, M. J. S. & P. L. McCall (eds), Biotic interactions in recent and fossil benthic communities. Plenum Press, New York, 479–625.
Tidal Stream Atlas for Plymouth Harbour and Approaches, 1991. Hydrographic Office, Taunton.
Warwick, R. M., J. D. Goss-Custard, R. Kirby, C. L. George, N. D. Pope & A. A. Rowden, 1991. Static and dynamic environmental factors determining the community structure of estuarine macrobenthos in SW Britain: Why is the Severn Estuary different? Journal of Applied Ecology 28: 329–345.
Wheatcroft, R. A., I. Olmez & F. X. Pink, 1994. Particle bioturbation in Massachusetts Bay: Preliminary results using a new deliberate tracer technique. Journal of Marine Research 52: 1129–1150.
Wiesner, D., 1995. EIA the Environmental Impact Assessment Process. What It Is and What It Means to You. Prism Press, Bridport.
Wright, J. F., 2000. An introduction to RIVPACS. In Wight, J. F., D. W. Sutcliffe & M. T. Furse (eds), Assessing the Biological Quality of Fresh Waters: RIVPACS and other techniques.
Ysebaert, T., P. Meire, P. M. J. Herman & H. Verbeek, 2002. Macrobenthic species response surfaces along estuarine gradients: Prediction by logistic regression. Marine Ecology Progress Series 225: 79–95.