Assessing ecological functioning in marine benthic communities

A thesis submitted to the University of Newcastle upon Tyne for the degree of Doctor of Philosophy

by

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January 2005

Abstract

With the advent of an ecosystem approach to marine management, the importance of developing methods to investigate ecological functioning is receiving increasing attention. This thesis develops a novel approach for describing ecological functioning in marine benthic systems. Biological traits analysis (BTA) uses a suite of life history, morphology and behaviour characteristics of species to describe aspects of their functioning. Comparison of BTA with two other approaches proposed for describing functioning in marine ecosystems established that BTA identified a range of biological attributes important for differentiating benthic communities and was better able to describe spatial patterns in assemblage composition than the other measures. Appraisal of the analytical tools proposed for use in BTA revealed they provided similar views of assemblage functioning, with the non-parametric tool being appropriate for providing a general picture of functioning, while the more complex parametric tools had greater power to detect anthropogenic impacts. Evaluation of the type and number of traits included in BTA showed it was sensitive to the number of traits selected for analysis, with optimal results being gained by maximising trait number. Examination of the relationship between functioning and environmental variability revealed that trait composition was related to changes in a number of environmental factors, although this relationship was complex and the nature of associations between traits and specific environmental factors varied depending on the location of assemblages. Further analyses focussed on the impacts of anthropogenic activities on benthic assemblage functioning. These revealed that assemblage functioning was impacted by fishing disturbance in both subtidal and intertidal assemblages. A number of traits were impacted by fishing, including some associated with vulnerability to physical stress and others related to resistance to disturbance, while other aspects of functioning remained unaffected. The thesis has increased our understanding of biological traits analysis as a tool for describing functioning in marine benthic systems. It has also contributed to some interesting ecological and management issues, such as the relationship between species and functioning and the importance of, information required for, and strategies available for conservation of ecological functioning in marine ecosystems.

Acknowledgements

I would like to thank my supervisors, Professor Chris Frid and Dr Stuart Rogers, for their continued support and contributions towards the compilation of this thesis and the work within it. I would like to acknowledge the Centre for Environment, Fisheries and Aquaculture Science (CEFAS), the University of Newcastle upon Tyne and the British Federation of Women Graduates, who provided finance for my PhD study. I am also grateful to Chris and Stuart, and my host institutions, for kindly providing the data that form the basis of this thesis and to Mike Nicholson, Jim Ellis and Steve Freeman for contributing biological information.

I owe a great deal of thanks to my family for support throughout my PhD and earlier. Especially to my Mum, Pat Bremner, and my brother Stewart Bremner, I can't tell you how far you've carried me. To my Gran, Ruby Collier and my Nana, Meg Stevenson; thank you for your love and for all the little things that helped so much along the way. To Mike, it's been a long road, and I'm glad you were on it with me for most of the way. Thank you for everything.

To all the enthusiastic people who carried endless buckets of mud and sand, your help was very much appreciated: Leanne Bailey, Silvana Birchenough, Tom Catchpole, Chris, Margaret Gill, Mike, John Knowles, Odette Paramor, Gemma Quilez-Badia, Leonie Robinson, Jill Shaw and, of course, Oscar and his rabbit. Extra thanks go to John for his field and lab expertise and to Peter Garwood for his invaluable assistance with invertebrate taxonomy.

To my friends who've come through these last few years with me, I would like to say thank you for your encouragement. To Gemma and Silvana, I'm glad to have shared all these times with you, muchas gracias y besitos, mis chicas bonitas. Dawn McCann, thanks for the cards and coffee. Louise Coppard, Jennifer Cameron, Matthew Wright and Sonia Kumar - look at us now, who'd have thought it?! To my Roxburgh Place gang, Frances Herron, Katy Milner and Barry Sewell, what can I say? You make Newcastle light up!

Finally, the staff and students in the Dove Marine Lab, who've made it such a great place to work and haven't been mentioned yet. To Andy Birchenough, Delphine Bonnet, Jane Delany, Stewart Evans, Judy Foster-Smith, Joseph Hornsby, Cliff Garside, Vicki Hendrick, Kim Last, Phil Percival, Catherine Scott, Paul Stebbing, Carol Weiss and Sue. It's been fun.

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Chapter 1

Biomonitoring and human impacts on marine ecosystems

INTRODUCTION

It is generally recognised that human activities are exerting intense pressure on marine ecosystems, which are subject to fishery exploitation, extractive activities, chemical pollution and nutrient enrichment (Sherman, 1994). Relatively little is known about the direction and extent of the effects of these human impacts, or the amount of stress marine ecosystems can tolerate, but compliance with legislation and international agreements requires sound information on these issues (Gislason *et al.*, 2000). The development of biomonitoring tools has allowed scientists to assess the levels of human impacts and their effects on receiving ecosystems, and to evaluate the success of management techniques initiated to remediate them. Good tools should be based on sound theory, applicable to different geographical areas and habitat types, able to ascribe causality to changes in the variable measured and able to separate the effects of different impact types (Doledec *et al.*, 1999). They should also have low implementation costs and be easy to apply for workers with little specialist scientific knowledge.

Marine ecosystems are composed of three units: (i) the physical environment (e.g. seabed structure, sediment composition, waves, currents and water temperature), (ii) the chemical environment (e.g. substances such as carbon, oxygen, nitrogen and phosphorus and properties such as salinity and pH) and (iii) the biotic environment (the assemblages of living organisms present in the system, ranging from microorganisms up to macroalgae, large marine mammals and humans).

Traditionally, approaches to the investigation of anthropogenic impacts on marine ecosystems have measured aspects of the individual ecosystem units (discrete approaches). Biomonitoring tools, in these instances, describe the structure of biological communities inhabiting marine ecosystems and their subsequent responses to human activity. However, ecosystem units do not exist in isolation. The physical, chemical and biological components interact with each other and the distinction between biotic and abiotic units is arbitrary (Lindeman, 1942). An alternative approach to ecosystem assessment uses integrative measures that attempt to combine information on, or indicators of, more than one ecosystem unit. This approach focuses on the ecological processes that cycle energy and substances through marine ecosystems, or on the maintenance and regulation of these processes (termed ecological functioning, after Naeem *et al.*, 1999). The methods used can provide information on both the effects of impacts on biological communities and the wider consequences of these impacts at the ecosystem level.

DISCRETE APPROACHES TO BIOMONITORING

The simplest measure used to assess change in biological assemblages is taxon richness. It is very widely used, often in combination with other univariate measures such as diversity indices, which account for both taxon richness and the distribution of abundance between taxa (Magurran, 1988). These are quick and easy to interpret and can be used to compare different habitats. However, an underlying assumption is that stress results in reduced taxon diversity, therefore low diversity is indicative of an impacted system. Stress does not always result in reduced diversity (Rapport *et al.*, 1985) and can, in some cases, have a positive effect (Connell, 1978). So, some levels of anthropogenic impact may also lead to increased diversity. Moreover, some systems may be naturally species-poor, so studies that describe a low-diversity assemblage may erroneously categorise it as impacted.

Other measures use the identity of component species to build-up a picture of community composition, assessing changes in composition in response to anthropogenic impacts. This approach has been used to examine the effects of most stressors occurring in marine environments. There is a large body of literature dedicated to assessing the effects of fishing on species composition in pelagic and demersal systems (Hutchings, 1990; Jennings & Kaiser, 1998; Johnson, 2002 and see special issues of the ICES Journal of Marine Science (Volume 57, Issues 3 and 5, 2000)) and it has also been applied to the assessment of fishery management practices (Edgar & Barrett, 1999) and other human activities such as dredging (Bonvicini Pagliai *et al.*, 1985) and nutrient enrichment (Bachelet *et al.*, 2000; Kitsyou & Karydis, 2000).

Taxonomic keys are widely available, making species composition a useful tool accessible to general workers. However, not all species have been identified (Vyerman *et al.*, 1996; Snelgrove *et al.*, 1997), which can limit the effectiveness of species-level investigations. Also, identification of organisms to species level can be difficult for non-specialists, particularly in benthic environments (Pearson & Rosenberg, 1978; Meyer-Reil & Koster, 2000). Mis-identification and inconsistency in identification can be common (Carney, 1996; Vecchione *et al.*, 2000) and this can impact on the reliability and compatibility of different studies. Moreover, there is debate over the way in which organisms are classified into species (Costello *et al.*, 1996; Vyerman *et al.*, 1996; Snelgrove *et al.*, 1997), making it difficult to compare studies that use different taxonomic identification methods.

Higher-level taxonomic assessments can help to address some of these problems. Family-level assessment is used extensively in studies examining the effects of fishing and fishery management measures on reef systems (Roberts & Polunin, 1992; McClanahan, 1994; Jennings *et al.*, 1996; Wantiez *et al.*, 1997) and may be as useful as (De Grave & Whitaker, 1999), and potentially more sensitive than (Olsgard *et al.*, 1997), species-level assessments. They are useful from a monitoring perspective as they are quicker and easier, thus cheaper and more reliable, than species-level studies (Warwick, 1988; Vecchione *et al.*, 2000). However, one problem inherent in using coarser groupings is a loss of information on small-scale structure, which can, in some cases, mask important changes in individual species (Dulvy *et al.*, 2000).

Another major drawback of the assessment of taxonomic composition is natural spatial and temporal variability, which can make it difficult to define baseline conditions in a system and, thus, harder still to attach causality to community changes (Underwood & Chapman, 1998; Rogers *et al.*, 1999a). This natural variability in marine assemblage composition is well established in intertidal and subtidal environments (see, for example, Underwood & Chapman, 1998; Rogers *et al.*, 1999b; Weslawki *et al.*, 1999). Focussing at higher taxonomic levels can lessen the problem, as these levels can be more stable than species analyses (Pearson & Rosenberg, 1978). Increased spatial and temporal replication can also help, but the scientific benefits of more intensive studies must be balanced against the financial and time costs involved.

INTEGRATIVE APPROACHES

These approaches attempt to combine information on more than one ecosystem unit into descriptions of ecosystems and their response to anthropogenic activity. Measurements of ecological processes place emphasis on the chemical components of ecosystems, whilst incorporating information on the roles of organisms and the physical environment in these processes. Measures of ecological functioning, in contrast, emphasise the roles played by organisms, but include information on their interactions with their chemical and physical environment.

Ecological processes

Marine biological communities are affected by cycling of, principally, N, P and C, the rates of which are themselves controlled by nutrient availability (Valiela, 1995). Some anthropogenic activities may affect biogeochemical cycles and the organisms involved (Schlesinger, 1991). Measuring changes in the rates of ecological processes in the presence of anthropogenic impacts will incorporate information on the chemical and biological components of ecosystems.

It would be extremely difficult to measure or even model impacts on entire biogeochemical cycles as they are complex and interlinked (Valiela, 1995). Monitoring strategies usually focus on the measurement of easily identified variables reflecting ecological processes (see, for example, Giller *et al.*, 2004). The approach has been applied to a diverse range of anthropogenic impacts including organic enrichment (Davanzo *et al.*, 1996; Harding & Perry, 1997; Kinney & Roman, 1998; Rask *et al.*, 1999; Voss *et al.*, 2000), climate change (Struyf *et al.*, 2004), anthropogenically-mediated invasion of non-indigenous species (Larned, 2003), sediment re-suspension (a phenomenon caused by trawling, dredging or mixing events) (Sloth *et al.*, 1996), fishing (McClanahan, 1995; Frid *et al.*, 2001; Jennings *et al.*, 2001a; Hermsen *et al.*, 2003) and fishery management practices (Babcock *et al.*, 1999).

There are several practical reasons why the approach is useful for biomonitoring purposes. Variables representing biogeochemical cycles are easy to measure (Davanzo *et al.*, 1996) and can be monitored over wide geographic areas (Joint & Groom, 2000), allowing large-scale impacts to be assessed. The approach can detect low levels of anthropogenic impact (Kinney & Roman, 1998) and short-lived change (Sloth *et al.*, 1996; Joint & Groom, 2000) in addition to longer-term responses (Babcock *et al.*, 1999). It can be used as an early-warning indicator, because changes in processes occur before changes in biotic structure (Rapport *et al.*, 1985) and can provide insight into the specific responses of individual biotic groups involved in ecological processes (Davanzo *et al.*, 1996; Sloth *et al.*, 1996; Kinney & Roman, 1998).

However, differential responses by different ecosystem components (see, for example, Borum & SandJensen, 1996; Jennings *et al.*, 2001a) may potentially impair the utility of the approach to detect anthropogenic impacts. Ecosystem responses to impacts such as enrichment may be defined by complex interactions between biotic groups (see Cognetti, 2001). Studies that monitor only one group may overlook conflicting and, sometimes, mediating responses of others, but measuring only whole-system response may mask differential reactions and hinder understanding of impact effects. In some situations, the approach may only be applicable when each component of the system is measured in conjunction with total response (Borum & SandJensen, 1996).

Additionally, causality can often only be inferred from changes in processes coinciding with changes in impact levels (Rosenberg, 1985; Voss *et al.*, 2000), which can be a major problem for environmental managers if it leads to doubt over the exact identity of drivers of ecosystem change. The lack of causality often originates from natural variability in ecological processes, with, for example, light availability, temperature, water flow, circulation patterns and natural enhancement of nutrient supply all influencing process rates (Schlesinger, 1991; Chen *et al.*, 2000; Reid *et al.*, 2001; Biles *et al.*, 2003). There is some evidence that short-term fluctuations can be separated from longer-term changes brought on by anthropogenic impacts (Harding & Perry, 1997), but this may require long-term studies (Davanzo *et al.*, 1996).

Lastly, separating the effects of different impact-types can also be difficult. For example, sediment resuspension can lead to decreased production in benthic sediments (Sloth *et al.*, 1996), but this can also be a consequence of nutrient enrichment (Borum & SandJensen, 1996; Meyer-Reil & Koster, 2000). In systems subject to both bottom trawling and nutrient enrichment, managers may not be able to separate the relative contribution of each.

Ecological functioning

Ecological functioning is defined as the maintenance and regulation of ecosystem processes (after Naeem *et al*., 1999). Approaches based on ecological functioning focus on the types of taxa present in marine communities and their responses to anthropogenic impacts. The methods employed to describe ecological functioning incorporate, either implicitly or explicitly, information on the ecological roles of taxa present in communities. Taxa interact in variable ways with their physical and chemical environment depending on the characteristics they express, and changes in the occurrence of these taxa have implications for ecological processes.

In its simplest form, the ecological functioning approach involves a taxonomic assessment of community composition, interpreted in terms of biological characteristics expressed by selected taxa. For example, Lotze and Schramm (2000) investigated the effects of nutrient enrichment on marine macroalgal communities in the Baltic, relating changes in dominance patterns to species' ecophysiological and ecological traits, while other authors have linked the impacts of sewage pollution, and subsequent management practices, to specific feeding, habitat-structuring and life-history characteristics (Poore & Kudenov, 1978; Grizzle, 1984; Soltan *et al.*, 2001). The methods have also been used to investigate fishing impacts such as trawling (Ramsay *et al.*, 1998; Hall-Spencer *et al.*, 1999), shellfish harvesting (Spencer *et al.*, 1998) and bait digging (Brown & Wilson, 1997), in environments ranging from coral reefs (McClanahan *et al.*, 1999) to rocky intertidal shores (Lasiak, 1998) and soft sediments (Rumohr & Kujawski, 2000).

Although the methods allow insight into the characteristics controlling organisms' responses to anthropogenic stress, these characteristics are considered post-analysis and the response of every taxon present in an assemblage is not considered, so links between them can only be implied. Organisms sharing particular characteristics are not always affected in the same way (Ramsay *et al.*, 1996; Bergmann *et al.*, 2002) and as the methods do not examine the responses of every taxon expressing a particular characteristic, it can be difficult to determine how general the responses are, thus compromising the ability of the methods to determine anthropogenic effects at the ecosystem level.

Other methods for describing ecological functioning explicitly incorporate information on the biological characteristics of resident fauna. The most commonly encountered of these methods are trophic group or functional group analyses. Trophic group analyses group taxa by their feeding modes, measuring changes in the relative proportions of these groups in response to anthropogenic stress. Functional group analyses extend trophic classifications to incorporate information on additional characteristics such as morphology or mobility. These methods have been used to monitor the effects of a variety of human impacts such as aquaculture-driven vegetation loss (Mistri *et al.*, 2000), habitat fragmentation (Eggleston *et al.*, 1999), pollution (Gaston *et al.*, 1998; Pagola-Carte & Saiz-Salinas, 2000), introduction of non-indigenous species (Ross *et al.*, 2003) and fishing (McClanahan, 1997; Garrison & Link, 2000).

The methods allow greater understanding of the factors controlling change in communities and can be effective in elucidating links between taxa and other ecosystem components (Bonsdorff & Pearson, 1999). They are useful for biomonitoring in systems with large numbers of species as they reduce complexity to manageable sizes (Padilla &

Allen, 2000) and have a relatively low data requirement, so are simpler and cheaper than other biomonitoring methods (Pagola-Carte & Saiz-Salinas, 2000).

One major issue associated with the use of trophic and functional group analyses is uncertainty over the nature of responses of these groups to natural and anthropogenic disturbance. Although functional group structure is stable over time in some biological communities (Steneck & Dethier, 1994), spatial variability has been documented in response to changes in sediment type, tidal influence and a range of other environmental conditions (Roth & Wilson, 1998; Bonsdorff & Pearson, 1999; Pinn & Robertson, 2003). There is some evidence that the methods are able to separate anthropogenic effects from environmental variability (Gaston *et al.*, 1998), but the issue is further complicated by the observation that, in some situations, groups may remain stable in the face of anthropogenic impacts (Garrison & Link, 2000). If change in trophic or functional groups does not always occur, or anthropogenic activities cannot be causatively linked with changes that do occur, this will affect the utility of trophic or functional group analyses for biomonitoring.

The assignment of organisms into groups can be subjective (Sale & Guy, 1992; Bonsdorff & Pearson, 1999), while categorisation can be complicated by the fact that species' habits may change over time, placing them in different groups at different life stages (Caddy & Sharp, 1986; Garrison & Link, 2000). Moreover, trophic interactions are not the only biological forces acting within systems (Caddy & Sharp, 1986). Functional group methods expand the focus from feeding modes to a few other organism characteristics, but these analyses may provide differing results depending on the functional trait examined (Lotze & Schramm, 2000). Many factors act in concert to shape ecosystems, with the relative importance of each varying in different systems (Jennings & Polunin, 1997). Trophic and functional group methods, that focus on only a small number of characteristics, may result in a loss of potentially important ecological information (Charvet *et al.*, 1998; Padilla & Allen, 2000) and are unlikely to provide a complete picture of change in natural or impacted ecosystems.

An alternative approach shows potential for addressing some of the problems associated with other measures of ecological functioning in marine ecosystems. The approach, biological traits analysis (BTA), originated in terrestrial and freshwater ecosystems (Olff *et al.*, 1994; Townsend & Hildrew, 1994; McIntyre *et al.*, 1995), but, until recently, has been largely ignored in marine ecology. BTA provides a picture of the biological characteristics, or traits, expressed by organisms in assemblages (termed biological trait composition). It differs from the taxonomic composition methods as it explicitly incorporates information on the attributes of all members of the assemblage, and from the trophic/functional group methods because it employs information on a wide range of attributes connected to organisms' interactions with each other and their physical and chemical environments, as well as their perceived responses to anthropogenic stress. It can also accommodate intraspecific variation in trait expression (Chevenet *et al.*, 1994), so overcoming the problems encountered in trophic or functional group analyses when taxa fit into more than one functional category.

Both freshwater and terrestrial applications of the approach have shown that BTA is resistant to the large scale geographic changes that can compromise the utility of taxon-based biomonitoring tools, with biological trait composition remaining stable over regional and continental scales (Charvet *et al.*, 2000; Statzner *et al.*, 2001; Hausner *et al.*, 2003). Additionally, studies have shown that BTA has the potential to identify the presence of human impacts (Charvet *et al.*, 1998; Doledec *et al.*, 1999; Ribera *et al.*, 2001; Usseglio-Polatera & Beisel, 2002), separate the effects of different impact types (Usseglio-Polatera *et al.*, 2000a; Kahmen *et al.*, 2002) and identify the primary traits governing responses of systems to human activities (Gayraud *et al.*, 2003; Hausner *et al.*, 2003). These attributes make BTA a promising candidate for describing ecological functioning in marine benthic assemblages and investigating the ecosystem effects of human activities, and Frid *et al.* (2000b) demonstrated that the approach could be applied in the marine environment.

The general aim of this thesis was to develop biological traits analysis for application to marine ecosystems. Presented herein are a series of individual papers that address different aspects of this development. The first step in the development of any novel biomonitoring tool is to determine how well the tool describes the property of interest, in this case ecological functioning. Chapter 2 (Bremner *et al.*, 2003b) critically compares BTA to other approaches proposed for assessing functioning in marine benthic assemblages. After its utility is determined, the next logical step is optimisation of analytical methods. This is accomplished in Chapter 3, where the various analytical tools proposed for use in BTA are compared and contrasted, and the sensitivity of the approach to changes in the traits included is assessed.

Anthropogenic impacts on marine ecological functioning must be placed within the context of changes occurring in response to environmental variability. So, to successfully apply new biomonitoring tools to the assessment of human impacts on a large scale, the nature of the relationship between functioning and environmental conditions should be examined. Chapter 4 investigates this relationship, addressing variability in functioning of benthic assemblages over a range of environmental conditions and examining the environmental parameters and biological traits most influential in determining associations between functioning and the environment.

Chapters 5 and 6 are concerned with the application of BTA to assessing the impacts of anthropogenic activities on benthic assemblage functioning. Fishing activities pose a large threat to marine ecosystems, potentially impacting on all ecosystem components. Chapter 5 examines changes in benthic ecological functioning concurrent with changing levels of fishing effort in a coastal fishing ground (Bremner *et al.*, 2004). Chapter 6 builds on this descriptive study, using an experimental approach to attribute causation to changes in functioning in intertidal assemblages subject to fishing disturbance. Chapter 7 discusses the general findings of the thesis in the context of ecosystem ecology and management and presents avenues for further research .

With the exception of Chapter 6, all analytical chapters utilise datasets previously gathered by the project partners. Data analysed in Chapters 2, 3 and 4 were provided to me by CEFAS Lowestoft, as tables of megainvertebrate biomass and environmental variables (CEFAS annual groundfish surveys, southern North Sea, eastern Channel and Irish Sea regions, 1998). Infauna abundance data used in Chapter 5 were taken from the Dove Marine Laboratory infauna timeseries (1971-2001) and fishing effort data for this chapter were provided by CEFAS Lowestoft.

The number of biological traits utilised varies between chapters, from nine in Chapter 2 to eighteen in Chapter 5. Several factors influence the number of traits selected for inclusion in biological traits analysis, such as the length of the taxon list utilised, the amount of information available on biological characteristics of these taxa and the time required for gathering the information (this issue is discussed in detail in Chapter 3). The influence of these factors varies between chapters, and this is reflected in the numbers of traits utilised.

Chapter 2

A comparison of approaches for describing ecological functioning in marine benthic ecosystems

ABSTRACT

Two methods traditionally employed to investigate ecological functioning in marine benthic ecosystems are relative taxon composition analysis, which interprets changes in the distribution of taxa in terms of the characteristics they exhibit, and trophic group analysis, which investigates differences in feeding mechanisms between assemblages. An alternative approach, biological traits analysis, considers a range of biological traits expressed by organisms to assess how functioning varies between assemblages. This study compares biological traits analysis to the relative taxon composition and trophic group approaches. Biological trait scores were assigned to a range of epibenthic invertebrate taxa from the southern North Sea and eastern Channel and differences in the relative proportions of these traits were investigated using multivariate methods. The traits important in differentiating stations were attachment, flexibility, body form, mobility, feeding method and life habit. Such assemblages were spatially heterogeneous and there was no obvious distinction between different geographical sectors. This contrasted with the results of the relative taxon composition approach, which showed broad patterns in assemblage distribution in the eastern Channel and southern North Sea. The biological traits approach provided information on a larger variety of ecological functions than the other techniques and revealed very different relationships between assemblages. It highlighted a greater diversity of assemblage types and was resistant to large-scale biogeographic variation. Therefore, it is potentially more useful than the traditional approaches for assessing ecological functioning on both large and small scales in benthic environments.

INTRODUCTION

Ecological functioning relates to the roles played by organisms in the maintenance and regulation of ecological processes (Naeem *et al.*, 1999). It incorporates interactions between organisms and their environment into a concept that can portray ecosystem-level structure in marine environments. In marine benthic ecosystems, ecological functioning has traditionally been addressed by describing the taxonomic composition of assemblages. Typically, a pattern in taxonomic composition is revealed and this is subsequently interpreted in the light of changes in a few ecological characteristics exhibited by the taxa, which are relevant to presumed functional roles.

This approach has been used to investigate the effects of different anthropogenic disturbances on functioning in marine systems. Studies have linked characteristics such as feeding mechanisms, longevity, body size and mobility to changes in species distribution in assemblages exposed to stressors such as sewage pollution (Poore & Kudenov, 1978; Grizzle, 1984), anoxia (Beukema *et al.*, 1999) and fishing (Brown & Wilson, 1997; Ramsay *et al.*, 1998; Spencer *et al.*, 1998; Hall-Spencer *et al.*, 1999).

Although the approach detects the responses of individual taxa to environmental stress, it can be difficult to confirm which ecological functions are driving those responses. Organisms that appear to perform similar ecological roles may not always respond to stressors in the same way (Ramsay *et al.*, 1998) because although they share some important attributes they are likely to differ in other, more subtle ways.

A more targeted approach proposed for the study of ecological functioning focuses specifically on feeding mechanisms, which are generally thought to be one of the central processes structuring marine ecosystems (Pearson & Rosenberg, 1978, 1987). Trophic group analyses combine taxa into guilds based on their feeding modes and investigate how these feeding guilds are distributed across assemblages. Such analyses have been used to investigate pollution effects (Gaston *et al.*, 1998; Cardell *et al.*, 1999; Mistri *et al.*, 2000; Mirto *et al.*, 2002), habitat modification (Schlosser, 1982), fishing impacts including dredging (Chicharo *et al.*, 2002) and bottom trawling (Garrison & Link, 2000) and natural variability in environmental parameters (Roth & Wilson, 1998; Desrosiers *et al.*, 2000).

Although this approach provides a stronger link between species and ecosystem functions than the relative taxon composition methods, the reduction of taxa to a small number of groups represents a loss of potentially important ecological information (Charvet *et al.*, 1998). Nor does it account for interactions other than feeding relationships, and other ecological functions performed by organisms that are important in structuring ecosystems may be overlooked (Mancinelli *et al.*, 1998).

Biological traits analysis takes these approaches further and considers a range of taxon characteristics across the entire assemblage. The approach has received little attention in the marine environment, originating in terrestrial plant (Olff *et al.*, 1994; McIntyre *et al.*, 1995) and freshwater invertebrate (Townsend & Hildrew, 1994; Castella & Speight, 1996) ecology. Biological traits analysis is based on habitat templet theory, which states that species' characteristics evolve in response to habitat constraints (Southwood, 1977). Assemblage structure is governed by habitat variability and the biological traits exhibited by organisms will provide information about how they behave and respond to stress (Lavorel *et al.*, 1997) and thereby indicate the state of the environment (Usseglio-Polatera *et al.*, 2000a).

The biological traits approach, which describes the contribution of a suite of ecological characteristics to species' abundance patterns, has a number of advantages over the more traditional measures of ecological functioning. It is based on sound ecological theory (Townsend & Hildrew, 1994) and there are strong links between functional traits and ecosystem processes (Diaz & Cabido, 2001; Coleman & Williams, 2002). As biological trait distribution can be directly related to ecosystem structuring mechanisms (Usseglio-Polatera *et al.*, 2000a), reasons for change in assemblages are highlighted directly and not merely inferred, as with the relative taxon composition approach.

Species replacements generally occur over extensive biogeographic gradients (Gee & Warwick, 1996; Engle & Summers, 1999; Lancellotti & Vasquez, 1999) and generalisations about assemblage structure and function can be difficult when taxon composition varies. Biological traits analysis uses the characteristics shared by many different taxa in an assemblage regardless of species composition and is a valuable approach for measuring ecosystem structure that is independent of biogeographic location (Doledec *et al.*, 1999; Charvet *et al.*, 2000; Usseglio-Polatera *et al.*, 2000a).

In freshwater systems, the approach has been shown to discriminate the effects of disturbance on biological traits (Charvet *et al.*, 2000). Trait structure appears to show a positive relationship with disturbance regimes, where the magnitude of response increases with the level of disturbance (Townsend *et al.*, 1997). Frid *et al.* (2000b) briefly investigated the use of biological traits analysis in marine benthic ecosystems, using epibenthic invertebrate data from the southern North Sea and eastern Channel. They showed that the traits approach had potential for describing ecological functioning in marine systems.

This study critically compares the biological traits approach with the relative taxon composition and trophic group composition approaches. It focuses on determining the extent to which the approaches can (i) identify the main ecological characteristics that distinguish epibenthic invertebrate assemblages from different sites and (ii) highlight differences between assemblages within an area. As the biological traits approach incorporates information on a large variety of ecological characteristics, it was predicted *a priori* that it would highlight the ecological functions most important for assemblage structure in the ecosystem to a greater degree than the other two approaches. It was also expected to identify more heterogeneity between stations than the other approaches because trait structure should be governed by environmental conditions on a smaller scale than taxonomic composition.

METHODS

Data collection

Epibenthic megafauna from ninety-nine subtidal stations in coastal waters (10-50m depth) of the southern North Sea and eastern Channel (ICES divisions IVc and VIId respectively) were sampled from the *RV Corystes* during August 1998. Trawls of 30 minutes duration, covering around 15,000m^2 (Ellis & Rogers, 2000) were carried out using a 4m beam trawl with a 40mm stretched cod-end, chain mat and flip-up rope (Rogers *et al.*, 1998).

Invertebrate taxa were identified to species where possible and the biomass of each recorded as wet weight (kg $hour^{-1}$). For small samples, the whole catch was processed whilst for larger samples, sub-samples of known weight were sorted and the resulting taxa biomass raised to that of the full catch weight.

To focus the investigation on the taxa that contributed most to similarity or variation between stations, the invertebrate dataset was reduced to those taxa found either (i) in the top 90% of biomass at any station or (ii) at more than 50% of stations. This incorporated taxa that were dominant in the biomass of any station in addition to those that were distributed widely but not necessarily of high biomass.

Data analysis

The software packages ADE-4 (Thioulouse *et al.*, 1997) and MINITAB® v.14 (MINITAB® and the MINITAB logo® are registered trademarks of Minitab Inc) were used for all analyses. Invertebrate biomass data were $\log_{10}(x+1)$ transformed prior to analysis to prevent dominant taxa from masking responses of lower-biomass organisms (Clarke & Warwick, 1994).

Relative taxon composition analysis

Centred (covariance) PCA was used to investigate patterns in the relative biomass of taxa over the stations. PCA is a linear ordination method based on actual differences in biomass between samples. Although non-parametric methods are more commonly used to investigate relative taxon composition in marine assemblages, PCA is calculated on the same basis as the methods used to describe biological trait structure (see below) and permits comparison of the relative taxon composition and trait ordinations.

Trophic group analysis

Each taxon in the study was classified as either deposit feeder, filter/suspension feeder, opportunist/scavenger or predator, based on information retrieved from literature sources and specialist knowledge (Table 2.1). Biomass values were then summed for each trophic group at each station. This resulted in a station by trophic group table that was assessed in the same way as the taxonomic data, using centred PCA.

Biological traits analysis

Nine biological traits were chosen for the analysis. These reflected life history (individual or colony size, relative adult longevity and reproductive technique), morphology (body flexibility and form) and behaviour (relative adult mobility, degree of attachment, adult life habit and feeding type) characteristics and were chosen for their potential to maximise differences between taxa. The 9 traits were sub-divided into categories, for example feeding type was separated into the categories ‘deposit feeder’, ‘filter/suspension feeder’, ‘scavenger/opportunist’ and ‘predator’ (Appendix 1(a)).

Individual taxa were then coded for the extent to which they displayed the categories of each trait using a ‘fuzzy coding’ procedure. Fuzzy coding, as described by Chevenet, Doledec and Chessel (1994), allows taxa to exhibit categories of a variable to different degrees. This takes account of variations in trait expression both between life stages and between individuals at each life stage (Castella & Speight, 1996; Charvet *et al.*, 2000).

The scoring range of zero to 3 was adopted, with zero being no affinity to a trait category and 3 being high affinity. For example, A*phrodita aculeata* (Linnaeus) are mostly scavenging organisms but may also deposit feed, so they were coded 1 (deposit), 0 (filter/suspension), 2 (scavenger), 0 (predator) for the trait variable ‘feeding type’. The resulting table of taxa by trait scores is included as Appendix 1(b). Information on biological traits was obtained from a variety of sources including primary and secondary literature and by consulting relevant experts. Where information on a particular trait

Table 2.1. Feeding mechanisms of southern North Sea and eastern Channel megabenthic taxa. Where a taxon exhibited more than one feeding method, it was classified by the preferred or most frequently documented method.

Deposit Feeder	Filter/Suspension Feeder	Opportunist/ Scavenger	Predator
Echinocardium cordatum *Spatangus purpureus*	*Acanthocardia spp.* *Aequipecten opercularis* *Alcyonidium diaphanum* *Alcyonium digitatum* *Ascidiacea* *Crepidula fornicata* *Chaetopterus variopedatus* *Flustra foliacea* *Hydroida* *Laevicardium crassum* *Metridium senile* *Mytilus edulis* *Ophiothrix fragilis* *Ostrea edulis* *Pecten maximus* *Pentapora foliacea* *Porifera* *Sabellaria spinulosa*	*Aphrodita aculeata* *Buccinum undatum* *Cancer pagurus* *Inachus* spp. *Hinia reticulata* *Homarus gammarus* *Liocarcinus depurator* *Liocarcinus holsatus* *Liocarcinus marmoreus* *Macropodia* spp. *Maja squinado* *Necora puber* *Ophiura albida* *Pagurus bernhardus* *Pagurus prideaux* *Psammechinus miliaris*	*Asteria rubens* *Crossaster paposus* *Philine aperta* *Urtica felina*

could not be obtained for a taxon, it was assigned the average score for that trait, so that it had no influence on the overall results (Chevenet *et al.*, 1994).

The links between the biomass of taxa at each station and the traits they showed were investigated using co-inertia analysis (Doledec & Chessel, 1994). Co-inertia analysis assesses the co-structure between two data tables by simultaneously ordinating them, maximising both the variance from the individual tables and the correlation between them (Doledec & Chessel, 1994). This produces scores for each station that incorporate both the biomass and trait information (Doledec *et al.*, 1999). These scores can be plotted on ordination maps in the same way as other multivariate techniques, with each point representing the biomass-weighted biological trait composition of each station. The co-inertia procedure was developed for biological traits analysis in freshwater systems. Although this procedure and the other parametric methods employed in the study may have some limitations in their ability to describe marine epibenthic assemblages, their use allows the results of the study to be compared with those obtained from the larger body of work dedicated to freshwater ecosystems.

Firstly, separate ordinations of the individual data tables were carried out. As before, centred PCA was used to investigate the relative taxon composition of the stations. However, for this analysis the table was transposed so that the taxa were in rows. Fuzzy Correspondence Analysis was used to assess the taxa by traits table. This is a form of Correspondence Analysis used when variables are fuzzy coded (Chevenet *et al.*, 1994). Co-inertia analysis was then carried out using both ordinations and the significance of the resulting co-structure examined with a random permutation test (Doledec & Chessel, 1994). This test randomly permuted the rows of the co-inertia table and re-calculated the inertia statistics 100 times. The observed co-inertia value was then compared to the frequency distribution of the randomly permuted values to assess if it was significantly larger.

Comparison of approaches

The relative taxon composition approach does not directly identify the biological characteristics involved in differentiating assemblages, so these were inferred by examining the biological characteristics of taxa shown by the PCA to make a large contribution to differences between stations. For the trophic group and biological trait approaches, important ecological functions were identified directly from the respective ordinations.

In order to investigate how each approach portrayed differences between assemblages within an area, four separate measures were devised. Initially, the number of distinct assemblage types present amongst the stations was identified for each approach. Complete-linkage cluster analysis was applied to the station scores from the first two axes of each of the three separate analyses (principal components 1 and 2 for the relative taxon composition and trophic group analyses and co-inertia axes 1 and 2 scores for biological traits analysis) (Reynaud & Thiouloiuse, 2000). This measure showed the degree to which each approach could identify different types of benthic assemblage, based on the information included in the analysis.

The other three measures compared the ability of each approach to detect spatial relationships between these assemblage types. The study area was split into four arbitrary sectors, the southern North Sea, north-eastern Channel, mid-eastern Channel and south-eastern Channel (see Ellis & Rogers, 2000). Within each sector, the number of assemblage-types present and the number of stations that differed from the modal assemblage-type were calculated in order to assess how each approach portrayed small-scale assemblage-type diversity. The number of stations within each sector that contained a different assemblage type to their nearest neighbour (using Euclidean distance) was then calculated to assess the ability of each approach to differentiate assemblages from similar geographical locations.

RESULTS

Relative taxon composition analysis

The first two principal components accounted for 43% of the variability in the composition of the benthic assemblages, with 27% on axis 1 and 16% on axis 2 (Table 2.2(a)). The cluster analysis identified 5 groups of stations on the basis of the principal component scores. When overlaid on the PCA ordination, two of these groups separated out from the others along axis 1 (Figure 2.1). Group 3 separated out to the right of the axis and group 5 towards the left. The organisms most influencing the differences between groups along this axis were *Asterias rubens* (Linnaeus), *Alcyonium digitatum* (Linnaeus), *Necora puber* (Linnaeus) and *Psammechinus miliaris* (Gmelin) (Table 2.2(a)). Group 5 had high biomass of all four species, whilst stations within group 3 exhibited relatively low biomass values across taxa.

On the second axis, groups 1 and 2 separated out from the other stations. Stations within these groups had relatively low biomass of *Alcyonidium diaphanum* (Hudson) and higher biomass of *Ophiothrix fragilis* (Abildgaard) and *Aequipecten opercularis* (Linnaeus) (Table 2.2(a)). Stations within group 1 were distinguished from those within group 2 by relatively higher proportions of *O. fragilis*.

Stations in the north-eastern Channel were quite homogenous in terms of their taxonomic composition (Figure 2.2). They differed from other stations in the region in that they shared relatively low biomass of *A. rubens*, *P. miliaris*, *A. digitatum* and *N. puber*. However, stations in the southern North Sea were more variable in their composition and although some were similar to the north-eastern Channel stations, several were members of other groups.

Megainvertebrate assemblages in parts of the south-eastern Channel were also heterogeneous, with stations around the port of Boulogne consisting of mixed assemblages representing all 5 of the cluster analysis groups. In contrast to the

Table 2.2. Principal components analysis of (a) taxon relative biomass and (b) trophic group composition of megabenthic assemblages from the southern North Sea and eastern Channel.

PCA Axes	Eigenvalue	Relative Inertia (%)	Cumulative Inertia (%)	Major Contributing Variables
a) Taxon relative biomass analysis				
1	1.1184	26.95	26.95	*Asterias rubens* *Alcyonium digitatum* *Necora puber* *Psammechinus miliaris*
2	0.6684	16.11	43.06	*Alcyonidium diaphanum* *Ophiothrix fragilis* *Aequipecten opercularis*
b) Trophic group analysis				
1	1.0678	60.74	60.74	Filter/suspension feeder Predator
2	0.4616	26.26	87.00	Filter/suspension feeder Predator

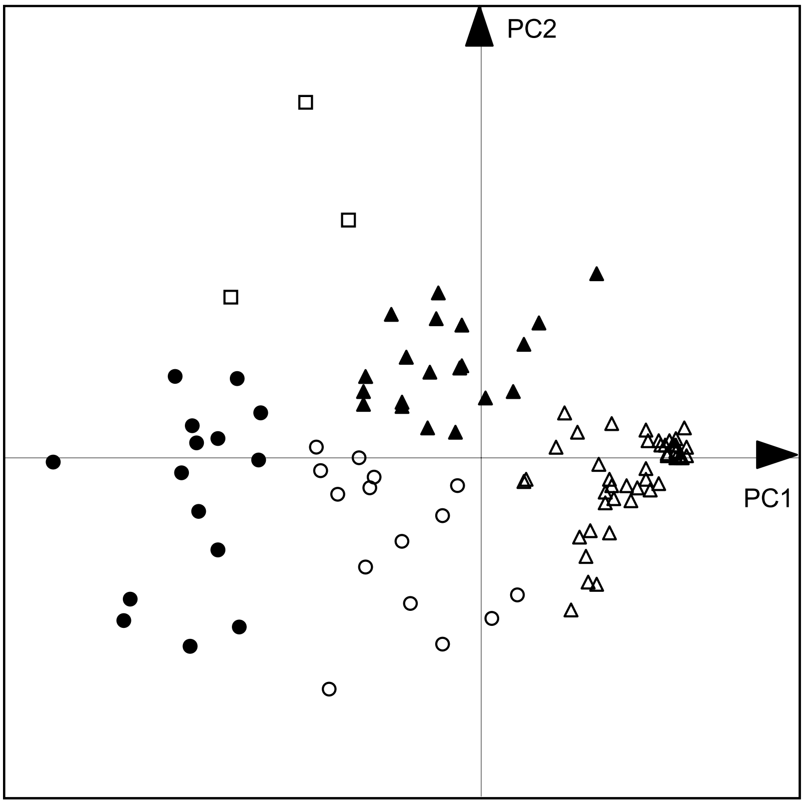


Figure 2.1. First plane PCA ordination of southern North Sea and eastern Channel benthic stations, based on the taxon relative biomass composition of macroinvertebrate assemblages. Stations are marked by groups identified from the cluster analysis; □ = group 1, ▲ = group 2, △ = group 3, ○ = group 4 and ● = group 5.

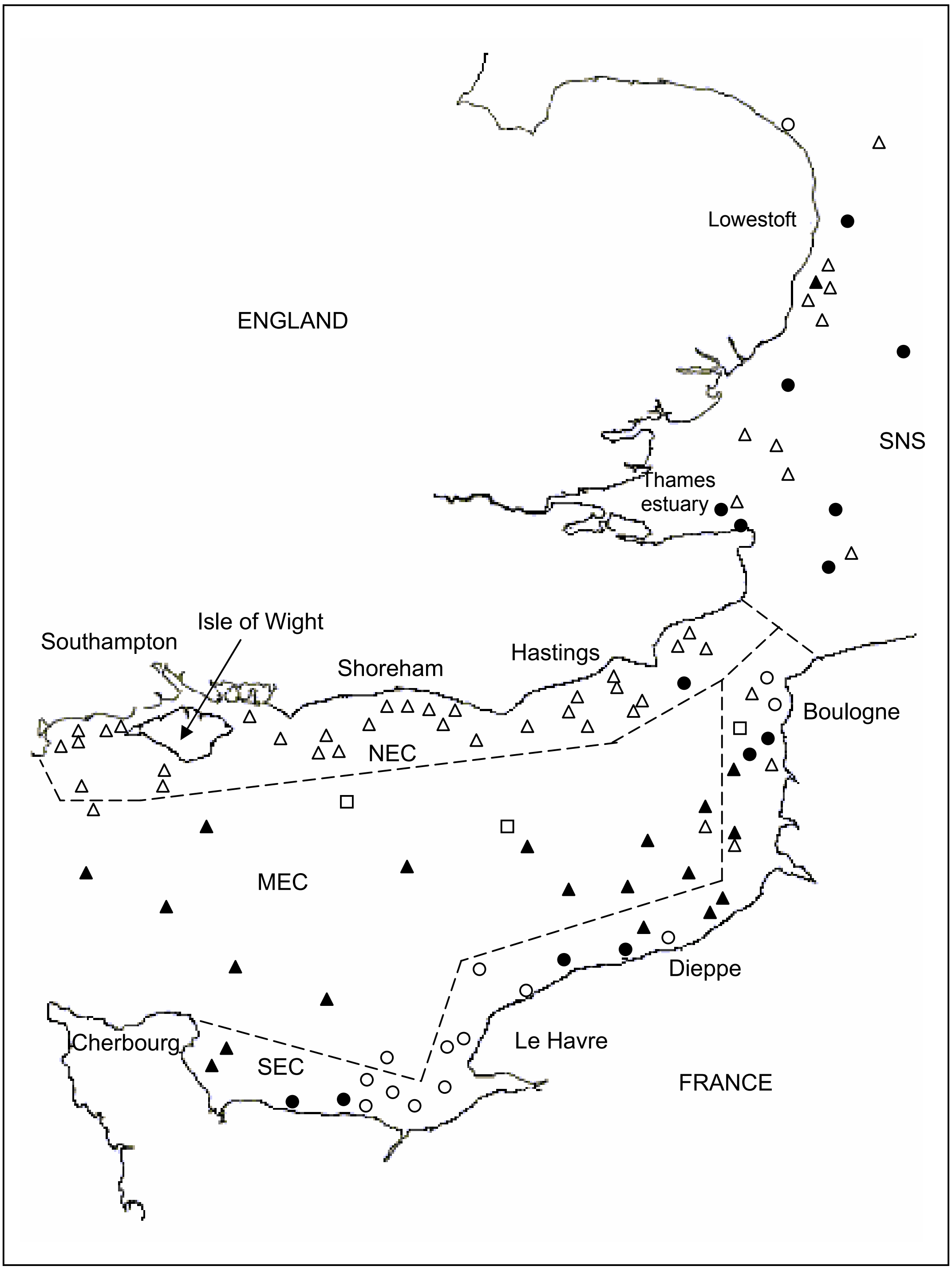


Figure 2.2. Assemblage types present in the eastern Channel and southern North Sea, based on the taxon relative biomass composition of benthic invertebrate assemblages (assemblage types as shown in Figure 1; □ = group 1, ▲ = group 2, △ = group 3, ○ = group 4 and ● = group 5). Sectors are as follows: SNS = southern North Sea, NEC = north-eastern Channel, MEC = mid-eastern Channel and SEC = south-eastern Channel (after Ellis & Rogers 2000).

north-eastern Channel, which was quite distinct in taxon composition from the deeper mid-eastern Channel, several of the south-eastern Channel stations south of Boulogne were quite similar to those located in the mid-eastern Channel region (group 2, Figure 2.2). These shared characteristically high biomasses of *O. fragilis* and *A. opercularis*. One exception to this was a cluster of stations around the Le Havre area (group 5, Figure 2.2), which displayed particularly high biomass of *A. rubens*.

Trophic group analysis

PCA of the trophic group composition showed that the first two axes accounted for 87% of variability between the stations, with 61% of this variability projected onto axis 1 and 26% on axis 2 (Table 2.2(b)). Five station groups were identified by the cluster analysis. Groups 3 and 4 separated out to the right of axis 1, whilst group 1 was distinguished towards the left (Figure 2.3). Group 5 showed some separation from the other groups along the second axis. Filter feeders and predators accounted for most of the variation along each of the first two axes (Table 2.2(b)), with predator biomass contributing most to projections along axis 1 and filter feeders to axis 2

As with the relative taxon composition analysis, stations around Le Havre grouped apart from the others, including nearby south-eastern Channel stations (group 4, Figure 2.4). These were characterised by a relatively higher predator biomass than the other stations. Stations around Boulogne were as variable trophically as they were in terms of taxon composition, again including representatives of all of the cluster analysis groups. There was also some continuity between the two approaches when stations in the mid-eastern Channel were examined. Many of the stations in the sector exhibited homogenous trophic group compositions (group 2, Figure 2.4).

Several differences between the approaches were however noted. Stations towards the eastern end of the mid-eastern Channel formed a distinct group (group 5, Figure 2.4). These stations had been similar in terms of taxon composition to the other mid-eastern Channel stations, but were now distinguished by a relatively low filter feeder biomass.

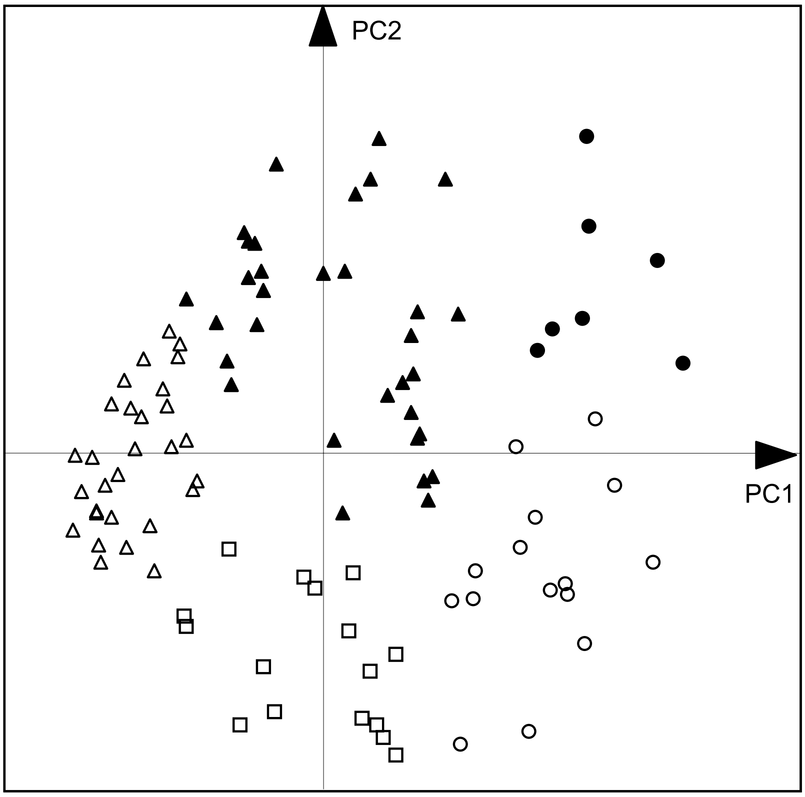


Figure 2.3. First plane PCA ordination of southern North Sea and eastern Channel benthic stations, based on the trophic group analysis of macroinvertebrate assemblages. Stations are marked by groups identified from the cluster analysis; △ = group 1, ▲ = group 2, ● = group 3, ○ = group 4 and □ = group 5.

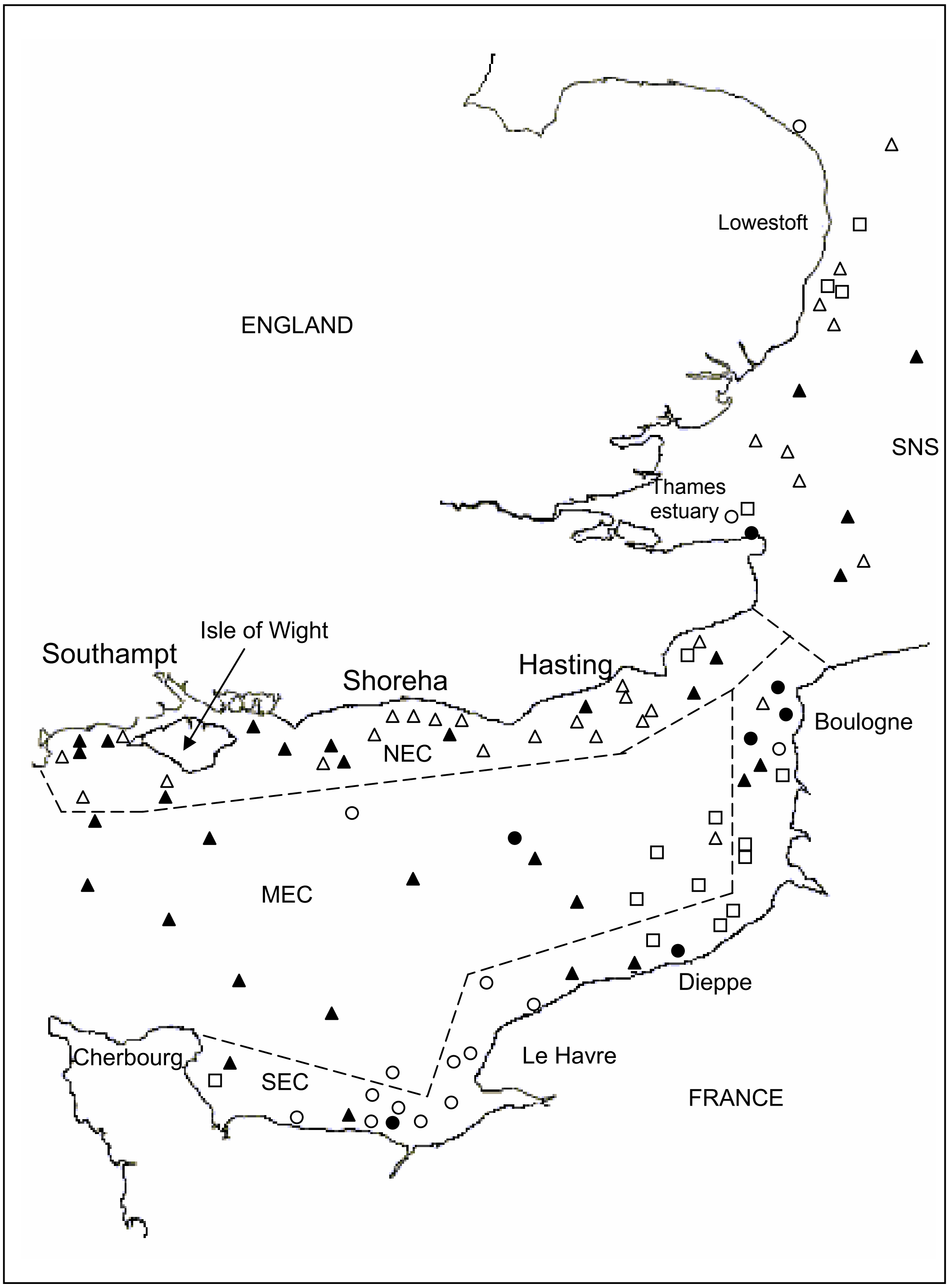


Figure 2.4. Assemblage types present in the eastern Channel and southern North Sea, based on trophic-group analysis of benthic invertebrate assemblages (assemblage types as shown in Figure 3; △ = group 1, ▲ = group 2, ● = group 3, ○ = group 4 and □ = group 5). Sector codes are as follows: SNS = southern North Sea, NEC = north-eastern Channel, MEC = mid-eastern Channel and SEC = south-eastern Channel (after Ellis & Rogers 2000).

This was also the case for stations between Boulogne and Dieppe, in the south-eastern Channel.

Some homogeneity in trophic group composition was noted in the north-eastern Channel, with stations in group 1 exhibiting low predator biomass. However, several stations in the sector, particularly around Southampton and the Isle of Wight, showed higher predator biomass then their coastal neighbours (group 2, Figure 2.4). These stations were more similar to the mid-eastern Channel assemblages in terms of their trophic group composition.

Biological traits analysis

The purpose of the co-inertia analysis was to combine information on taxon distributions over the study area with information on some of the biological traits that they exhibited. The analysis expressed the taxon composition of each station in terms of the component taxa's biological traits, producing a table of the biomass-weighted biological trait composition of each station. Analysis of the table showed how stations varied in terms of their trait composition.

Axes 1 and 2 of the Co-inertia analysis accounted for 79% of the variability in biological trait composition between the stations, with 59% of inertia projected along axis 1 and 20% along axis 2. The random permutation test confirmed that the distribution of biological traits between stations was not random (estimated $P<0.05$). The cluster analysis identified 5 station groups. Groups 1 and 2 separated from the others along axis 1 of the ordination and groups 4 and 5 showed some distinction along the second axis (Figure 2.5).

The traits with the greatest influence on variability between groups of stations were identified by plotting the individual co-inertia scores for each trait category (Figure 2.6). Traits contributing to the variation along axis 1 were attachment, flexibility and body form, with groups 1 and 2 being characterised by permanently attached organisms, highly

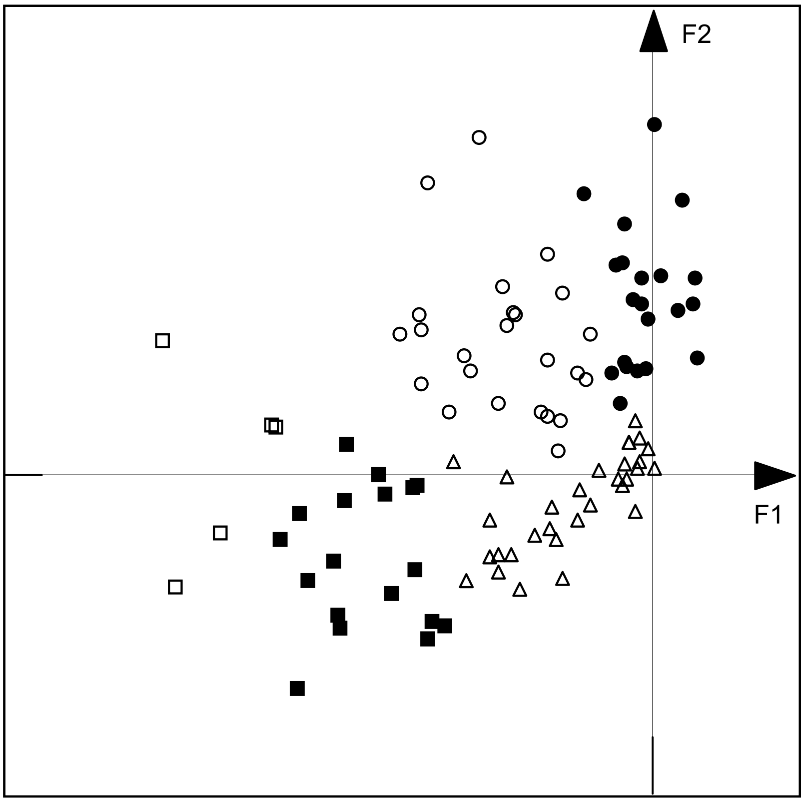


Figure 2.5. First plane co-inertia ordination of southern North Sea and eastern Channel benthic stations, based on biological trait structure of macroinvertebrate assemblages. Stations are marked by groups identified from the cluster analysis; ■ = group 1, □ = group2, △ = group 3, ○ = group 4 and ● = group 5.

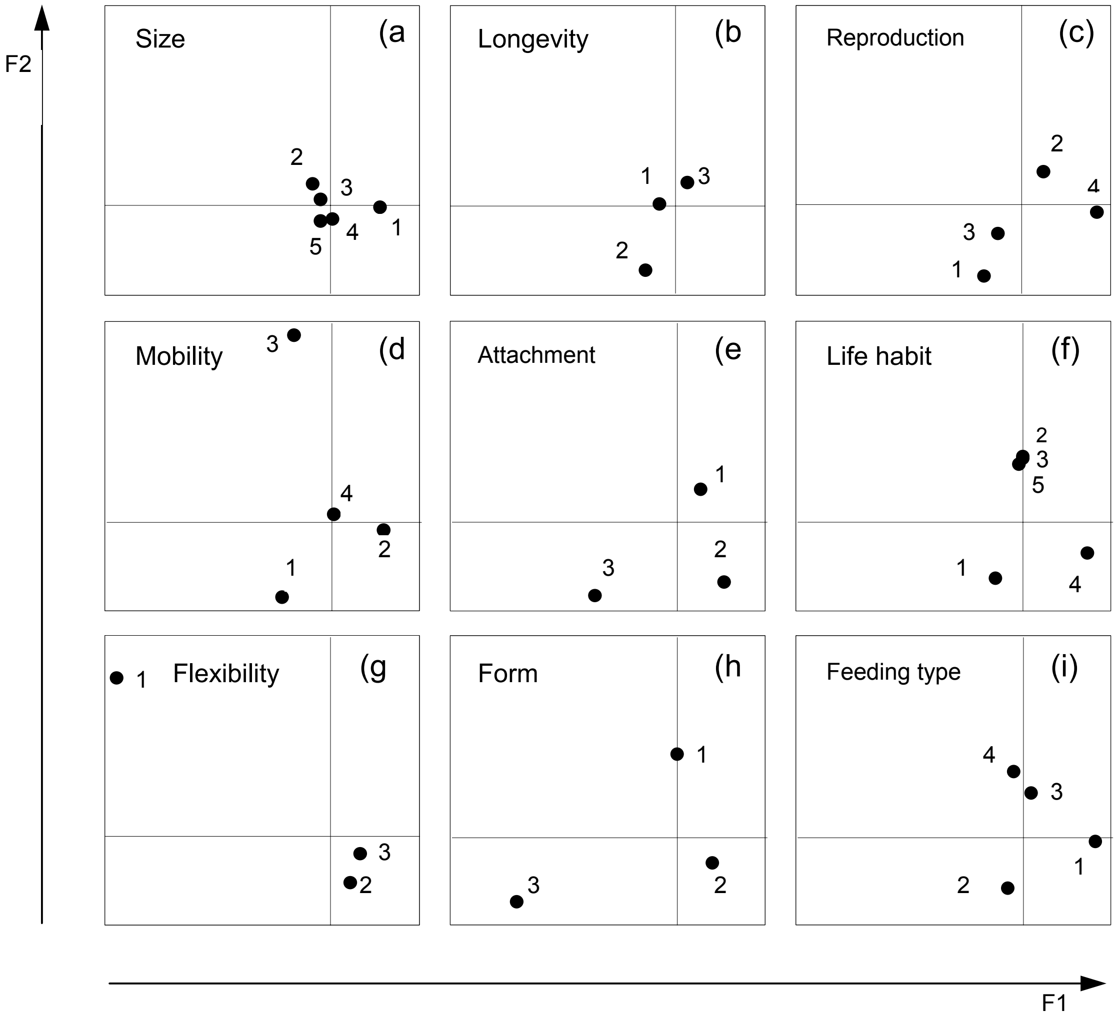


Figure 2.6. Ordination of the biological trait categories from the co-inertia analysis. Trait variables are (a) individual/colony size, (b) relative adult longevity, (c) reproductive technique, (d) relative adult mobility, (e) degree of attachment, (f) adult life habit, (g) body flexibility, (h) body form and (i) feeding type. Trait categories are described in Appendix 1(a).

flexible organisms and those of erect stature (Figure 2.6(e), (g) and (h)). Groups separating along axis 2 were differentiated by a number of traits: mobility, flexibility, body form, feeding habit and adult life habit. Groups 4 and 5 were characterised by high biomass of very flexible organisms, those that were flat and those of medium mobility (Figure 2.6(d), (g) and (h)). They also had relatively higher biomass than other stations of organisms that swam, crawled or dwelled in crevices and those that were predators or opportunists/scavengers (Figure 2.6(f) and (i)).

Stations grouped together differently when described by their biological trait composition rather than by their taxon or trophic group composition (Figure 2.7). The distinct mid-eastern Channel grouping highlighted by both previous analyses was no longer evident. Several of these stations were similar in their trait structure to those around Le Havre in the south-eastern Channel (group 4, Figure 2.7). These were dominated by flexible, flat, moderately mobile predators or scavengers that were swimming, crawling or crevice-dwelling.

In the north-eastern channel, two-thirds of the stations were similar in their trait composition (group 3, Figure 2.7), however stations around Hastings exhibited a variety of trait structures. A cluster of stations between Shoreham and Southampton were distinguished from those nearby by a relatively higher biomass of permanently attached, erect, flexible organisms (group 1, Figure 2.7).

In keeping with the spatial arrangement of stations described in the relative taxon composition and trophic groups analyses, areas of heterogeneous trait composition were evident in stations around Boulogne and Lowestoft. However, using the biological traits approach these heterogeneous areas were extended, south towards the Thames estuary in the southern North Sea and southwest to Dieppe in the south-eastern Channel.

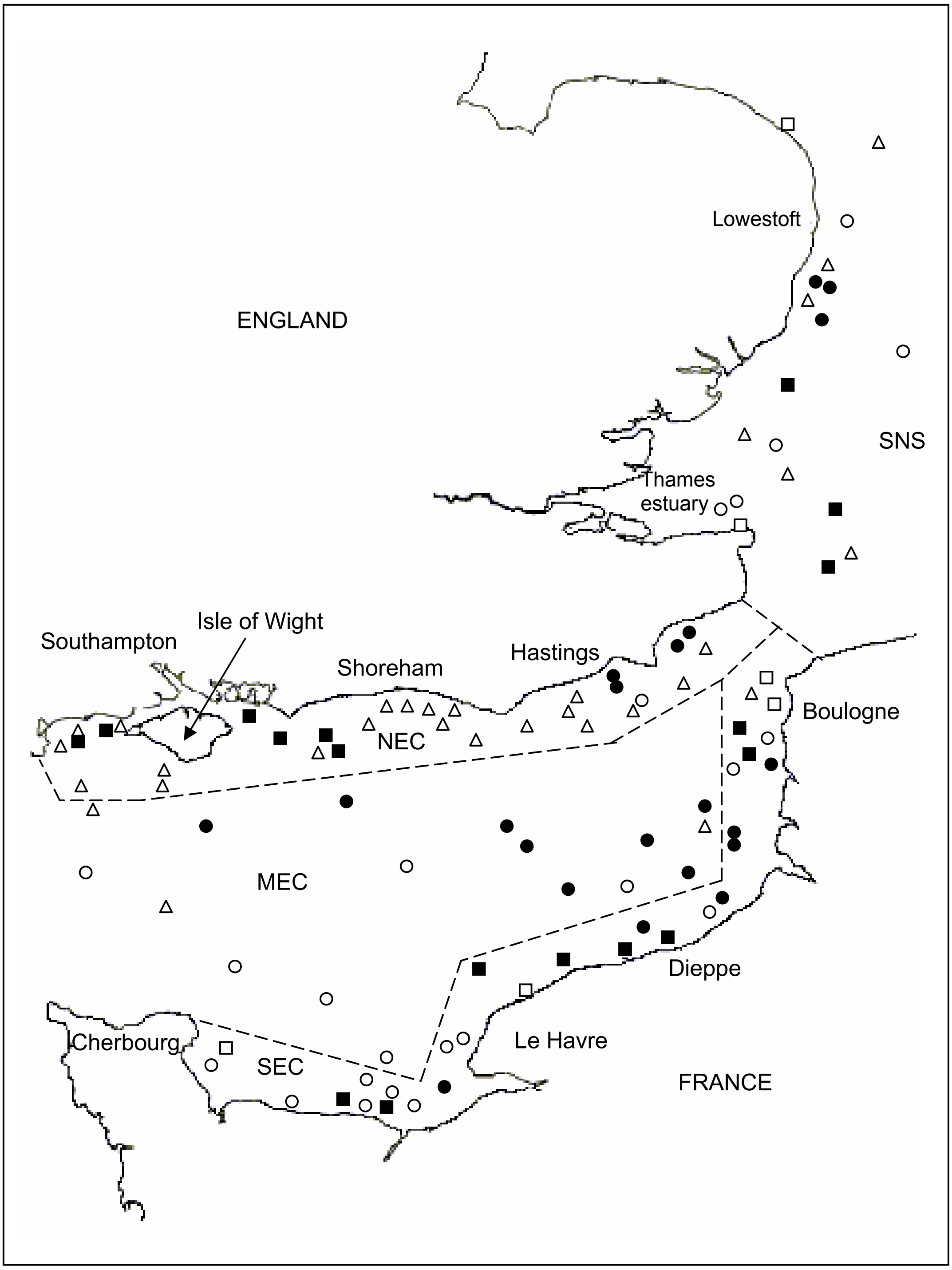


Figure 2.7. Assemblage types present in the eastern Channel and southern North Sea, based on the biological trait structure of benthic invertebrate assemblages (assemblage types as shown in Figure 2.5; ■ = group 1, □ = group 2, △ = group 3, ○ = group 4 and ● = group 5. Sector codes are as follows: SNS = southern North Sea, NEC = north-eastern Channel, MEC = mid-eastern Channel and SEC = south-eastern Channel (after Ellis & Rogers 2000).

Comparison of approaches

There was little difference between the approaches in their ability to identify assemblage types over the whole region, with each approach identifying 5 different types of assemblage at a distance of 0.5 (50%). Within each geographic sector, assemblage types were more evenly distributed when defined by biological traits than by relative taxon composition or trophic groups (Figure 2.8), but only in the north-eastern Channel were relatively more assemblage types identified by the biological traits approach than by both of the others (Table 2.3).

The biological traits approach provided consistently more spatial heterogeneity than the relative taxon composition approach. Within each sector, the number of stations differing from the modal assemblage type increased between the relative taxon composition and biological traits analyses, as did the number of stations differing from their nearest neighbour in the north-eastern, mid-eastern and south-eastern Channel (Table 2.3).

When the biological traits approach was compared to the trophic group approach, there was an increase in the number of stations differing from their nearest neighbours in the southern North Sea, mid-eastern and south-eastern Channel (Table 2.3). The number of stations differing from the modal assemblage type increased between the two approaches in the southern North Sea and mid-eastern Channel. Within the north-eastern Channel however, the number of stations differing from their nearest neighbour and from the modal assemblage type both decreased between the trophic group and biological traits analyses.

DISCUSSION

The relative taxon composition approach aims to describe epibenthic functioning by relating changes in composition to characteristics of selected taxa. With it's incorporation of information on the biological roles of all component taxa, the biological traits approach would seem to offer several advantages over relative taxon composition

Table 2.3. Assemblage type and spatial heterogeneity for stations within each sector of the southern North Sea and eastern Channel, as described by taxon relative biomass, trophic group and biological trait analyses. Each approach identified 5 assemblage types, based on a distance of 50% derived from cluster analysis.

	Community types present (%)	Stations differing from nearest neighbour (%)	Stations differing from modal community type (%)
Southern North Sea			
Taxon Relative Biomass	80	73.7	47.4
Trophic Group	100	68.4	57.9
Biological Traits	100	73.3	68.4
North-east Channel			
Taxon Relative Biomass	40	3.1	3.1
Trophic Group	60	50.0	40.6
Biological Traits	80	28.1	34.4
Mid-east Channel			
Taxon Relative Biomass	60	53.0	29.4
Trophic Group	100	47.1	47.1
Biological Traits	60	58.8	52.9
South-east Channel			
Taxon Relative Biomass	100	50.0	56.7
Trophic Group	100	60.0	63.3
Biological Traits	100	76.7	60.0

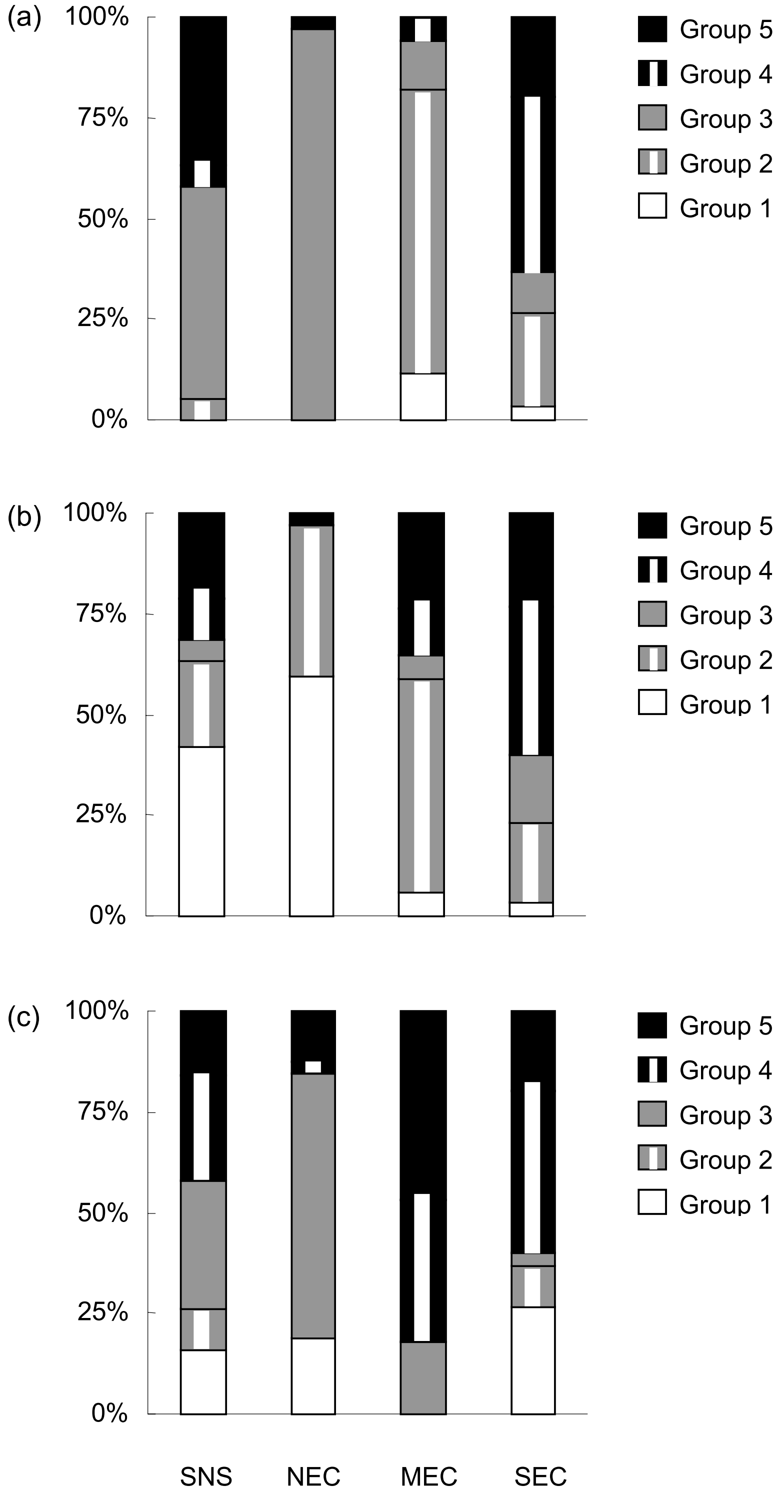


Figure 2.8. The distribution of assemblage types in the southern North Sea and eastern Channel, based on (a) taxon relative biomass composition, (b) trophic group composition and (c) biological trait composition. Sectors are as follows: SNS = southern North Sea, NEC = north-eastern Channel, MEC = mid-eastern Channel and SEC = south-eastern Channel.

analysis in terms of characterising differences in the underlying structure of the epibenthic assemblages of the southern North Sea and eastern Channel. The first two axes of the relative taxon composition PCA accounted for less than 50% of variance in the assemblages. This suggests that more than half of the variation between stations was explained by subtle differences in taxon distributions. However, around 80% of variance was accounted for in the first two axes of the biological traits ordination, indicating that the majority of the variability in trait structure between the assemblages was governed by distinct changes in a number of ecological functions. The fact that so much more of the variation between sites was accounted for by consideration of the biological traits than taxon composition suggests that there may be general trends in ecological functioning across benthic assemblages that are not revealed using taxon identities alone.

Biological traits analysis also highlighted more small-scale heterogeneity than the relative taxon composition analysis, with more stations in general differing from their nearest neighbour and an increase in functional diversity, both in terms of assemblage-type richness and ‘evenness’ (stations differing from the modal assemblage-type).

There was some evidence of a geographical gradient in relative taxon composition within the region, with a high degree of similarity in the north-eastern Channel and the southern North Sea, but differences between these sectors and the mid-eastern and south-eastern Channel. Other studies have identified geographical variation in both fish (Rogers *et al.*, 1998) and invertebrate (Holme, 1961, 1966; Dyer *et al.*, 1982) taxon composition in the North Sea and Channel, linked to large-scale processes such as tidal action, sand transport, circulation patterns and temperature gradients (Dyer *et al.*, 1983; Sanvicente-Anorve *et al.*, 1996).

The role of smaller-scale factors such as substrate type and seabed morphology in determining differences in taxon composition of assemblages is not certain. Some authors have identified a relationship (Ford, 1923; Brown *et al.*, 2002; Sanvicente-Anorve *et al.*, 2002) but others argue that it is not universal (Seiderer & Newell, 1999; Newell *et al.*, 2001). Recent evidence suggests that species’ distributions are influenced by habitat on a small scale, however the relationship is complex and incorporates multiple factors (Freeman & Rogers, 2003). The lack of geographical gradients and the increase in local heterogeneity in biological trait structure suggest that ecological functioning is driven primarily by small, local-scale differences in environmental conditions and that it is robust in the face of large-scale geographical influences. In addition to providing information on the scales of organism-environment relationships, this makes traits analysis potentially useful for investigations of trends in ecosystem functioning on large scales that are not practical using relative taxon composition analysis.

Any analysis of multi-species data sets using advanced statistical techniques will always be prone to two confounding factors. Firstly, the mathematical techniques used will always introduce some level of bias and different approaches will bring different distortions to the output. Secondly, ecological effects, whether they are natural (e.g. geographic gradients, salinity clines) or anthropogenic in origin are likely to operate on a continuum and so multivariate analyses must often distinguish gradients rather than discrete changes. The three approaches are increasingly explicit in their incorporation of information on ecological functioning. The consistency in the direction of change between the approaches, particularly the dampening of the biogeographic gradient and the increase in functional diversity, leads to the conclusion that the results presented here do have real ecological significance and are not just artefacts of the statistics used.

Freshwater studies have shown that biological trait composition is more stable than taxonomic composition in semi-natural systems (Charvet *et al.*, 2000), but this functional composition is affected by human impacts (Doledec *et al.*, 1999; Charvet *et al.*, 2000). The benthos of the North Sea and Channel are subject to several types of human disturbance, including fishing (Rijnsdorp *et al.*, 1991; Rijnsdorp *et al.*, 1998), minerals extraction (Desprez, 2000; van Dalfsen *et al.*, 2000; ICES, 2001) and pollutants/contaminants (Jones & Franklin, 2000), the distribution of which are patchy and localised in nature. Local differences in the severity of these impacts may well have an influence on the biological traits expressed in assemblages, leading to functional differences between neighbouring assemblages.

It is difficult to say whether the observed differences in trait structure are influenced by human impacts. Resistance/resilience traits that may increase in impacted systems, e.g. mobility and avoidance mechanisms, robustness and opportunistic life history tactics (Frid *et al.*, 2000a; Bradshaw *et al.*, 2002), are not necessarily excluded from stable or unimpacted assemblages (Townsend *et al.*, 1997). Investigating changes in the relative proportions of biological traits over time may provide the only reliable means of identifying impact-driven alterations to ecological functioning.

Some of the traits linked to resistance/resilience were important in differentiating assemblages. Groups 4 and 5 were distinguished by high biomass of moderately mobile, flexible animals that swam or crawled. However, most of the differences between stations were accounted for by traits associated with structure-forming organisms, i.e. permanent attachment and erect stature. Changes in the proportions of these organisms have been linked to fishing (Auster *et al.*, 1996), but in the present study insufficient information on fishing effort was available to investigate this link. Kaiser *et al.* (1999) linked the occurrence of sessile, structure-forming fauna to water depth, and stations characterised by permanently attached organisms did appear limited to shallow, coastal areas of the study (Figure 2.7).

Feeding interactions have been promoted as the most important factor structuring invertebrate assemblages (Pearson & Rosenberg, 1987) and organisms' feeding mechanisms can dictate their response to impacts such as fishing (Rumohr & Kujawski, 2000; Chicharo *et al.*, 2002). In this respect, trophic analysis should be useful in differentiating assemblages in the region. However, the low range of feeding types encountered in the study, combined with the recent suggestion that trophic interactions are not always altered in impacted systems (Ramsay *et al.*, 1996; Ramsay *et al.*, 1998; Jennings *et al.*, 2001b) casts doubt on the usefulness of the trophic group approach in monitoring human impacts. Traits analysis showed that feeding mechanisms were influential in determining differences between the assemblages, but they were less important than attachment, body form and mobility.

Body size has also been implicated in assemblage structure in impacted systems (Jennings *et al.*, 1999; Kaiser *et al.*, 2000). It is perhaps surprising that body size does not appear to be an important factor in differentiating these assemblages (but see Frid *et al.*, 2000a). Usseglio-Polatera *et al.* (2000b) found that two traits connected to species' life cycles (life duration and aquatic stages), which were thought *a-priori* to be important in generating differences between groups of benthic invertebrates, were in fact relatively unimportant. It seems that a whole range of biological traits, not just those currently viewed as important, contribute to variation in benthic assemblages.

In this respect, biological traits analysis is more useful than the relative taxon composition and trophic group approaches. Relative taxon composition can only address functioning indirectly and to a limited extent. A restricted number of characteristics (commonly feeding preferences and body size) are chosen to interpret changes in taxon biomass, the characteristics are only applied post-analysis and only on selected taxa. So although the approach includes a degree of information on ecological characteristics, the method is subjective and only ever allows a superficial insight into the functioning of the system. The trophic group approach incorporates biological characteristics into the initial phase of the analysis, but because it focuses only on feeding interactions, it has limited potential to capture functioning in the epibenthic system. The important point about biological traits analysis is that it is an objective measure of ecological functioning, directly incorporating into the analysis information on a range of ecological characteristics exhibited by the full complement of taxa.

It is interesting to note the species replacements do not always lead to changes in ecological functioning. Stations around Le Havre, characterised by high biomass of *A. rubens*, differed in relative taxon composition from those in the mid-channel. However, they were quite similar in terms of their biological trait structure. In this area, other organisms were fulfilling the same functions as *A. rubens*. Ecological functioning persisted even when the species composition had altered. This consistency of functional structure will have consequences for ecosystem monitoring, management and conservation where geographical gradients in taxonomic composition make these difficult on a large scale. The present study addressed only one component of marine benthic ecosystems, the large epifauna. The usefulness of the approach in this respect highlights it's potential for providing insights into functioning of other system components, such as infauna (see Chapters 5 and 6, Bremner *et al.*, 2004) and perhaps, in future, of the marine benthic ecosystem as a whole.

Biological traits analysis provides more information on the ecological functions performed by organisms in marine benthic assemblages than both the relative taxon relative composition and trophic group approaches. Biological trait structure is less affected by the large-scale geographic influences that hamper studies of relative taxon composition and is linked more to small, local-scale environmental conditions. It provides a robust method for studying ecological functions of benthic systems that has the potential to be applied at both local and international scales.

Chapter 3

Methods for conducting biological traits analysis in marine benthic ecosystems

ABSTRACT

Biological traits analysis (BTA) is a method recently proposed for describing ecological functioning of marine benthic assemblages. It incorporates information on species' distributions and the biological characteristics they exhibit, to produce a summary of the biological trait composition of assemblages. The approach provides a link between species, environments and ecosystem processes, and is potentially useful for the investigation of anthropogenic impacts on ecological functioning. As part of the development of BTA for application to marine systems, two aspects of the approach were investigated here; the comparative applicability of three analytical tools proposed for conducting BTA, and the sensitivity of the approach to the number and type of trait selected for analysis. The three tools, fuzzy correspondence analysis (FCA), co-inertia analysis (CoI) and non-metric multidimensional scaling (nmMDS) portrayed trait composition of benthic assemblages in similar ways, however nmMDS had less power to discriminate between assemblages with varying trait composition than FCA or CoI. For the thirteen biological traits investigated, the number of traits selected for analysis had more of an effect on the ability of BTA to describe variability in trait composition than the identity of the traits themselves. Ultimately, selection of biological traits for inclusion in BTA will be based on a trade-off between their efficacy for describing variability in ecological functioning and the time and effort required to gather biological information for the taxa studied. The choice of analytical tool is a balance between the power of the tool to describe changes in trait composition and the ease with which results can be interpreted. nmMDS is appropriate for providing a general picture of functioning in marine assemblages, whereas FCA and CoI have greater power to detect the effects of human impacts, but are more difficult to interpret. Including as many traits as possible will lead to the most useful description of ecological functioning, as will selecting traits sensitive to anthropogenic impacts or closely linked to important ecosystem processes.

INTRODUCTION

With the advent of an ecosystem approach to marine monitoring and management, the importance of developing methods to investigate ecological functioning is receiving increasing attention. Several approaches have been proposed for assessing functioning, including trophic group analysis (Roth & Wilson, 1998; Desrosiers *et al.*, 2000), functional group analysis (Mancinelli *et al.*, 1998; Bonsdorff & Pearson, 1999; Padilla & Allen, 2000; Pearson, 2001) and integrative indices such as the index of biotic integrity (Borja *et al.*, 2000), the ecological evaluation index (Orfanidis *et al.*, 2003) and the ecofunctional quality index (Fano *et al.*, 2003).

One of the most promising of the recently proposed approaches is biological traits analysis (BTA) (Statzner *et al.*, 1994). Biological traits analysis uses a series of life history, morphological and behavioural characteristics of species present in assemblages to indicate aspects of the functioning of biological assemblages. These biological characteristics can be shared by organisms that differ widely in their taxonomic identity (Usseglio-Polatera *et al.*, 2000b), so BTA can be applied over large geographic ranges where there are gradients in species composition (Charvet *et al.*, 2000; Statzner *et al.*, 2001) and to different taxonomic groups (Doledec & Statzner, 1994). In freshwater systems, where the approach was initially developed, there is mounting evidence that BTA has the capacity to both identify the presence of an anthropogenic impact (Charvet *et al.*, 2000) and separate the contrasting effects of different impact types (Doledec *et al.*, 1999).

The approach can be used to address ecological functioning in marine ecosystems. It performs well in comparison to more traditional assessment methods (Chapter 2, Bremner *et al.*, 2003b) and initial marine applications suggest it can be used to provide a view of the effects of impacts such as fishing on benthic assemblage functioning (Chapters 5 and 6, Bremner *et al.*, 2004).

BTA uses multivariate ordination to describe patterns of biological trait composition over entire assemblages, using information on species' distributions and the biological traits they exhibit (Charvet *et al.*, 1998). Several ordination tools are available. The two most widely used are fuzzy correspondence analysis (FCA, Chevenet *et al.*, 1994) and co-inertia analysis (CoI, Doledec & Chessel, 1994).

FCA is a parametric linear ordination method that uses eigenanalysis to investigate differences between samples, based on the biological traits exhibited by species present in the assemblages, weighted by their abundance or biomass. CoI is also based on eigenanalysis, however it differs from FCA in that it investigates patterns in species' distributions and their biological traits separately, searching for covariation between them (Doledec & Chessel, 1994). Both FCA and CoI allow the traits that contribute most to differences in functioning between assemblages to be identified and visualised. Additionally, CoI provides a measure of the strength of the relationship between species' distributions and the biological traits they exhibit (Doledec & Chessel, 1994).

Non-metric multi-dimensional scaling (nmMDS) is a non-parametric ordination method frequently used in the analysis of marine assemblage composition (Clarke, 1993). Unlike FCA and CoI, which utilise absolute distance between samples as a measure of the difference between them, nmMDS is based on the rank similarities of samples and produces an ordination plot showing relative differences in biological trait composition. nmMDS does not explicitly identify the biological traits most important for differentiating assemblages, nor does it provide a measure of the relationship between species distributions and traits. However, it is very widely used in marine ecology and management and has the potential for use in BTA. Each ordination method will have advantages and disadvantages, and initial stages of development of BTA must include an appraisal of the tools available.

The selection of biological traits for BTA is important. A wide variety of traits are potentially available for describing ecological functioning, but they will not all be equally useful. Ideally, monitoring tools should utilise traits that exhibit low variability in natural, reference conditions but respond to anthropogenic stressors (Doledec *et al.*, 1999). However, most coastal ecosystems are subject to human impacts in some form, and it is very difficult to find examples of entirely natural conditions, and consequently to identify traits that are stable under these conditions. In this case, traits that capture the largest amount of variability in ecological functioning between different assemblages will be more useful for monitoring the effects of human impacts than those that show little change.

Trait selection is constrained by the amount of information available (Gayraud *et al.*, 2003) and the costs of processing it. For example, in benthic systems, species' feeding methods and relative mobility have implications for resource utilisation and energy transfer (Pearson, 2001) and are useful for examining functioning. Information on these traits is relatively easy to find for benthic fauna (see, for example, Pearson & Rosenberg, 1978; Fauchald & Jumars, 1979). Other traits, such as movement methods, mucous production and the ability to form biogenic structures, are extremely important for nutrient cycling and substrate stability (Austen *et al.*, 2002; Reise, 2002; Widdows & Brinsley, 2002). However, these traits have received less attention in benthic studies, so are much harder to characterise for the diversity of fauna making up typical benthic assemblages.

Different traits can describe different aspects of ecological functioning and some are intimately linked to particular functions, whereas others serve only as indirect indicators (Lavorel & Garnier, 2002). The type of trait included in analyses has the potential to affect the way benthic assemblages are viewed, so the number and type of traits chosen for BTA should not be an arbitrary decision. Development of BTA must also include an assessment of which traits provide the most useful description of ecological functioning so that selection is optimised.

This paper describes the development of BTA to describe the functioning of ecological assemblages. I compared the three analytical tools that have been proposed for BTA, considered their power to discriminate between assemblages having different trait compositions, and assessed the sensitivity of BTA to the number and type of traits selected.

METHODS

Dataset 1

Dataset 1 contained biomass (kg hour^{-1} trawling) data for megabenthic invertebrate assemblages sampled at ninety-nine subtidal stations in the southern North Sea and eastern Channel (see Chapter 2, Bremner *et al*. (2003b) for details of sampling and dataset preparation). Nine biological traits were utilised in the initial analysis (relative individual/colony size, adult longevity, reproductive method, relative adult mobility, degree of attachment, adult movement method, body flexibility, body form and feeding habit; Appendix 2(a)), with individual taxa scored for the extent to which they displayed the categories of these traits using fuzzy-coding (Chevenet *et al*., 1994) (Appendix 2(b)). The two resulting data tables, containing taxa biomass for each station and biological trait scores for each taxon, formed the basis of the analysis.

Dataset 2

To address whether the analytical tools had the power to detect differences in biological trait composition between benthic assemblages, a simulated dataset was created where trait composition could be manipulated in both subtle and extreme ways. This was achieved by manipulating the biomass of all taxa that exhibited a single trait category (using the taxa by trait table from dataset 1), hence manipulating the frequency of that trait category within an assemblage.

A consequence of manipulating the biomass of taxa exhibiting the selected trait category is that other trait categories shown by these taxa will also be affected. This will lead to changes in the frequency of several trait categories, masking the manipulations of the selected category. The greater the number of taxa exhibiting the selected category, the more pronounced this effect will be. Therefore, the following steps were taken to minimise this potentially confounding factor.

First, trait categories that were common to a large number of taxa were removed from the dataset. Second, where several categories of a trait were expressed by taxa, these traits were also excluded from the dataset. This resulted in a reduced set containing the traits relative adult mobility, degree of attachment, body form and feeding method. Next, the species by trait table was simplified to limit the number of trait profiles included. A trait profile is the pattern of trait categories exhibited by individual taxa. This simplification was achieved by removing taxa that were the only representatives of a given trait profile. Finally, the trait category 'low relative adult mobility' was selected for further manipulation, as it was the category shown by the fewest taxa. The resulting species by traits table is shown in Table 3.1.

A species biomass table was created by assigning arbitrary biomass values of between 100-200kg hr^{-1} to each species in Table 3.1, over a series of 30 samples. Six different treatments were adopted for the analysis, simulating scenarios of increased frequency, decreased frequency and complete removal of low mobility fauna from the dataset (Table 3.2). These manipulations were not designed to be ecologically relevant, merely to provide groups of samples with pre-determined differences in the frequency of a single trait category (low-mobility fauna).

Comparison of analytical tools (dataset 1)

Like most standard ordination methods, FCA and nmMDS are applied to a single data table, so an initial weighting step was required to combine the information from the taxon biomass table and the biological traits table. To do this, the trait category scores for each taxon present at a station were weighted by their biomass at that station. The category scores were then summed over all taxa present at the station, resulting in a sample by trait table showing the overall frequencies of biological traits at each station (Charvet *et al.*, 1998). This table was ordinated using FCA (Chevenet *et al.*, 1994) and

Table 3.1. Trait scores for taxa used to create the simulated biological traits dataset (trait category names are shown in Appendix 2(a)).

	Relative adult mobility				Degree of attachment			Body form			Feeding habit			
	1	2	3	4	1	2	3	1	2	3	1	2	3	4
Alcyonidium diaphanum	3						3			3		3		
Cancer pagurus				3	3			1	2				2	1
Flustra foliacea	3						3			3		3		
Hydroida	3						3			3		3		
Inachus spp.		3			3			1	2				3	
Liocarcinus depurator				3	3			1	2				2	1
Liocarcinus holsatus				3	3			1	2				2	1
Liocarcinus marmoreus				3	3			1	2				2	1
Macropodia spp.		3			3			1	2				3	
Mytilus edulis	3						3		3			3		
Pagurus bernhardus			2	1	3				3				3	
Pagurus prideauxi			2	1	3				3				3	
Pentapora foliacea	3						3		3			3		
Sabellaria spinulosa	3						3		3			3		

Table 3.2. Manipulations of fauna exhibiting the trait category ‘low adult mobility’ (extreme increase to removal), used to investigate the ability of the analytical tools to detect differences in biological trait composition between benthic assemblages. Only biomass of low mobility fauna was altered, all other fauna were assigned randomly-generated biomass values between 100-200kg hr^{-1}.

Treatment	Number of samples	Biomass alteration
Baseline (B)	15	No change
Removal of low mobility fauna (R)	3	0kg hr^{-1}
Extreme decrease low mobility fauna (X-)	3	0-50kg hr^{-1}
Subtle decrease low mobility fauna (S-)	3	70-80kg hr^{-1}
Subtle increase low mobility fauna (S+)	3	220-230kg hr^{-1}
Extreme increase low mobility fauna (X+)	3	250-300kg hr^{-1}

nmMDS (Clarke, 1993). CoI was carried out on the taxon biomass and biological traits tables directly, using the procedure set out in Chapter 2 (Bremner *et al.*, 2003b). The CoI results show the extent of the relationship between the distribution of taxa over samples and the traits they exhibit.

The ordination plots produced by the three tools were compared, and the agreement between the outputs formally assessed by Spearman's rank order correlations (r^2) of sample co-ordinates from the first axis or dimension of each ordination. As the order of nmMDS dimensions are arbitrary, scores from both the first and second nmMDS dimensions were used in correlations. The orientation of nmMDS plots is also arbitrary (Clarke & Warwick, 1994) so only the significance and strength, not the direction of the correlations were assessed.

Power of the analytical tools (dataset 2)

To investigate whether the analytical tools had the power to detect pre-determined differences in trait composition, the simulated data were ordinated by FCA, CoI and nmMDS. Differences in trait composition (summarised as first-axis/dimension sample scores from each ordination) between each of the treatments were assessed using analysis of variance (ANOVA). In the case of nmMDS, analysis was once more carried out on scores from both the first and second dimensions.

Sensitivity of BTA (dataset 1)

Two aspects of sensitivity were investigated, (a) the effect of the type of trait utilised in BTA on it's ability to describe variability between assemblages, and (b) whether the number of traits included in the analysis had an affect on the variability described, irrespective of their identity. Station by traits tables were prepared using different combinations of traits, and the variability described by BTA was calculated based on these combinations.

Mean Euclidean distance between stations, calculated on the station by trait table, was used as an indicator of variation in functioning between assemblages. Low mean distance showed that little variability was described by a trait combination, whereas the highest mean distance between stations described the most variability in the dataset.

The importance of the identity of traits selected for BTA was analysed by removing each of the 9 traits in turn from the station by traits table. This produced 9 reduced station by traits tables (each containing 8 biological traits). Mean variability calculated from these tables was compared with that calculated from the full table, indicating how much each individual trait contributed towards variability.

Assessment of the sensitivity of BTA depends on the selection of a comprehensive list of biological traits. To address whether the 9 biological traits originally selected were adequate for capturing variability over assemblages, dataset 1 was expanded to incorporate four other biological traits identified from the literature as important for benthic species' roles in ecological processes and responses to disturbance. These traits were migration potential, sociability, living habit and sexual differentiation (Appendices 2(a) and 2(b)). The 4 extra traits were added sequentially to the original station by traits table, producing 4 increased station by traits tables (each containing 10 traits). Mean variability was calculated for each, and compared to the original traits table.

Studies of ecological functioning often group traits by the aspect of species biology they describe, the most commonly investigated trait types being behaviour, life history and morphology. The expanded trait table was used to assess whether traits describing behaviour, life history or morphology were equally useful for capturing variability within the dataset. Mean distances were calculated and compared for BTA using only behaviour traits (feeding method, mobility, movement, degree of attachment, living habit, migration potential and sociability), only life history traits (reproductive method, longevity and sexual differentiation) and only morphology traits (individual or colony size, degree of flexibility and body form). As there were many more behaviour than life history or morphology traits (n = 7, n = 3 and n = 3 respectively), the comparison was standardised by repeating the analysis using 3 randomly selected behaviour traits.

Subsequently, the sensitivity of BTA to the number of traits included, irrespective of their identity, was investigated. One to 12 traits were selected at random from the expanded station by trait table. This procedure was repeated 5 times. Mean distance between stations was calculated for each trait selection and also the full trait set. Trait number was plotted against mean distance. It was expected that, at some point, the addition of extra traits would fail to capture further variability in the dataset. Non-linear regression techniques (Curve Expert v1.34, http://www.curvexpert.webhop.biz/) were used to fit a curve to the data, so the position of the asymptote could be determined. FCA, centred PCA and CoI were carried out in the ADE-4 software package (Thioulouse *et al.*, 1997) and the other procedures in PRIMER v5.2.2 (PRIMER-E Ltd, Plymouth).

RESULTS

Comparison of analytical tools

The first two FCA axes accounted for 65% of the variability in biological trait composition between the stations, 50% along axis 1 and 15% along axis 2. The traits with the greatest influence on variability between stations were mobility, degree of attachment and body form. In contrast, CoI accounted for 59% of variability in the data along axis 1 and 20% on axis 2, and showed that traits contributing most to variability between stations were mobility, degree of attachment, body form and flexibility. The permutation test confirmed that the distribution of biological traits between stations was non-random (estimated $P<0.05$). nmMDS resulted in an adequate representation of the patterns in the data, with a minimum 2D stress of 0.06.

Correlation analysis determined whether the three tools portrayed the patterns of variability in biological trait composition in the same ways. Tools showing strong correlations presented similar views of differences in trait composition as they placed stations in similar relative positions in the ordination plane. However, tools showing weak correlations represented the relationships between assemblages in different ways.

FCA and CoI provided similar views of patterns in trait composition, with axis 1 scores showing a relatively strong correlation (r^2 = -0.651, P <0.001). CoI and nmMDS were also alike in their representation of relationships between assemblages, with correlations between CoI axis scores and both the first (r^2 = 0.509, P<0.001) and second (r^2 = 0.665, P<0.001) nmMDS dimension scores. The strongest correlation existed between FCA axis 1 scores and nmMDS dimension 2 scores (r^2 = 0.985, P<0.001), however, no relationship was found between the first axis/dimension scores for these tools.

Power of the analytical tools

Assessment of the power of the analytical tools to detect changes in biological trait composition was achieved by applying each tool to a simulated traits dataset with predetermined differences in the frequency of a selected biological trait category. The power of each tool lies in its ability to detect and represent these differences, and identify the trait category responsible.

FCA accounted for most of the variability in the simulated data (87% along axis 1 and 9% on axis 2) and identified, as expected, that this was caused by differences in the relative proportions of low-mobility fauna (Table 3.3). On the ordination plot, the manipulated samples were well separated from baseline samples (Figure 3.1(a)). Samples with subtle and extreme increases were especially distinct from the others, as were those with subtle decreases in low-mobility fauna. Samples with low-mobility fauna removed or extremely reduced were not distinct from each other. These differences in trait composition were significant in all cases, except where low-mobility fauna were removed or extremely reduced (ANOVA F = 95.02, DF = 5, P<0.001).

CoI accounted for 85% of variability in the simulated data along axis 1 and 10% along axis 2 and confirmed that low mobility fauna were important determinants of the

Table 3.3. The amount of variability in the abundance-weighted biological trait data explained by the first two fuzzy correspondence axes and the contribution of each trait to this variability.

	Axis 1	Axis 2
Relative inertia (%)	87.21	8.77
Correlation Ratio (r)		
Mobility	0.046	0.003
Attachment	0.005	0.001
Body form	0.003	0.000
Feeding method	0.008	0.001

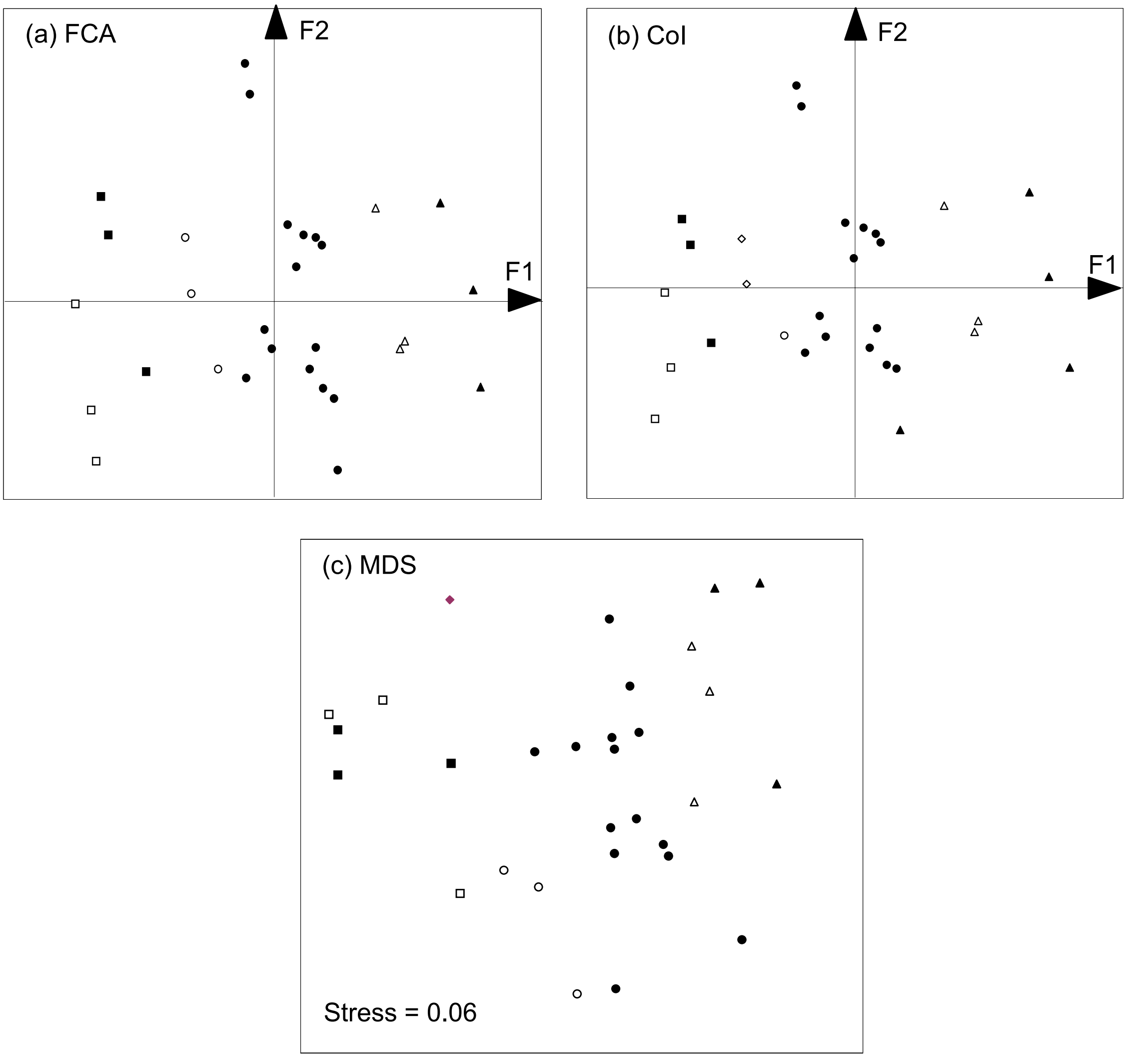


Figure 3.1. Ordination plots of biological trait composition of faunal assemblages, based on (a) FCA, (b) CoI and (c) MDS of dataset 2 (simulated biological traits data). Symbols represent manipulations of low mobility fauna biomass; □ = complete removal, ■ = extreme decrease, ○ = subtle decrease, Δ = subtle increase, ▲ = extreme increase, ● = baseline samples.

variation. The permutation test confirmed a non-random distribution of traits over samples (estimated $P<0.05$). The CoI ordination was quite similar to the FCA plot (Figure 3.1(b)). Again, samples with subtle and extreme increases in low-mobility fauna separated out to the right of axis 1 and those with subtle and extreme decreases or a removal of low-mobility fauna to the left. Differences in axis 1 scores were significant (ANOVA F = 82.96, DF = 5, $P<0.001$) for all treatments, except those where low-mobility fauna were extremely reduced or removed and those with subtle or extreme decreases.

Overall, the nmMDS ordination presented a similar view of the treatments to FCA and CoI, and very little difference was noted between tools along the second axes/dimensions (Figure 3.1(c)). However, nmMDS was less able than the other two tools to separate the treatments in dimension 1. Samples with removal and extreme reductions in low-mobility fauna overlapped in this dimension, as did those with subtle and extreme increases. The subtle reduction and increase treatments were not obviously separated from baseline samples in the dimension.

nmMDS dimension 1 scores for all treatments, except those with subtle reductions in low-mobility fauna, differed from baseline conditions (ANOVA F = 36.12, DF = 5, $P<0.001$), but these differences were less apparent than for FCA or CoI and there was no significant difference between dimension 2 scores. Similarity of percentages (SIMPER) analysis applied to the manipulated dataset indicated that low-mobility fauna were instrumental in determining differences in trait composition between baseline conditions and removal, subtle increase and extreme increase treatments, but not between baselines and subtle or extreme reductions (Table 3.4).

Sensitivity of BTA

The effect of the identity of traits selected on the description of variability produced by BTA was assessed by comparing the reduced station by trait tables with the full original table. In each case, removal of a trait reduced the variability described by BTA in

Table 3.4. SIMPER analysis of trait categories that contributed most (cumulative contribution) to dissimilarity between samples subject to manipulations of low-mobility fauna. Average proportion data are expressed as the abundance-weighted occurrence of trait categories in the samples. B = baseline conditions, R = removal, X^- = extreme reduction, S^- = subtle reduction, S+ = subtle increase and X+ = extreme increase of low-mobility fauna.

Trait	Category	Average proportion difference	Cumulative %
B v R			
Mobility	Low	-908.53	19.48
Feeding method	Scavenger	-836.62	37.49
Attachment	None	-808.68	54.93
B v X-			
Attachment	None	-942.22	19.95
Feeding method	Scavenger	-916.99	39.24
Mobility	Low	-744.19	54.88
B v S-			
Attachment	None	-509.98	15.87
Feeding method	Scavenger	-485.36	30.86
Mobility	Low	-451.43	44.83
B v S+			
Mobility	Low	449.29	16.47
Feeding method	Scavenger	355.68	29.81
Attachment	None	330.88	42.72
B v X+			
Mobility	Low	785.4	20.01
Feeding method	Scavenger	595.94	35.20
Attachment	None	540.25	49.14

comparison to the full original table (Figure 3.2). Removal of the trait longevity had the most effect on the description of variability provided (7.18% reduction) and individual or colony size the least (4.14% reduction).

The addition of extra traits always led to an increase in the amount of variability described by BTA, compared to that described by the full original station by trait table (Figure 3.2). Addition of the trait sexual differentiation led to the largest increase in mean Euclidean distance (6.88% increase) and living habit had the least effect (1.44% increase).

Analysis of randomly selected traits showed that the amount of variability described by BTA increased with the number of traits included, irrespective of the identity of those traits (Figure 3.3(a)). The increase in variability was more pronounced at low trait numbers, differences becoming smaller as trait number increased. Although extrapolation to T = 100 did not result in an asymptote for the modelled distance values, the amount of extra variability described by increasing trait number dropped below 20% of that initially shown after T = 34 (Figure 3.3(b)).

BTA using only behavioural traits led to better representation of variability between assemblages than when only life history or morphology traits were used (Figure 3.4). Using only behaviour or life history traits described more variability than using the same number of randomly selected traits (i.e. n=7 or n=3), however this was not the case for morphology traits (see Figure 3.3a). When the behaviour group was corrected for the large number of traits included, mean distance reduced to less than that of the life history traits and the differences between the groups became less pronounced (Figure 3.4).

DISCUSSION

BTA is an important and useful approach to investigating ecological functioning, which potentially has the power to show the links between organisms and their environment, and provide information on the impacts of human activities. The choice of analysis tool

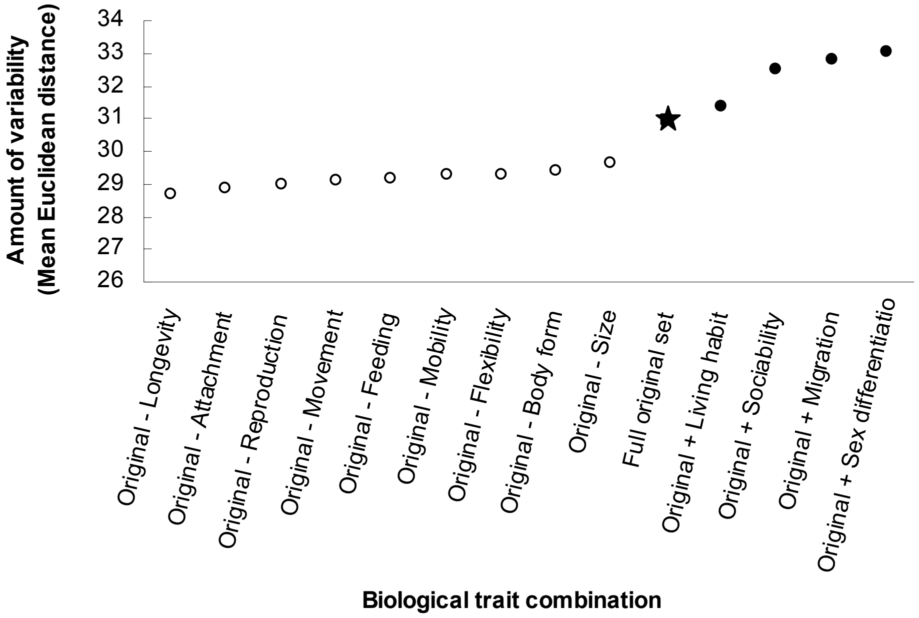
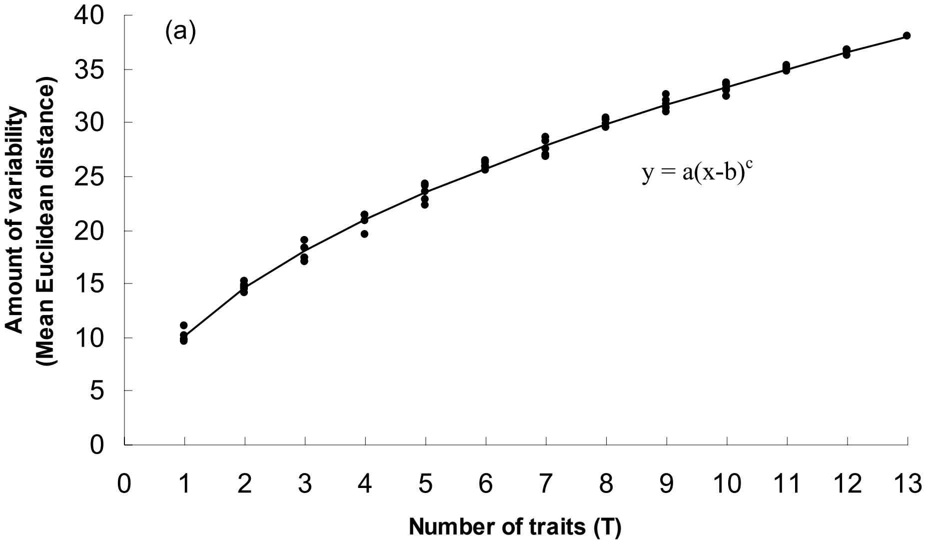


Figure 3.2. The amount of variability described by BTA after removal or addition of biological traits, compared with BTA based on the full original trait list (original trait set n = 9, trait removals n = 8, trait additions n = 10). Trait removals and additions are ranked according to their relative effects on variability.



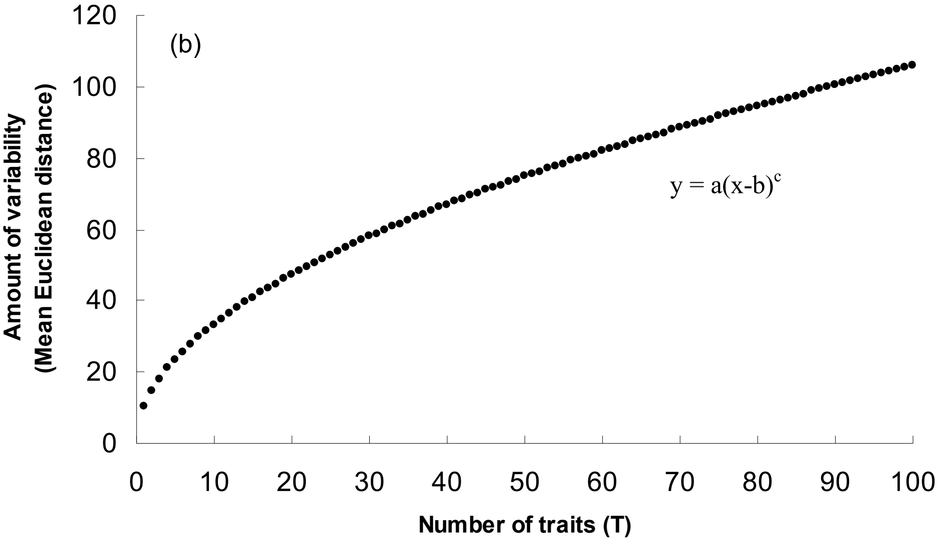


Figure 3.3. The effect of trait number (T) on the amount of variability described by BTA. Plots show (a) the relationship between the number of traits selected and mean Euclidean distance and (b) the fitted curve ($y=a(x-b)^c$), with modelled data extrapolated to T = 100.

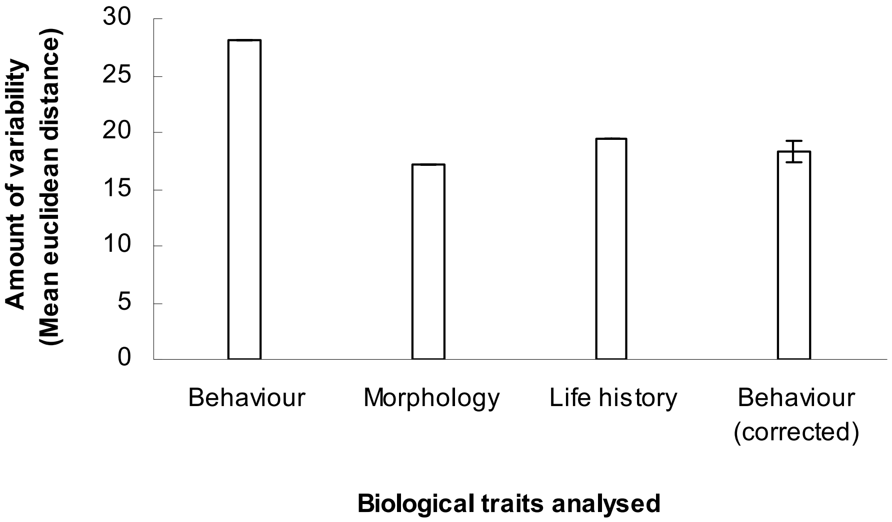


Figure 3.4. Comparison of the amount of variability described by BTA when only morphology, life history, or behaviour traits were selected for analysis (n = 3, n = 3 and n = 7 respectively). BTA using 3 randomly selected behaviour traits was also compared, to correct for the relatively large number of behaviour traits (value shown is $\bar{x} \pm$ 95% C.I. of mean Euclidean distance). Definitions of morphology, life history and behaviour traits are listed in the text.

for BTA and the sensitivity of the approach to the traits analysed are important issues that must be addressed during development of the methodology.

The number of traits selected for BTA was closely linked to the amount of variability in trait composition described by the approach, with rising trait number leading to an increase in variability between the benthic assemblages. It is clear that including as many traits as possible will give a more informative picture of ecological functioning, and conversely, limiting the number of traits used could impact on the ability of the approach to accurately describe functioning over the assemblages. Studies that include few biological traits risk producing a misleading view of assemblage functioning. For example, Bellwood *et al.* (2002) found that labrid reef fish exhibited global-scale homogeneity in functional characteristics, based on analysis of one biological trait related to fin morphology and habitat use. However, they conceded that species similar in their fin morphology were often very different when other characteristics were considered. In order to account for this variation between taxa, a larger number of traits would need to be analysed.

A potential problem with including large numbers of traits in BTA relates to the time required for carrying out the analysis. Theoretically, preparing large trait databases should not be an issue for monitoring situations, as finding information and coding traits would only require an initial, one-off investment of time and resources. However, in reality, trait information is not static. New research can broaden our knowledge of species biology. Biological traits can also change within species over time, in response to both fluctuating environmental conditions and anthropogenic stress (Jennings & Kaiser, 1998). Trait databases will thus be dynamic and require updating after the initial coding to ensure information remains up to date.

This problem will be amplified by the size of the species pool being investigated. One of the most exciting potential applications of BTA is as a monitoring tool over large geographical scales. Biological trait composition of natural freshwater invertebrate assemblages is generally stable at both catchment (Charvet *et al.*, 2000) and regional

(Statzner *et al.*, 2001) scales and there is some preliminary evidence of stability in the face of environmental gradients in marine assemblages (Chapters 2 and 4, Bremner *et al.*, 2003b). However, taxon composition varies over large geographic scales (Gee & Warwick, 1996; Engle & Summers, 1999; Lancellotti & Vasquez, 1999), requiring trait coding for a large number of species and thus a substantial input of time and resources. Limiting the number of traits used would mitigate the potential time and resource costs of preparing and updating traits databases for large numbers of species. So how do we decide which traits should be retained and which discarded?

One obvious solution would be to select those traits that capture the most variability in functioning over assemblages. Somerfield and Gage (2000) showed that, although certain groups of species contributed most to spatial patterns in sea loch macrofauna, assemblage structure could not be described adequately by considering only those species. In the same way, looking only at high-variability traits may not encompass different aspects of functioning. Even if it was appropriate to select only the most variable traits, the cut-off point at which traits were included or removed would be subjective.

Another method for limiting the number of traits included in BTA would be to remove those traits that vary in the same way. Merigoux *et al.* (2001) found correlations between several traits such as size at maturity and fecundity or body height and egg size in their study of juvenile neotropical fish. They used these correlations to reduce trait numbers in further analyses, but noted that some species did not conform to the correlations and exhibited theoretically opposing traits. Limiting trait number based on traits that behave in similar ways will only be useful when the traits always behave in this manner. At present, in marine systems at least, we do not know enough about the nature of the relationships between traits to enable that judgement to be made.

Alternatively, traits can be selected based on the requirements and aims of individual studies, whether these be to describe assemblage functioning, identify the presence and effects of anthropogenic impacts, or a combination of both. Lavorel and Garnier (2002) define two forms of biological trait that can be used for these purposes; ‘effect’ traits (traits that have important effects on ecosystem functions) and ‘response’ traits (those that respond in a specific way to environmental factors).

Kahmen *et al*. (2002) used this rationale to select traits for a study of the effects of different grassland management techniques on plant assemblages. They chose 8 traits based on their assumed sensitivity to the management treatments. Seven of the eight traits responded to the treatments, but one did not. Traits responding in both expected and unexpected ways were also encountered in fishing-impacted invertebrate assemblages, where some traits assumed to be sensitive to fishing responded as predicted, whereas others did not (Chapter 5, Bremner *et al*., 2004). Although selecting traits based on either particular ecosystem functions or responses to environmental disturbance is a powerful method for limiting trait number in BTA, it must be used with caution until we know more about the relationships between traits and functioning.

No matter what method is adopted for selection of biological traits, the way trait composition is analysed may have a bearing on the description of functioning provided. Comparison of the three analytical tools proposed for BTA showed that they were all similar in their portrayal of the direction of change in station scores, and hence biological trait composition of the benthic assemblages in the southern North Sea/eastern Channel dataset. This suggests there is very little to choose between the three tools in terms of how they portray patterns of ecological functioning. This outcome is not limited to trait composition of assemblages. Gamito and Raffaelli (1992) found that, although several metric and non-metric multivariate methods produced ordination plots that differed in their appearance, they all identified the same main gradients underlying species composition. Although they all provide a similar picture of functioning over these assemblages and are, in this respect, interchangeable, there are other issues that must be considered.

The power of analytical tools to detect differences between or changes within assemblages will have implications for their application to studies of anthropogenic impacts. nmMDS had less power to detect pre-determined changes in biological trait composition in the simulated dataset than FCA or CoI. It separated extreme changes in the frequency of low-mobility fauna from baseline trait composition, but could not detect the more subtle manipulations.

This lack of power to detect subtle changes in trait composition is surprising, given that multivariate methods based on ranks are useful for downplaying the effects of extreme values (Clarke & Warwick, 1994), which can often hide more subtle relationships. Metric ordination methods are useful for identifying distinct groups of samples, whereas the strength of nmMDS lies in portraying the overall relationships between samples (Kenkel & Orloci, 1986). The treatments adopted during the analysis were deliberately designed to be distinct from each other, which may explain why the metric methods performed better in this respect. The manipulations were not designed to be ecologically relevant, and it is unclear how important this issue would be during analysis of change in real, impacted, biological assemblages.

It is also important to consider whether the tools available are appropriate for the type of data being analysed. Metric ordination methods such as FCA or CoI are based on the assumption that the data have a linear structure. If, as is often the case in ecological systems, the data are structured in a non-linear way, metric ordinations can produce a misleading view of relationships (Pielou, 1984). However, other studies have shown that metric methods are able to describe complex patterns in biological trait composition (e.g. Doledec & Statzner, 1994; Townsend *et al.*, 1997) and if the purpose of the ordination is not to test formal hypotheses but to explore patterns in the data, these tools may be justifiably used (Dytham, 1999).

The concept of linear ordination is well established and methods such as principal components analysis or correspondence analysis are familiar to most community ecologists, however the execution of FCA and particularly CoI can be complicated and their outputs difficult to interpret (see, for example, Usseglio-Polatera & Beisel, 2002). nmMDS, on the other hand, is easy to understand and straightforward to compute using available software (Kenkel & Orloci, 1986; Clarke, 1993). Although this is not necessarily an issue in academic studies, monitoring strategies developed for management purposes should be understandable without the need for high levels of initial training.

Ultimately, the selection of biological traits for BTA will be based on a trade-off between the amount of variability described by the traits and the time and effort required to gather information, whilst the choice of analytical tool will be a balance between the power of the tool to describe changes in trait composition and the ease with which results can be interpreted. nmMDS is appropriate for providing a general picture of functioning in marine assemblages. FCA and CoI may have greater power to detect the effects of human impacts on trait composition, but are more difficult to interpret than the nmMDS methods familiar to most benthic ecologists. Including as many traits as possible will lead to the most useful description of ecological functioning, as will selecting those traits sensitive to anthropogenic impacts or closely linked to important ecosystem processes.

Chapter 4

Does ecological functioning in marine benthic assemblages change with environmental conditions?

ABSTRACT

Environmental variability is important for structuring species composition in benthic assemblages, but it is unclear whether or how this variability influences ecological functioning. The aim of this study was to establish and explore the relationship between environmental variability and ecological functioning in megafaunal assemblages from the Irish Sea and eastern Channel. Biological traits analysis was used to describe ecological functioning. Multivariate methods were employed to match patterns of trait composition to environmental conditions, and subsequently examine the nature of the relationship. Biological trait composition was related to environmental conditions over the two regions; with salinity, sea surface temperature (SST), annual temperature range (ATR) shell content, fish richness and fishing effort, and the traits 'small size', 'short lifespan', 'sexual reproduction producing mini-adults', 'moderate mobility', 'moderate to high flexibility', 'opportunistic feeding', 'non-sociability' and 'permanent-burrow inhabiting', being the most important determinants of this relationship. These traits were, in general, negatively correlated with salinity, SST, ATR and fishing, and positively associated with fish richness and shell content over the regions. Within this, reductions in ATR and shell content between the two regions were associated with low frequencies of short-lived, moderately mobile, flexible, solitary, opportunistic, directly-developing and permanent-burrow dwelling fauna. On a local scale, increases in shell content and fishing effort were associated with low frequencies of moderately mobile and moderately to highly flexible fauna over the eastern Channel, but high frequencies of these traits over the Irish Sea. These changes in ecological functioning have implications for ecosystem processes, with reductions in permanent-burrow dwellers in the eastern Channel potentially compromising the ability of these assemblages to process and store chemicals and waste products. However, the nature of the relationship between functioning and the environment is complex and incorporates many factors, which require further, experimental, investigation to determine the extent and consequences of the relationship.

INTRODUCTION

In benthic systems, invertebrate species distributions and assemblage composition are strongly influenced by the physico-chemical environment over a range of scales (Hall *et al.*, 1994). On large scales, the species complement of benthic assemblages changes over geographic gradients, both latitudinally (Gray, 2002; Hillebrand, 2004) and longitudinally (Heip *et al.*, 1992). In the northeast Atlantic region, within the Channel and North and Irish Sea regions; depth, temperature, water movement patterns and sediment type are considered the primary factors controlling species composition (Kunitzer *et al.*, 1992; Rees *et al.*, 1999; Sanvicente-Anorve *et al.*, 2002). Sediment mobility and the amount of organic carbon and chlorophyll *a* present have also been implicated as influential factors at the regional scale (Basford *et al.*, 1989; Eleftheriou & Basford, 1989; Heip *et al.*, 1992; Sanvicente-Anorve *et al.*, 1996). Elsewhere, salinity can be an important determinant of large-scale invertebrate assemblage composition (Giberto *et al.*, 2004).

On a more localised scale, benthic species composition is linked to sediment grain size (Brown *et al.*, 2002). However, this is not a universal phenomenon (Newell *et al.*, 2001) and sediment type has variable importance in determining individual species abundance patterns (Seiderer & Newell, 1999; Thrush *et al.*, 2003), and hence in determining the distribution of benthic assemblages. Seabed morphology is also important for structuring species assemblages at a local scale (Thrush *et al.*, 2001; Barros *et al.*, 2004), although there may be multiple factors involved in complex species-environment relationships at this scale (Snelgrove & Butman, 1994; Freeman & Rogers, 2003).

The biological environment experienced by species will also have an effect on their distributions. For benthic invertebrate assemblages, the principal biotic factors affecting species composition are fish and algae. Fish prey on benthic invertebrates (Ellis *et al.*, 1996) and changes in the fish assemblages lead to altered predation pressure on and hence potentially drive changes in the species composition of benthic assemblages (Frid *et al.*, 1999b). The presence, degree of cover and type of vegetation found in an area can affect the composition of invertebrate assemblages (Bostrom & Bonsdorff, 1997; Sfriso *et al.*, 2001) and the quantity of algal material in an area therefore can act as a relatively simple index of habitat type.

Anthropogenic disturbances can be viewed as components of the environment experienced by benthic invertebrate assemblages. Exposure to bottom trawling modifies assemblage composition (see reviews in Hutchings, 1990; Jennings & Kaiser, 1998; Johnson, 2002), as does materials extraction (Kenny & Rees, 1994; Desprez, 2000; van Dalfsen *et al.*, 2000) and organic enrichment (Pearson & Rosenberg, 1978).

Increasingly, the focus of studies assessing relationships between environmental conditions and benthic assemblages has been shifting from species composition towards the ecological functioning of benthic systems. Ecological functioning, defined here as the maintenance and regulation of ecosystem processes (after Naeem *et al.*, 1999), encompasses interactions between and within the biotic components (e.g. macrofauna, meiofauna, microfauna) of a system and between species and the environment. Important processes involving benthic assemblages include carbon, oxygen and nutrient cycling and decomposition of dead matter or waste materials (Snelgrove *et al.*, 1997; Austen *et al.*, 2002).

It is unlikely that functioning of all biotic components of benthic systems can be addressed simultaneously. Issues of scale make the concurrent assessment of micro- to megafauna assemblages methodologically difficult. One alternative is to focus on a single component. Invertebrate assemblages are heavily involved in the regulation of ecosystem processes (Snelgrove, 1998), so provide a useful study unit. Functioning in these assemblages will be dependent on the biological characteristics, or traits, exhibited by constituent species, because these determine how the species contribute to ecological processes. For example, certain types of feeding and movement exhibited by benthic invertebrates (primarily deposit feeding and burrowing activities) can disrupt sediments, increasing the depth of oxygen and detritus penetration and consequently enhancing organic matter decomposition (Pearson, 2001). Therefore, a logical approach to describing ecological functioning is to focus on the characteristics, or traits, expressed by members of invertebrate assemblages.

Recent evidence suggests that environmental conditions are intricately linked to biological traits, and hence ecological functioning. Physical factors such as water turbulence and wind-driven wave action can influence functioning, by controlling the dominant feeding methods exhibited by benthic invertebrates. Filter feeders dominate assemblages in areas of high turbulence and wave action, and this has implications for the turnover of organic matter and regulation of plankton assemblages (Davoult *et al.*, 1998). Water flow may also affect functioning through its influence on the behaviour of burrowing organisms (Biles *et al.*, 2002), because bioturbation occurring in sediments regulates carbon degradation and bentho-pelagic nitrogen cycling (Biles *et al.*, 2002; Widdicombe *et al.*, 2004).

The contribution a benthic species makes to ecosystem processes is most likely to be determined by a combination of biological characteristics (Webb & Eyre, 2004a), so a number of traits will be involved in ecological functioning. Additionally, several characteristics can be involved in organisms' responses to individual environmental variables. For example, responses to benthic trawling have been linked to traits such as feeding methods, body size, flexibility, mobility and burrowing activities (Kaiser *et al.*, 1998; Hall-Spencer *et al.*, 1999; Rumohr & Kujawski, 2000; Bradshaw *et al.*, 2002; Thrush & Dayton, 2002; Wassenberg *et al.*, 2002).

A multi-trait approach is therefore useful for capturing and describing ecological functioning in invertebrate assemblages. One such approach, termed biological traits analysis (BTA), performs well in comparison to other methods used to describe functioning (Chapter 2, Bremner *et al.*, 2003b), and has shown potential for assessing the effects of environmental change on benthic assemblages (Chapter 5, Bremner *et al.*, 2004). The approach could be useful for describing the relationship between ecological functioning and environmental conditions. The initial aim of this study was to assess whether ecological functioning of benthic invertebrate assemblages altered over a range of environmental conditions and, if so, to determine the environmental factors most closely associated with these changes. Subsequently, relationships between the biological traits driving these changes in functioning and the associated environmental factors were examined.

METHODS

Invertebrate data

Invertebrate benthic megafauna were collected by the *RV Corystes* from 122 stations in the Channel and Irish Sea regions, during two cruises undertaken in 1998 (Figure 4.1). Thirty-seven stations in the eastern Channel were sampled in August 1998, from the mid-eastern and north-eastern Channel sectors (MEC and NEC respectively). Eighty-five stations were sampled from the Irish Sea north (ISN), Irish Sea south (ISS), Irish Sea west (ISW), St George's Channel (SGC) and inner Bristol Channel (BCI) sectors during September 1998.

Epifauna were collected using a 4m beam trawl with a 40mm stretched cod-end, chain mat and flip-up rope (Rogers *et al.*, 1998). The trawl was towed for 30 minutes at each station, covering an area of approximately 15,000m^2 (Ellis & Rogers, 2000). Invertebrates recovered from the trawl were identified to species where possible and the biomass of each recorded as wet weight (kg hour^{-1}). For small samples, the whole catch was processed whilst for larger samples, sub samples of known weight were sorted and the resulting taxa biomass raised to that of the full catch weight.

The dataset was reduced to retain only those taxa found either (i) in the top 90% of biomass at any station or (ii) at more than 50% of stations, thus selecting taxa that were dominant (high biomass) at individual stations or widely distributed over the region. This excluded taxa that were not well-sampled by the beam trawl.

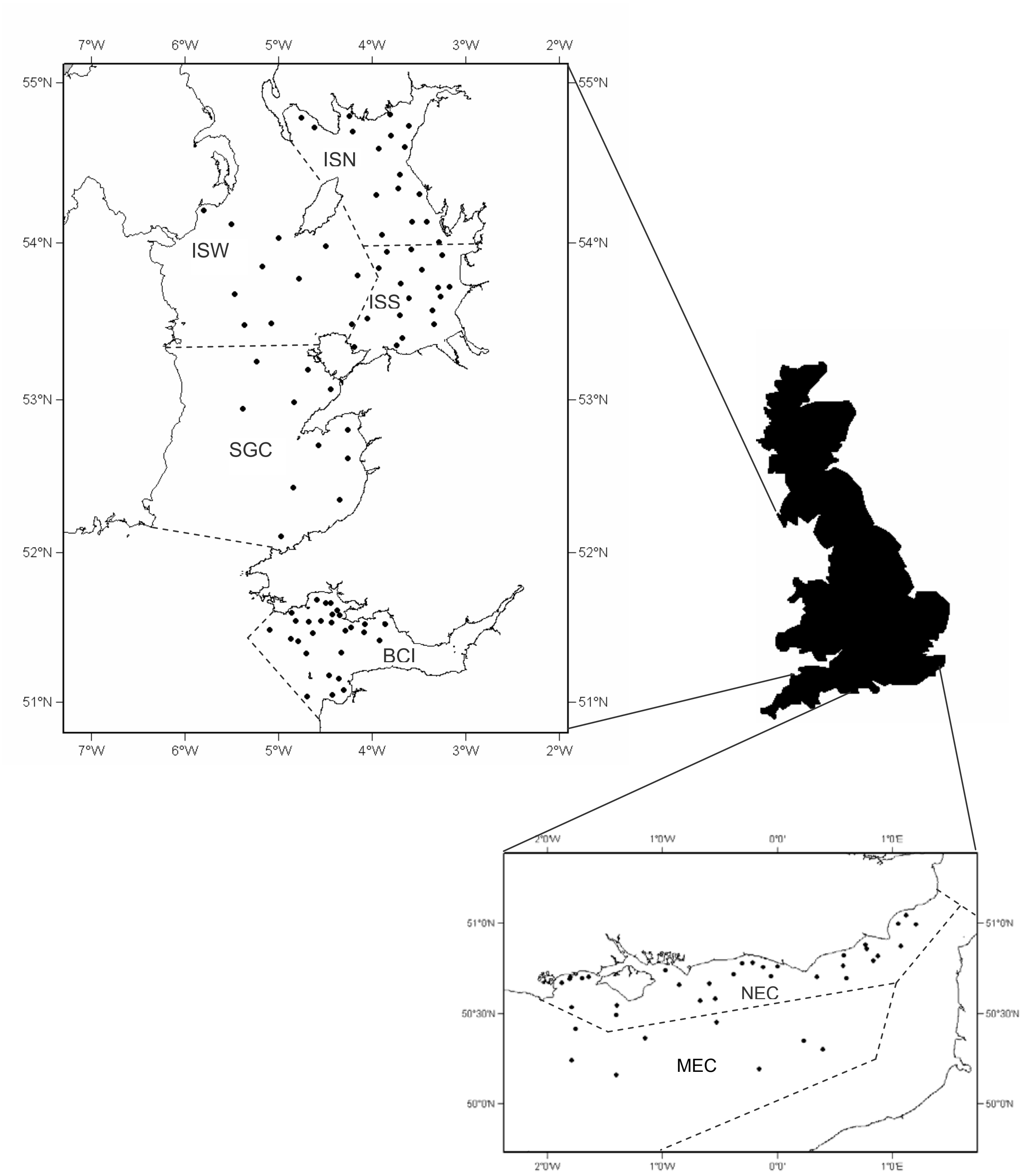


Figure 4.1. Map of the Irish Sea and eastern Channel benthic stations considered in the study. Sectors within each region are marked on the map (NEC = north-eastern Channel, MEC = mid-eastern Channel, ISN = Irish Sea North, ISW = Irish Sea west, ISS = Irish Sea south, SGC = St George's Channel and BCI = inner Bristol Channel).

Environmental data

Thirteen variables, characterising the environment, were selected for analysis. Sea surface temperature (SST) and salinity (measured using a continuous data recorder), water depth and the weights of rock/stones, broken shells and algae (*Laminaria* spp. (Lamouroux)) collected in each trawl were measured at the stations sampled during the research cruises, to provide a description of the physical habitat. Other physical habitat variables selected were seabed shear stress, mean annual temperature range (ATR) and sediment type.

Seabed shear stress (m s^{-1}) was estimated for each station by squaring tidal water velocity (Dyer, 1986). Water velocity estimates were obtained from the POLPRED offshore tidal prediction system. This system provides values at 7-mile intervals, so the water velocity value nearest to each sample station (identified using MapInfo) was used. Mean annual temperature range (calculated as the difference between mean winter minimum and summer maximum temperatures) and underlying sediment type were recorded for each station using information obtained from marine charts (Lee & Ramster, 1981).

Additionally, the total abundance and taxon richness of fish caught in trawls at each station were included as a measure of the biotic environment encountered by epibenthic invertebrates. Latitude was recorded for each station to act as a proxy for the biogeographic gradient over the region. Lastly, an index of fishing effort in the vicinity of each station was calculated from observations by British Fishery Protection flights monitoring commercial fishing activity in the UK Exclusive Economic Zone (Rogers *et al.*, 2001).

Data analysis

Environment

Twelve of the thirteen environmental variables were quantitative and could be analysed together. However, underlying sediment type was recorded qualitatively. This variable was dealt with separately (see below). Normalised principal components analysis (PCA) was used to investigate the variations in environmental conditions over the region and to determine which variables differed most between the stations (Pielou, 1984). There were clear differences in latitude between the two regions investigated (see Figure 4.1), so latitude was likely to dominate the PCA ordination and obscure more subtle patterns in other variables. For this reason, it was excluded from this stage of the analysis. The PCA and all further analyses were carried out using PRIMER v5.2.2 (PRIMER-E Ltd, Plymouth).

Taxa and the environment

Similarities in taxon composition over the stations were described using non-metric multidimensional scaling (nmMDS), after 4th root transformation of taxon biomass and calculation of Bray-Curtis similarity coefficients between stations (Clarke, 1993). Links between taxon composition and environmental variables were investigated using the RELATE and BIO-ENV procedures. RELATE tests for the degree and significance of agreement between two datasets (Clarke & Ainsworth, 1993). It calculates rank correlations between the elements of two similarity/distance matrices and produces a matching coefficient (ρ), which is then used in a permutation test. BIO-ENV identifies subsets of variables from one dataset that show the best match with patterns from a second dataset (Clarke & Ainsworth, 1993). It is based on the same principle as RELATE, calculating the rank correlation between the two datasets, however it uses different combinations of variables from the first dataset, in order to identify the variables producing the highest rank correlations with the second dataset.

These procedures were used to investigate the significance of any relationship between taxon composition and environmental conditions, and identify the environmental variables best matched to the distribution of taxa. Spearman rank order correlations (R_s) were used for both procedures, with Bray-Curtis similarity measures calculated for the taxon data and normalised Euclidean distance for the environmental data. Information on the type of underlying sediment at each station was overlaid on the nmMDS plot, to allow a coarse visual investigation of any relationship between sediment type and taxon composition.

Functioning and the environment

Thirteen biological traits were chosen for the analysis. These reflected life history characteristics (relative adult individual or colony size, relative adult longevity, reproductive technique and sexual differentiation), morphology (degree of flexibility and body form) and behaviour (relative adult mobility, movement type, degree of attachment, adult life habit, sociability, migration potential and feeding type) and were chosen for their perceived importance for ecological functioning and potential to maximise differences between taxa. The traits were sub-divided into categories (see Appendix 2(a)) and individual taxa coded for the extent to which they displayed each category using fuzzy-coding (see Chapter 2, Bremner *et al.*, 2003b). The table of taxa by trait scores is included as Appendix 3.

Trait category scores for each taxon present at a station were weighted by their biomass at that station. These biomass-weighted trait category scores were then summed over all taxa present at the station, to provide a measure of the frequency of trait categories at that station (Charvet *et al.*, 1998). This weighting procedure was repeated for each station in the dataset, resulting in a station by trait table. When no information on a particular trait was available for a taxon, zero values were entered for each trait category and the taxon did not contribute to the calculation of trait weightings (Usseglio-Polatera *et al.*, 2000a).

Following the methods used to analyse taxon composition, 4th root transformation, Bray-Curtis similarities and nmMDS were applied to the table of trait frequencies. This allowed a description of similarities between stations in terms of their biological trait composition, and is useful for providing a general picture of functioning in marine benthic assemblages (see Chapter 3). As before, the nmMDS plot was overlaid with information on the underlying sediment types at each station.

RELATE was used to measure the degree of agreement between biological trait composition and environmental conditions over the stations. BIO-ENV was used to identify the environmental variables best matched to biological trait patterns. In addition, the BVSTEP routine was used to identify the biological traits best matched to environmental conditions (BVSTEP is similar to BIO-ENV, but uses a stepwise procedure to combine variables from the first dataset (i.e. the station by trait table), so is better suited to datasets with large numbers of variables (Clarke & Warwick, 1998).

RESULTS

Environmental variables

The first two principal components accounted for 42% of variability in environmental conditions over the stations, with 26% on axis 1 and 16% on axis 2. SST, salinity and fish taxon richness were important determinants of differences between stations along the first axis, whilst depth, algae and weight of rocks in the catch were influential along axis 2 (Table 4.1). ATR and fish abundance were important along both axes.

The largest differences in environmental conditions existed between the Irish Sea and eastern Channel regions (Figure 4.2). The eastern Channel stations had higher SSTs ($\bar{x}$ 18.03^{O}C ± 0.18 C.I. v 16.29^{O}C ± 0.20 C.I.), ATRs ($\bar{x}$ 9.54^{O}C ± 0.3 C.I. v 3.82 ^{O}C ± 0.14 C.I.) and salinity ($\bar{x}$ 34.25 ± 0.11 C.I. v 33.34 ± 0.19 C.I.) than Irish Sea stations, but lower fish abundances ($\bar{x}$ 173.35 ± 65.87 C.I. v 794.48 ± 203.10 C.I.) and richness ($\bar{x}$ 8.81 ± 1.00 C.I. v 14.01 ± 0.90 C.I.). The BCI stations appeared to be intermediate in general between the Channel and Irish Sea regions, especially in terms of temperature, salinity and fish assemblages, although they were more similar to other Irish Sea sectors than to eastern Channel stations.

Stations within the ISW differed from the ISN and ISS sectors along the second PCA axis (Figure 4.2). These stations were deeper and contained more rock, but had less algae, lower fish abundance and ATRs in general (Table 4.1). On average, these stations had the

Table 4.1. PCA of environmental conditions at benthic stations in the eastern Channel and Irish Sea regions.

	PCA axis	
	1	2
Eigenvalue	2.81	1.77
Relative Inertia (%)	25.5	16.1
Cumulative Inertia (%)	25.5	41.6
Eigenvectors		
Depth (D)	0.034	0.620
Seabed shear stress (SS)	-0.034	0.257
Salinity (S)	0.405	0.097
Sea surface temperature (SST)	0.459	-0.238
Average temperature range (ATR)	0.473	-0.329
Weight of shell (WOS)	-0.221	-0.052
Weight of rock (WOR)	0.003	0.330
Weight of algae (WOA)	0.077	-0.331
Fish abundance (FA)	-0.407	-0.315
Fish richness (FR)	-0.378	-0.206
Amount of fishing (F)	0.191	0.108

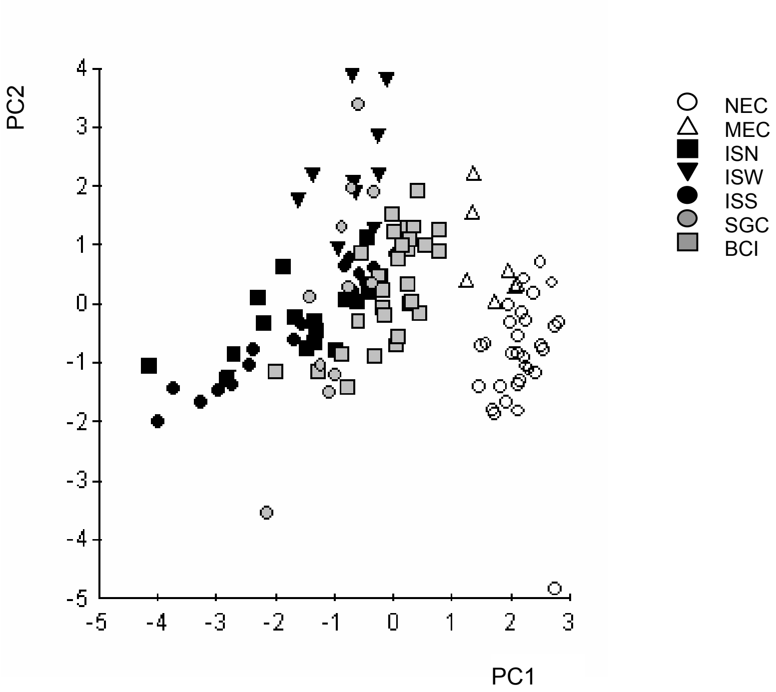


Figure 4.2. First plane PCA ordination of environmental conditions at benthic stations in the eastern Channel and Irish Sea regions. Stations are marked by sector identifiers (NEC = north-eastern Channel, MEC = mid-eastern Channel, ISN = Irish Sea North, ISW = Irish Sea west, ISS = Irish Sea south, SGC = St George's Channel and BCI = inner Bristol Channel).

greatest depths ($\bar{x}$ 63.09 ± 14.48 C.I.) and lowest ATRs ($\bar{x}$ 2.91 ± 0.56 C.I.) of all sectors analysed. Stations in the ISN, ISS and SGC were not differentiated from each other on the basis of their environmental conditions.

Taxa and the environment

Most of the stations from the north-eastern Channel separated from the Irish Sea sectors based on taxon composition (Figure 4.3(a)). However, MEC stations were often more similar to those from the Irish Sea region than to the NEC stations. BCI stations grouped apart from the ISN, ISS and ISW sectors, exhibiting an assemblage structure intermediate between these and the NEC. Although taxon composition was variable over the ISN, ISS and ISW, these sectors were not differentiated from each other on the nmMDS plot.

There was a significant correlation between taxon composition and environmental conditions over the stations (RELATE; $\rho = 0.412$, $P<0.01$). The best correlation between environment and taxa was given by a combination of ATR, SST, latitude, fish richness and depth ($\rho = 0.546$). Associations between environmental conditions and taxon composition were weaker when environmental variables were considered individually; the variable most associated with taxon composition was ATR (Table 4.2).

Superimposition of the underlying sediment types on the nmMDS plot indicated some differences in taxon composition between stations with differing sediments (Figure 4.3(b)). Stations with rock/sand/gravel sediments were largely separated from those with other sediment types, although there was overlap with sand/gravel assemblages. Stations with sand, gravel or mud sediments were also relatively well differentiated from each other on the plot.

Functioning and the environment

The biological trait composition of assemblages from the NEC was distinct from the other sectors (Figure 4.4(a)). Stations in the MEC differed in trait composition from those

Table 4.2. BIO-ENV analyses showing the correlations (ρ) between individual environmental variables and (i) taxon composition or (ii) biological trait composition.

	BIO-ENV comparison	
	Environment / taxa	Environment / traits
Variables	Correlation (ρ)	Correlation (ρ)
Latitude (L)	0.380	0.215
Depth (D)	0.141	-0.006
Seabed shear stress (SS)	0.005	-0.046
Salinity (S)	0.126	0.164
Sea surface temperature (SST)	0.407	0.201
Average temperature range (ATR)	0.478	0.240
Weight of shell (WOS)	0.037	0.081
Weight of rock (WOR)	0.036	-0.061
Weight of algae (WOA)	0.119	0.070
Fish abundance (FA)	0.039	0.167
Fish richness (FR)	0.230	0.142
Amount of fishing (F)	0.060	0.067

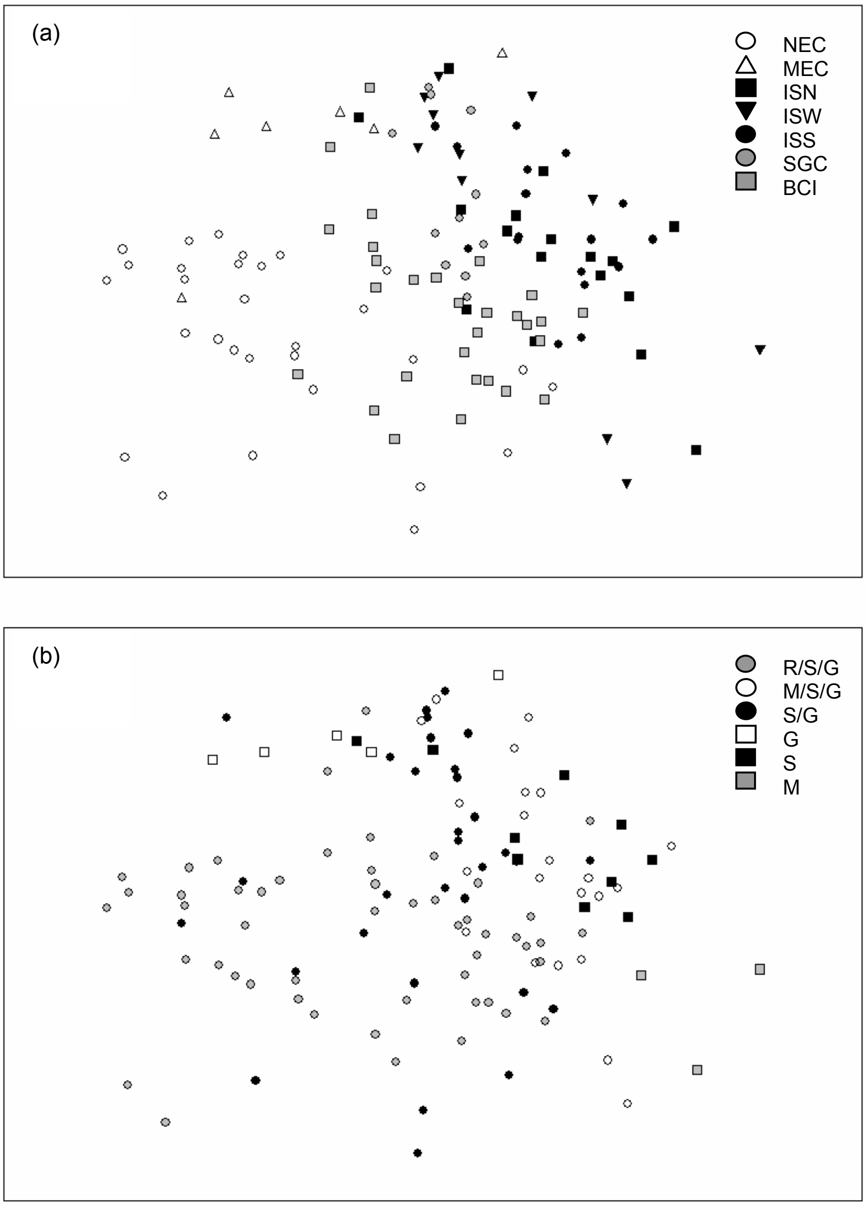
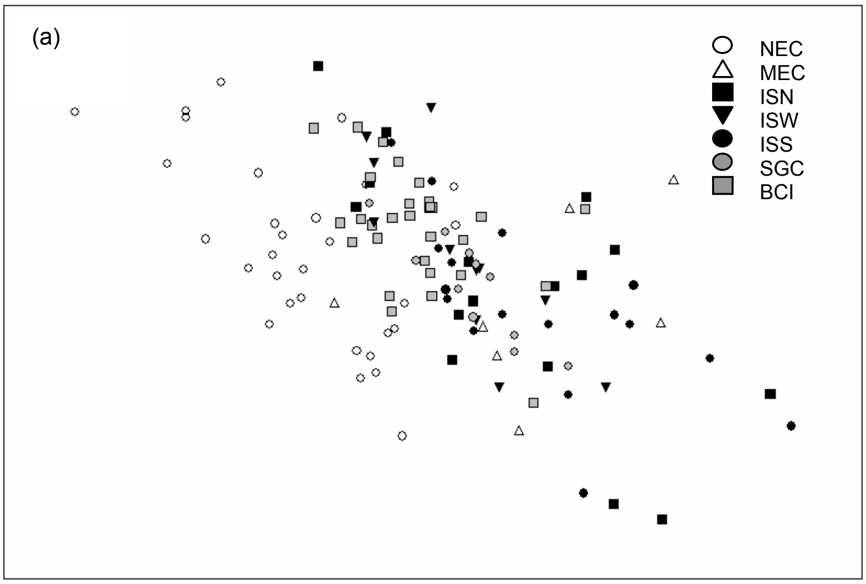


Figure 4.3. nmMDS ordination of relative taxon composition over the Irish Sea and eastern Channel stations, with (a) sector identifiers (NEC = north-eastern Channel, MEC = mid-eastern Channel, ISN = Irish Sea North, ISW = Irish Sea west, ISS = Irish Sea south, SGC = St George’s Channel and BCI = inner Bristol Channel) and (b) underlying sediment types (R/S/G = rock/sand/gravel, M/S/G = mud/sand/gravel, S/G = sand/gravel, G = gravel, S = sand and M = mud) superimposed.



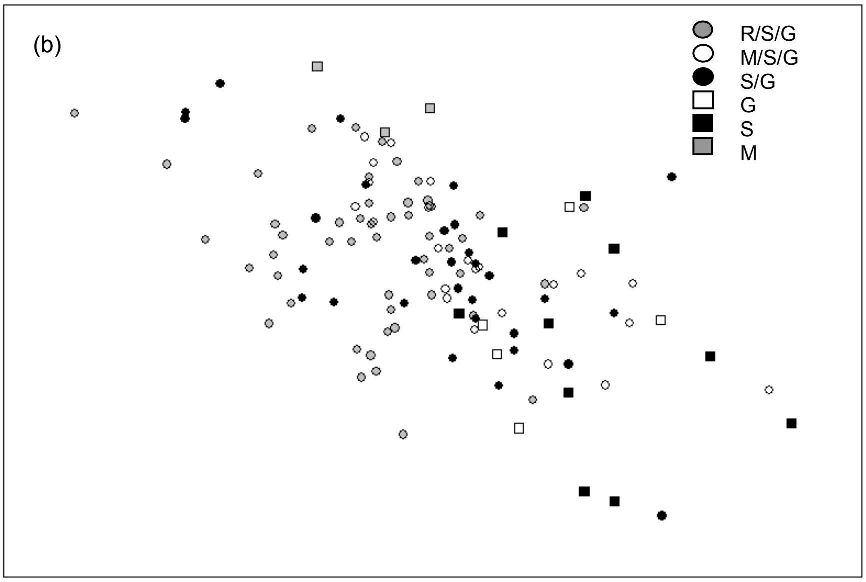


Figure 4.4. nmMDS ordination of relative biological trait composition over the Irish Sea and eastern Channel stations, with (a) sector identifiers (NEC = north-eastern Channel, MEC = mid-eastern Channel, ISN = Irish Sea North, ISW = Irish Sea west, ISS = Irish Sea south, SGC = St George's Channel and BCI = inner Bristol Channel) and (b) underlying sediment types (R/S/G = rock/sand/gravel, M/S/G = mud/sand/gravel, S/G = sand/gravel, G = gravel, S = sand and M = mud) superimposed.

in the NEC, though they were not distinct from the Irish Sea sectors. There was some differentiation between SGC and the BCI stations, with some of the stations from these sectors grouping apart from each other. Biological trait composition was variable in the ISN, ISS and ISW stations. There was little differentiation between these sectors, and they overlapped with the BCI and SGC.

No obvious patterns emerged when sediment types were overlaid on the biological trait nmMDS plot (Figure 4.4(b)). Stations with sand or gravel sediments generally separated from those with mud and rock/sand/gravel substrates; however, they were not clearly differentiated from each other or from other sediment types.

The RELATE procedure confirmed a significant association between biological trait composition and environmental conditions ($\rho = 0.334$, $P<0.01$). The combination of environmental variables providing the strongest association with trait composition comprised salinity, SST, ATR, weight of shell in the catch, fish richness and the amount of fishing ($\rho = 0.417$); showing that trait distributions responded simultaneously to a range of environmental conditions. When considered individually, ATR provided the best correlation with trait composition, but this association was much weaker than the multivariate combination (Table 4.2).

According to the BVSTEP procedure, the biological traits providing the strongest correlation with environmental conditions were size (small), longevity (<2 years), reproductive method (sexual: mini-adults), relative mobility (moderate), flexibility ($>45^{O}$ and $10\text{-}45^{O}$), feeding method (opportunistic), sociability (solitary) and living habit (permanent burrows) (BVSTEP; $\rho = 0.417$). These traits were expressed by many of the taxa sampled, with the exception of ‘permanent burrows’ and ‘sexual production of mini-adults’, which were expressed by only three taxa respectively (‘permanent burrows’ = *Echinocardium cordatum* (Pennant), *Nephrops norvegicus* (Linnaeus) and *Spatangus purpureus* (Muller) ‘sexual production of mini-adults’ = *Buccinum undatum* (Linnaeus), *Eledone cirrhosa* (Lamarck) and *Neptunea antiqua* (Linnaeus)). In general, relationships between these traits and environmental variables were negative, with high salinity, sea surface temperature, temperature range and fishing effort being associated with low frequencies of the traits (Table 4.3). However, in stations with high fish richness and a lot of shell, the traits occurred more regularly.

Values for the environmental and trait variables identified by the BIO-ENV and BVSTEP procedures were overlaid onto geo-referenced plots of the sampling stations, so that the environment/trait relationships could be studied at regional and sectoral scales. Although the level of differentiation in trait composition between regions or sectors was not as great as that of environmental conditions (compare Figures 4.2 and 4.4(a)), the geo-referencing procedure highlighted some general patterns that occurred at both scales.

Regionally, ATR and the amount of shell present appeared to be the most important drivers of differences in environmental conditions between stations (Figure 4.5), and these differences were reflected in most of the traits selected by the BVSTEP procedure, with the exception of ‘small body size’ (Figure 4.6). Eastern Channel stations had less shell overall, consistently higher and more homogenous ATRs, and generally fewer short-lived, moderately mobile, flexible and solitary individuals. They also contained fewer opportunistic feeders, permanent burrow inhabitants and individuals producing directly-developing offspring. Irish Sea stations, in contrast, had lower temperature ranges, more shell, and more of these organism types.

Shell content was also related to trait distribution at a local scale, as was fishing effort, although the relationships were complex and differed between the regions (Figures 4.5 and 4.6). High shell content and fishing effort were associated with decreased frequencies of moderately mobile and moderately to highly-flexible fauna towards the eastern reaches of the eastern Channel, whilst in the Irish Sea the reverse was true. Here, the northern-most stations tended to have high shell contents and increased fishing activity, associated with increases in the frequency of moderately mobile and moderately to highly-flexible organisms.

Table 4.3. Correlations (R_s) between environmental variables and biological traits identified by BIO-ENV and BVSTEP as best describing the relationship between trait composition and environmental conditions. Environmental variables selected were salinity (SAL), sea surface temperature (SST), average temperature range (ATR), weight of shell in the catch (WOS), fish richness (FR) and amount of fishing (F). Biological traits selected were ‘small body size’ (S), ‘longevity of less than 2 years’ (<2), ‘sexual reproduction producing mini adults’ (MIN), ‘moderate mobility’ (MMB), flexibility of ‘>45^{o}’ (>45) and ‘10-45^{o}’ (10-45), ‘opportunistic feeding’ (OPP), ‘absence of sociability’ (SOL) and ‘permanent burrows’ (PBR). Significance levels of the correlations are shown at P<0.1 (*), P<0.05 (**) and P<0.01(***)

	Environmental variable					
	SAL	SST	ATR	WOS	FR	F
Biological trait						
S	-0.222**	-0.219	-0.078***	0.284**	0.196***	-0.273***
<2	0.165*	0.171*	0.173*	-0.085	0.028	-0.125
MIN	-0.349***	-0.559***	-0.455***	0.552***	0.442***	-0.128
MMB	-0.448***	-0.618***	-0.514***	0.461***	0.457***	-0.257***
>45	-0.415***	-0.293***	-0.208**	0.258***	0.423***	-0.329***
10-45	-0.330***	-0.500***	-0.457***	0.269***	0.339***	-0.292***
OPP	-0.465***	-0.594***	-0.566***	0.517***	0.534***	-0.173*
SOL	-0.453***	-0.557***	-0.474***	0.438***	0.534***	-0.283***
PBR	-0.168*	-0.374***	-0.354***	0.225**	0.129	0.107

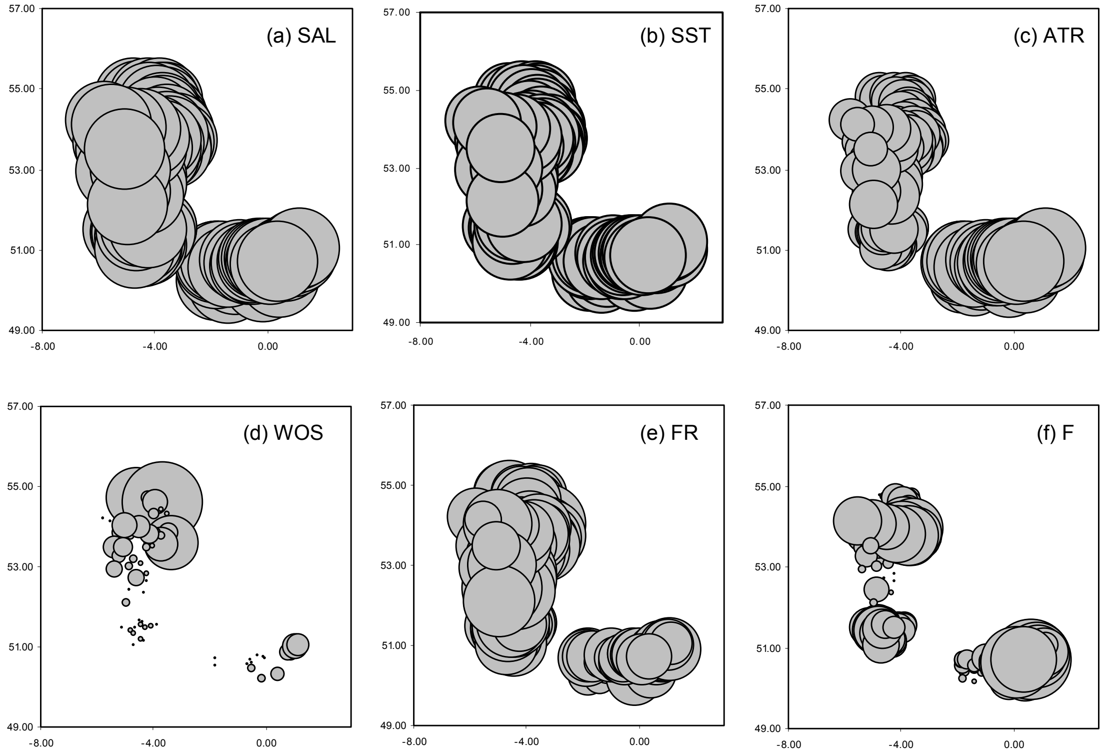


Figure 4.5. Environmental variables selected by the BIO-ENV procedure as providing the best correlation with biological trait composition in the eastern Channel and Irish Sea, overlaid on the benthic sampling stations. Stations are plotted by their geographical location. Environmental variables selected were; (a) salinity (SAL), (b) sea surface temperature (SST), (c) average temperature range (ATR), (d) weight of shell in the catch (WOS), (e) fish richness (FR) and (f) amount of fishing (F)

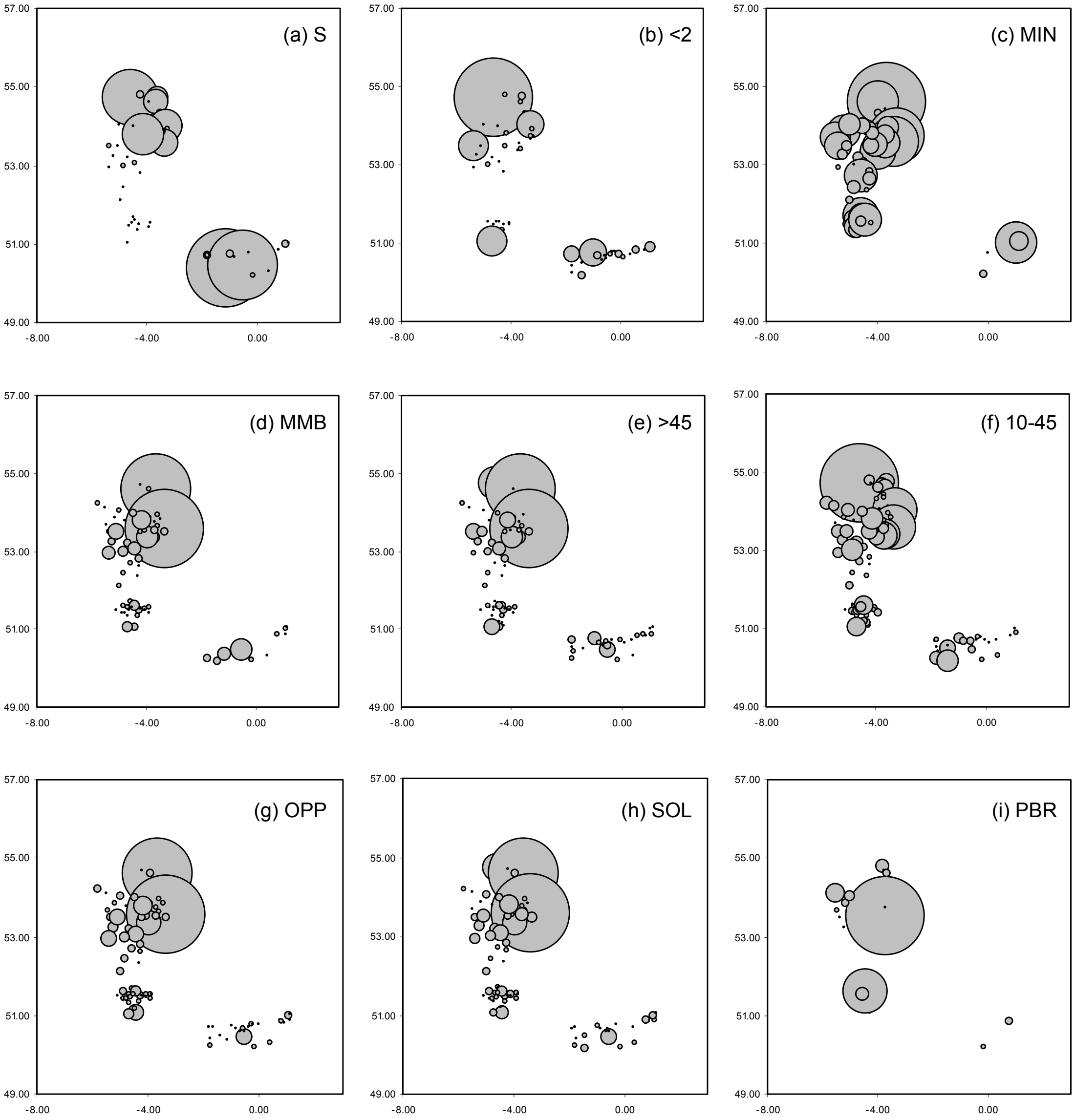


Figure 4.6. Biological traits selected by the BVSTEP procedure as providing the best correlation with environmental conditions in the eastern Channel and Irish Sea, overlaid on the benthic sampling stations. Stations are plotted by their geographical location. Trait variables selected were; (a) ‘small body size’ (S), (b) ‘longevity of <2 years’ (<2), (c) ‘sexual reproduction producing mini-adults’ (MIN), (d) ‘moderate mobility’ (MMB), (e) flexibility of ‘>45^{o}’ (>45) and (f) ‘10-45^{o}’ (10-45), (g) ‘opportunistic feeding’ (OPP), (h) ‘absence of sociability’ (SOL) and (i) ‘permanent-burrows’ (PBR).

DISCUSSION

Ecological functioning of benthic assemblages is central to the maintenance of ecosystem processes and the links between benthic and pelagic systems. The need for management measures to protect ecological functioning is well accepted. In practice, biodiversity and functioning cannot be directly managed, what can actually be managed are the human activities that impact on them. Therefore, to effectively manage for ecological functioning, we must understand how functioning relates to the natural and anthropogenic forces that impinge on benthic systems.

Ecological functioning varied over the regions, with changes in functioning being associated most closely with differences in salinity, sea surface temperature, the amount of shell present, fish richness and fishing intensity. However, although latitude was related to taxon composition in the regions studied, there was little evidence for a biogeographic effect on functioning. This finding supports earlier observations on a smaller scale, within the eastern Channel and southern North Sea (see Chapter 2, Bremner *et al.*, 2003b).

That taxon composition varied latitudinally over the regions is not surprising, as this phenomenon is well-documented in both the Channel (Holme, 1961, 1966) and Irish Sea (Ellis & Rogers, 2000) and is a feature of several other marine benthic systems (Hillebrand, 2004). However, the lack of relationship between latitude and functioning is, perhaps, surprising, given that ecological interactions, and hence functioning, have been proposed as a possible explanation for biogeographic changes in taxon composition (Hillebrand, 2004).

For example, Connolly and Roughgarden (1998) deduced a relationship between latitude and competitive interactions from changes in the cover of competitively dominant species on intertidal sites in the northwest United States, whilst Hillebrand (2004) showed that marine latitude/diversity relationships were affected by the size, mobility and feeding methods exhibited by fauna, with large, mobile, carnivorous or omnivorous fauna exhibiting stronger gradients than small or sessile organisms, or those at lower trophic levels such as autotrophs. Patterns of size, feeding and mobility traits did vary over the assemblages studied here, but the assertion that latitudinal changes cause these variations in functioning does not hold true for this temperate benthic system.

This lack of consistency in response of taxon and trait composition to latitudinal change, if a general phenomenon in marine benthic systems, is very important as it suggests that functioning is conserved in the face of changes in the species complement. Anthropogenic impacts such as pollution, fishing and climate change all have documented effects on species composition but if, albeit within certain limits, these changes do not alter functioning, the challenges for marine ecosystem management are considerably simplified.

However, the nature of the relationship between species and functioning is the subject of much debate (Emmerson *et al.*, 2001; Loreau *et al.*, 2001; Giller *et al.*, 2004). One recently proposed view is that it is not so much species diversity itself that is important, more the diversity of functional types (Bengtsson, 1998; Bolam *et al.*, 2002; Biles *et al.*, 2003; Raffaelli *et al.*, 2003). This is because several different species perform similar roles within assemblages, and reductions in the frequency of a species performing a particular role may be compensated for by increases in other similar species (Frost *et al.*, 1995). If this were the case, ecosystem management would focus on maintaining the levels of particular functional groups or types within assemblages, and not preserving each individual species (see, for example, Borja *et al.*, 2000; Pavluk *et al.*, 2000), because functioning would be conserved as long as each functional type was represented.

There is some suggestion of compensation in this study. For example, ten taxa exhibited ‘life-stage migration’ in the eastern Channel, compared to only eight in the Irish Sea, but frequencies of the trait did not generally differ between the regions. However, this was not a general phenomenon. Three species in the dataset produced directly-developing offspring (*B. undatum*, *E. cirrhosa* and *N. antiqua*). All three were found in the Irish Sea, whilst only *B. undatum* was found in the eastern Channel. In this instance, reductions in the frequency of the trait were noted, and compensation did not occur. The extent of compensation will be governed by how functionally-similar taxa are to each other in reality, when a variety of traits are considered; although the above-mentioned species were similar when migratory abilities or reproductive methods were considered, they expressed these traits to differing degrees and varied in terms of a number of others.

The changes in trait frequencies observed between the Irish Sea and eastern Channel (i.e. reductions in short-lived, moderately mobile, flexible or solitary organisms, or those feeding opportunistically, living in permanent burrows or producing mini-adults) have implications for ecosystem processes and bentho-pelagic dynamics. The low occurrence of organisms inhabiting permanent burrows in the eastern Channel is particularly notable. Burrows made by benthic fauna can range in size from single tubes to extensive systems (Reise, 2002). They are important features of coastal benthic assemblages, and have crucial roles in the processing of detritus and regeneration of nutrients. Burrows provide microenvironments that differ from the surrounding substrate and promote microbial biomass (Marinelli *et al.*, 2002), leading to increased organic matter decomposition and nutrient cycling (Snelgrove *et al.*, 1997). In addition, the unique physical properties of burrow walls allow them to act like molecular sieves, permitting oxygen and other particles to be transported into and through the sediments (Aller, 1983; Reise, 2002). The low frequencies of burrow-builders observed in the eastern Channel may reduce the ability of these benthic assemblages to process and store chemicals and waste materials.

The nature of the relationship between these changes in functioning and the environmental conditions measured is not intuitive. For instance, although ATR and shell content were implicated by the BIO-ENV procedure, it is difficult to find an explanation for direct effects of large temperature ranges on the construction of burrows within sediments. Moreover, burrow production requires soft, penetrable substrates; two of the three burrow-builders recorded in this study (*E. cordatum* and *N. norvegicus*) require sandy or muddy sediments (www.marlin.ac.uk). The presence of shell on benthic surfaces should inhibit burrow construction, so reductions in shell litter would logically be associated with higher, not lower, frequencies of burrow-builders.

This point illustrates a fundamental limitation of analyses studying organism-environment relationships: it is very difficult to determine whether it is the environmental parameters included in the analysis that drive the faunal patterns observed, or whether other environmental variables not measured, but correlating with those included, actually cause ecological patterns (Clarke, 1993). In this case, the low frequencies of permanent burrow inhabitants noted in the eastern Channel are likely to be related to sediment properties, which may be correlated with patterns of temperature range and shell content over a regional scale. Although sediment type was considered in the analysis, the low resolution of the information available precluded the formation of useful conclusions - the sediment data used were derived at a regional scale and, as such, may not adequately describe the substrate present at individual sampling stations.

A variety of environmental parameters act, in concert, to shape taxon composition (Thrush *et al.*, 2001; Freeman & Rogers, 2003) and, as evidenced here, ecological functioning. Even if observational studies identify the combinations of factors that are most closely associated with faunal patterns, there is no way, using such studies, of determining which parameters are individually most important, how the parameters measured interact with each other or the mechanisms by which they shape functioning. Observational studies are most useful for describing general patterns in functioning and environmental conditions, and identifying aspects of functioning that appear to respond to specific environmental factors, so the nature of these relationships can then be investigated experimentally.

In spite of the limitations imposed by the observational nature and limited spatial extent of the study, it has shown that ecological functioning changes with environmental conditions in temperate invertebrate assemblages. The factors primarily linked to this include physico-chemical (temperature, shell content and salinity), biotic (fish community structure) and anthropogenic parameters (demersal fishing); changes in these being associated with traits related to size, longevity, reproduction, mobility, flexibility, and feeding, social and living habits of the benthic megafauna. The links between environmental conditions and ecological functioning now require further experimental investigations to determine the nature, extent and ecosystem consequences of these complex relationships.

Chapter 5

Biological traits of the North Sea benthos – does fishing affect benthic ecological functioning?

ABSTRACT

The impact of fishing on benthic species and habitats has been well documented, but effects on the way the ecosystem functions are less well understood. The roles performed by benthic species contribute to ecological functioning, and changes in the types of species present may have implications for the whole ecosystem. Biological traits analysis, which uses a wide range of biological characteristics, is employed to investigate the effects of fishing on the variety of roles performed by benthic taxa. Eighteen biological traits were chosen to represent aspects of the morphology, life history, feeding and habitat use of benthic infauna from the western North Sea. Differences in relative frequency of the traits were assessed in relation to changes in fishing pressure over a 30-year period. The assemblages were dominated throughout by organisms exhibiting opportunistic traits. These traits responded positively to an initial increase in fishing effort, then remained relatively stable for the remainder of the study. Traits predicted to be associated with vulnerability to fishing impacts, such as long life spans, large oocytes and shelled body designs decreased in proportion in response to elevated fishing effort. Those organisms with high regeneration potential and asexual reproduction also responded negatively. Traits related to taxa's feeding modes and interactions with the benthic habitat remained relatively stable throughout the study. I conclude that fishing has altered the biological trait composition of this benthic assemblage in both predictable and unexpected ways over the last three decades. Some aspects of functioning may have been affected, while others, including those related to trophic relationships and habitat usage have been preserved in spite of changes in taxon composition. It is not yet clear what the larger scale implications of these trait changes may be to ecosystem functioning, fisheries management, or indeed to the management of anthropogenic activities in the sea. What is clear is that studies of the biological trait compositions of other marine ecosystem components are now required.

INTRODUCTION

International agreements require countries to manage the marine benthos to protect biodiversity at a level that includes both species diversity and the essential functions performed by ecosystems (Secretariat of the Convention on Biological Diversity, 1992; OSPAR Commission, 1998). Ecological functioning relates to physical processes and the organisms mediating these processes (Naeem *et al.*, 1999). As well as species diversity and physical aspects of the habitat, it incorporates the roles played by organisms, their interactions with each other and their interactions with their environment.

The impacts of trawl fishing on benthic habitats have been well documented, with trawling disturbing the substrate surface (Watling & Norse, 1998), displacing rocks (Engel & Kvitek, 1998), damaging sedimentary structures (Auster *et al.*, 1996) and moving particulate matter into the water column (Riemann & Hoffmann, 1991; Pilskaln *et al.*, 1998). The effects of trawling on biological assemblages are equally demonstrable, with reductions in total abundance/biomass and richness and alterations in relative species composition (Hutchings, 1990; Jennings & Kaiser, 1998).

How fishing affects the types of organisms inhabiting benthic systems is, however, less well understood. Structure-forming organisms, which provide a refuge from predation and perform important nursery functions for fish and invertebrate species, can be heavily impacted by the passage of trawl gear (Turner *et al.*, 1999; Collie *et al.*, 2000a). Direct damage also reduces large, long-lived and fragile taxa (Hall-Spencer *et al.*, 1999; Kaiser *et al.*, 2000; Bradshaw *et al.*, 2002), whilst indirect impacts include increases in opportunists and scavengers such as crabs and whelks that take advantage of increased dead benthos and discarded bycatch (Kaiser *et al.*, 1998; Rumohr & Kujawski, 2000).

Although changes to the types of organism present will have implications for the functioning of benthic systems, the magnitude of the impacts is still unclear. Not all taxa predicted to respond to disturbance in a particular manner actually do. Different species of scavenging taxa may respond in contradictory ways to increases in fishing, or may respond positively in some habitats but not others (Ramsay *et al.*, 1996; Ramsay *et al.*, 1998). Species defined as vulnerable to fishing may show no response or even increase in abundance in impacted systems (Frid *et al.*, 2000a).

Characteristics that make some species types vulnerable to fishing may be offset by other characteristics that impart resistance. Some upright, sessile organisms are able to withstand trawl disturbance because they also possess the ability to regenerate lost appendages or quickly re-colonise post-impacted areas (Bradshaw *et al.*, 2002). There are also indications that additional characteristics such as flexibility (Wassenberg *et al.*, 2002), sediment reworking activities (Coleman & Williams, 2002) and sediment depth ranges (Bergmann & Hup, 1992) may be important in determining how such taxa respond to stress.

Biological traits analysis is a method capable of investigating the wide range of biological characteristics involved in determining how organisms respond to fishing. The approach, which originates in lotic ecosystems (Townsend & Hildrew, 1994), incorporates organisms' interactions both with each other and with their environment, and can be a potentially valuable tool for investigating the effects of anthropogenic disturbance at the ecosystem-functioning level (Doledec *et al.*, 1999; Charvet *et al.*, 2000).

This paper uses the biological traits approach to investigate the potential effects of bottom-trawling on the ecological functioning of an infaunal assemblage located within a fishing ground in the western North Sea. The assemblage has been sampled over a time period of some 30 years and there is evidence of fishing impacts at the species level (Frid *et al.*, 1999a). Preliminary analysis provided indications of changes in functioning over time, compared to a neighbouring, unfished, assemblage (Bremner *et al.*, 2003a, see Appendix 5). The present study builds upon these findings by focussing on the benthic assemblage inside the fishing ground; making a detailed examination of temporal changes in biological trait composition, and investigating whether these changes could be related to fluctuations in fishing pressure. Specific predictions were made about the response of each biological trait to fishing pressure, based on current ideas about the characteristics that make benthic organisms vulnerable to or tolerant of disturbance (Table 5.1). For example, it was predicted that traits linked to opportunistic lifestyles, such as short lifespans, early maturity, asexual reproduction, scavenging and body regeneration would respond positively to increased fishing, whereas long lifespans, shelled body forms, filter feeding and large size would be impacted.

METHODS

Study area

The study station is located at 55°07'N, 01°15'W, some 18.5km (11.5 miles) off the northeast coast of England, UK (Figure 5.1). It is located in 80m of water, with predominantly silt and clay sediments. The station has been sampled annually in late winter since 1971. At least five samples of 0.1m^2 area were taken on each occasion using a van Veen grab. These were passed through a 0.5mm mesh sieve and taxon abundance recorded per square metre (Buchanan & Warwick, 1974). With the exception of 1977 and 1998, data were available from all years since 1971.

In order to overcome difficulties arising from mis-identification and changes in taxonomy over the 30-year period, the taxa were analysed at the genera level or above (Clark, 2000). To simplify the analysis, the dataset was reduced to the most abundant taxa by retaining only those that represented 3% or more of abundance at the station in any two or more years. On average, 3% of the total taxa present met this criterion in each individual year, resulting in a subset of 15 taxa (Table 5.2).

Fishing pressure

The station lies within a *Nephrops norvegicus* (Linnaeus) (Dublin Bay prawn) fishing ground. It is trawled principally by the UK, but Danish, Dutch and Swedish vessels have fished in the vicinity. The area is trawled for *N. norvegicus* in the autumn, winter and spring, although *Gadhus morhua* (Linnaeus) (cod), *Melanogrammus aeglefinus*

Table 5.2. The most abundant taxa found in the benthic infauna assemblage off the northeast English coast. Relative abundance is the average abundance of each genus, expressed as a percentage of total fauna abundance and averaged over the study period.

Taxa	Relative abundance ($\bar{x}$ ± 95% C.I.)
Abra spp.	3.0 ± 1.0
Amphiura spp.	2.5 ± 1.3
Chaetozone spp.	4.8 ± 1.0
Glycera spp.	1.6 ± 0.4
Harpinia spp.	2.9 ± 0.6
Heteromastus spp.	31 ± 3.9
Levinsenia spp.	11 ± 3.8
Lumbrineris spp.	2.3 ± 0.3
Nemertea spp.	2.9 ± 0.6
Oligochaeta spp.	2.2 ± 1.0
Ophelina spp.	3.7 ± 1.1
Paramphinome spp.	2.2 ± 0.6
Praxillella spp.	9.4 ± 1.8
Prionospio spp.	2.6 ± 0.6
Spiophanes spp.	1.7 ± 1.1

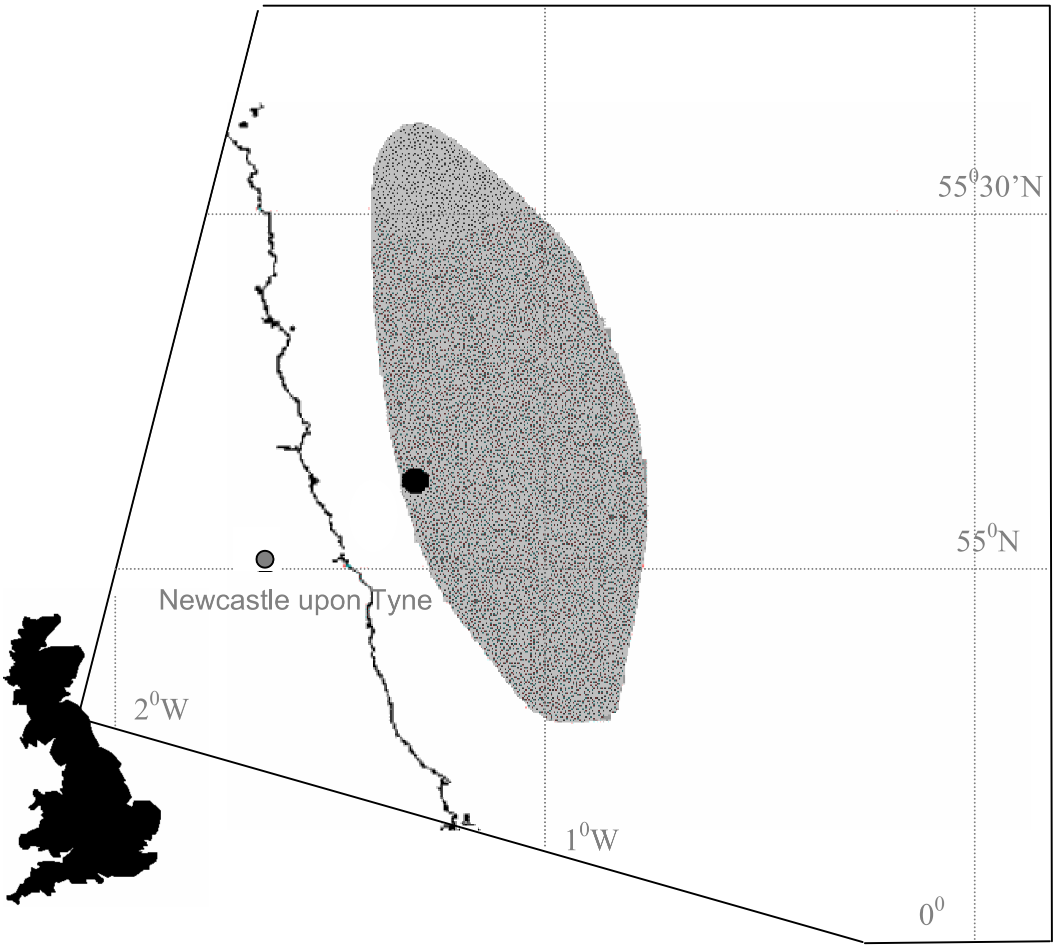


Figure 5.1. The location of the benthic sampling station off the northeast coast of England, western North Sea (the shaded area represents the *Nephrops norvegicus* fishing ground).

(Linnaeus) (haddock) and *Merlangius merlangus* (Geoffroy) (whiting) are also taken year round (Robson, 1995). The fishery has landed around 1,000 tonnes locally for the past 5-6 years (MAFF, 1995, 1996, 1997, 1998; DEFRA, 2000). It is based primarily around otter trawling, although some beam trawling was also carried out during the 1990s.

Fishing effort data for the *N. norvegicus* fishery, measured as total hours fished per annum (hpa) within ICES rectangle 39E8, were provided by the Department for Environment, Food and Rural Affairs (DEFRA) (Figure 5.2). Effort ranged from approximately 12,000 to 92,000hpa ($\bar{x}$ = 51,809.6hpa ± 7,435.9 S.E.), equating to between 5.7 and 8.9 hours per day trawled.

The fishing effort data were split into five phases, defined by changes in effort over the period 1972-2001. Effort was low during the initial years of the study, from 1972 to 1981 (Phase one: $\bar{x}$ = 37,509.3hpa ± 6,994.3 S.E.). It then rose to moderate levels (Phase two: $\bar{x}$ = 65,256.6hpa ± 13,830.1 S.E.) from 1982 to 1986. The years 1987 to 1989 (Phase three) saw the highest levels of trawling, on average 90,259.3 hours per annum (± 3,583.6 S.E.), before a drop to more moderate levels (Phase four: $\bar{x}$ = 63,837.2hpa ± 12,895.1 SE) between 1990 and 1994. Phase five contained the years from 1994 to the end of the study period, where effort was once more reduced to low levels (Phase five: $\bar{x}$ = 37,563.9hpa ± 5,062.9 S.E.).

Biological traits analysis

Eighteen biological traits were chosen to represent aspects of the benthic organisms' morphology, life history and interaction with each other and their environment, and each trait broken down into categories (Table 5.1). Individual taxa were coded for their affinity to each category of the biological traits using fuzzy coding (Chevenet *et al.*, 1994) (Appendix 4). Fuzzy coding is particularly useful when taxa are, as is the case here, aggregated to the genus level or above. For example, nemerteans were only identified to phylum, but fuzzy coding allowed differences between taxa within the phylum to be reflected in the trait categories. Thus, nemerteans mostly have non-planktonic

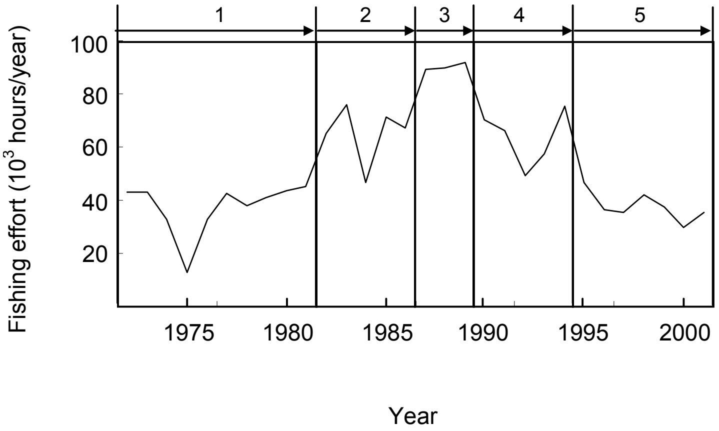


Figure 5.2. Fishing effort from 1972 to 2001 in ICES statistical rectangle 39E8. Effort is divided into five levels; Level one = initial low effort (1972-1981), Level two = initial moderate effort (1982-1986), Level three = high effort (1987-1989), Level four = subsequent moderate effort (1990-1994), Level five = subsequent low effort (1995-2001).

development, but may sometimes exhibit short or extended planktonic development. They can be coded 3,1,1 for the trait category 'duration of planktonic development phase'.

Each taxon's trait category scores were weighted by their abundance in each year of the study, and these weighted scores were summed over all 15 taxa (Charvet *et al.*, 1998). This resulted in a year by trait table, showing the frequency of each trait category within the assemblage for each year of the study. When no information on a particular trait was available for a taxon, zero values were entered for each trait category and the taxon did not contribute to the calculation of trait weightings (Usseglio-Polatera *et al.*, 2000a).

The faunal dataset was 4th root transformed in order to downweight the influence of traits exhibited by very abundant taxa. It was then split into five groups, according to the different phases of fishing effort. Differences in trait composition over the study period were investigated using non-metric multidimensional scaling (nmMDS) on the year by trait table (Clarke, 1993). One-way analysis of similarities (ANOSIM) was used to test for differences in biological trait composition between the fishing effort phases, and similarity of percentages (SIMPER) analysis employed to determine the traits most responsible for any differences. The analyses were carried out using PRIMER v.5.2.2 (PRIMER-E Ltd, Plymouth).

RESULTS

The benthic assemblage at the sampling station was the *Brissopsis lyrifera* (Forbes)-*Amphiura chiajei* (Forbes) variant of the classic *Amphiura filiformis* (OF Müller) community type (Petersen & Boysen-Jensen, 1911) Of the 15 most abundant taxa, 10 were polychaetes (Table 5.2). Nemerteans and oligochaetes were also represented, as was one genus of mollusc (*Abra* spp. (Lamark)), crustacean (*Harpinia* spp. (Boeck)) and echinoderm (*Amphiura* spp. (Forbes)). Most trait categories were expressed by several taxa, with the exception of long lifespans and shelled body forms, exhibited only by *Amphiura* spp. and *Abra* spp. respectively.

Based on the relative proportions of biological traits, nmMDS highlighted several changes in biological trait composition within the benthic assemblage. There was evidence of a directional trend in trait composition during the early years of the study, however the assemblage did not follow a consistent trajectory over the whole period (Figure 5.3(a)). Differences were more marked when the years were grouped by the level of fishing effort (Figure 5.3(b)). The largest changes in trait composition occurred between the first two phases, when effort rose from low to moderate. Trait composition also altered during the mid to late 1980s, when effort became high. Changes after this period were more gradual, and even though fishing effort was similar, the assemblage remained subtly different during the subsequent low effort phase than that encountered at the beginning of the study. Differences in trait composition were significant between all fishing phases (ANOSIM Global R=0.492, P<0.01), except between phases three and four (Table 5.3).

The benthic assemblage was characterised by short-lived, sessile, vermiform taxa with monotelic reproduction and extended reproductive seasons. These organisms dominated throughout the study, as did deposit feeders and animals with low regeneration potential. Proportions of these trait categories were similar within fishing phases, although, with the exception of deposit feeders, they increased between low and high effort, then reduced between Phases three and five (Figures 5.4 and 5.5). One or more of these trait categories were exhibited by all taxa to some degree and *Chaetozone* spp. (Malmgren), *Heteromastus* spp. (Eisig), *Levinsenia* spp. (Mesnil), *Ophelina* spp. (Oersted), *Prionospio* spp. (Malmgren) and *Spiophanes* spp. (Grube) strongly expressed each of the seven categories.

Organisms displaying consistent reductions in response to increased fishing effort included those exhibiting high regeneration potential, polytelic reproduction (more than one reproductive episode per year), production of large oocytes (more than 301µm), asexual reproduction by budding and shelled body design (Table 5.4). These organisms decreased in proportion between the initial low and high effort phases, then increased

Table 5.3. Comparison of biological trait composition between different fishing effort phases for north-eastern English coast benthic assemblages by ANOSIM (Phase 1 = initial low effort, Phase 2 = initial moderate effort, Phase 3 = high effort, Phase 4 = subsequent moderate effort, Phase 5 = subsequent low effort). Significance levels are shown at P<0.1 (*), P<0.05 (**), P<0.01 (***) and P<0.001 (****).

Fishing phases	R-value
Phase 1 to Phase 2	0.781^{****}
Phase 2 to Phase 3	0.959^{**}
Phase 3 to Phase 4	-0.087
Phase 4 to Phase 5	0.451^{***}
Phase 1 to Phase 3	0.35^{*}
Phase 3 to Phase 5	0.704^{**}

Table 5.4. SIMPER analysis of the biological traits that contributed most (cumulative contribution) to differences in trait structure between fishing effort phases. Average difference is the change in the average frequency of each trait category in the assemblage between the fishing phases.

Trait	Category	Average difference	Cumulative %
Phase 1 to Phase 3 (low to high effort)			
Reproductive mode	Budding	220.33	3.7
Body design	Shell	77.50	6.9
Oocyte size	301+ μm	328.67	9.6
Reproductive events	Polytelic (> 1)	372.22	12.2
Maturity	0-12 months	985.44	14.8
Reproductive mode	Fission	273.28	17.3
Regeneration potential	High	289.50	19.6
Duration reproduction	Continuous	295.11	21.8
Oocyte size	201-300 μm	257.89	23.8
Movement	Crawl	178.95	25.8
Phase 3 to Phase 5 (high to low effort)			
Body design	Shell	-339.00	4.2
Longevity	12+ years	-286.67	8.1
Body design	Armour/scales	-592.00	11.8
Regeneration potential	High	-706.67	15.4
Reproductive events	Polytelic (>1)	-555.33	18.7
Longevity	8-11 years	-143.33	22.0
Oocyte size	301+ μm	-313.00	24.5
Aggregation potential	Medium	-404.33	26.7
Movement	Crawl	-364.33	29.0
Reproductive mode	Budding	-88.33	31.1
Phase 1 to Phase 2 (low to moderate effort)			
Reproductive mode	Planktonic	4878.36	2.4
Duration reproduction	Short episodic	4071.16	4.7
Life habit	Burrow-dweller	3910.73	7.0
Aggregation potential	High	4075.39	9.2
Reproductive season	Spring	3853.43	11.5
Substrate location	11-20cm	3889.12	13.6
Maturity	13-24 months	4306.73	15.7
Size	ML	2197.87	17.7
Oocyte size	0-100 μm	2201.84	19.7
Mobility	Low	1792.17	21.6

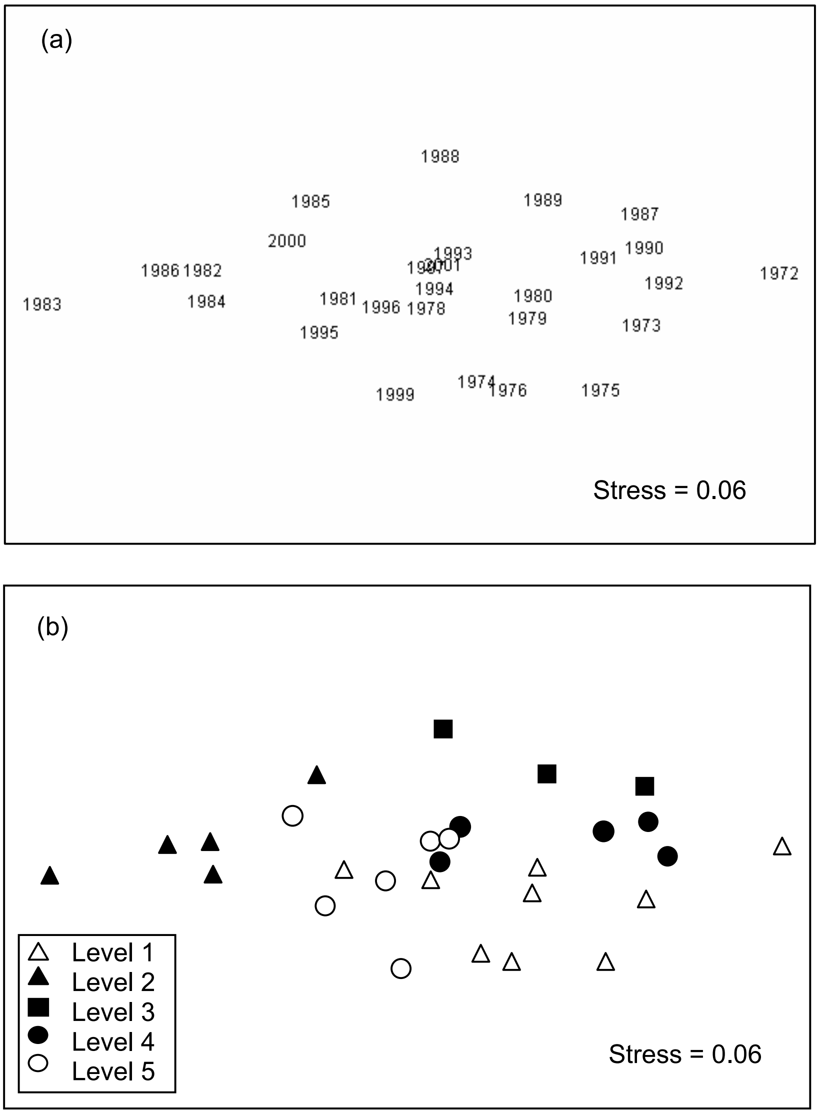


Figure 5.3. nmMDS of the biological trait composition of a benthic assemblage from the northeastern English coast during the period 1972-2001. Plot (a) shows the pattern of change over the years, while (b) shows the relationship between the years when labelled by the level of fishing effort (Level one = initial low effort, Level two = initial moderate effort, Level three = high effort, Level four = subsequent moderate effort, Level five = subsequent low effort).

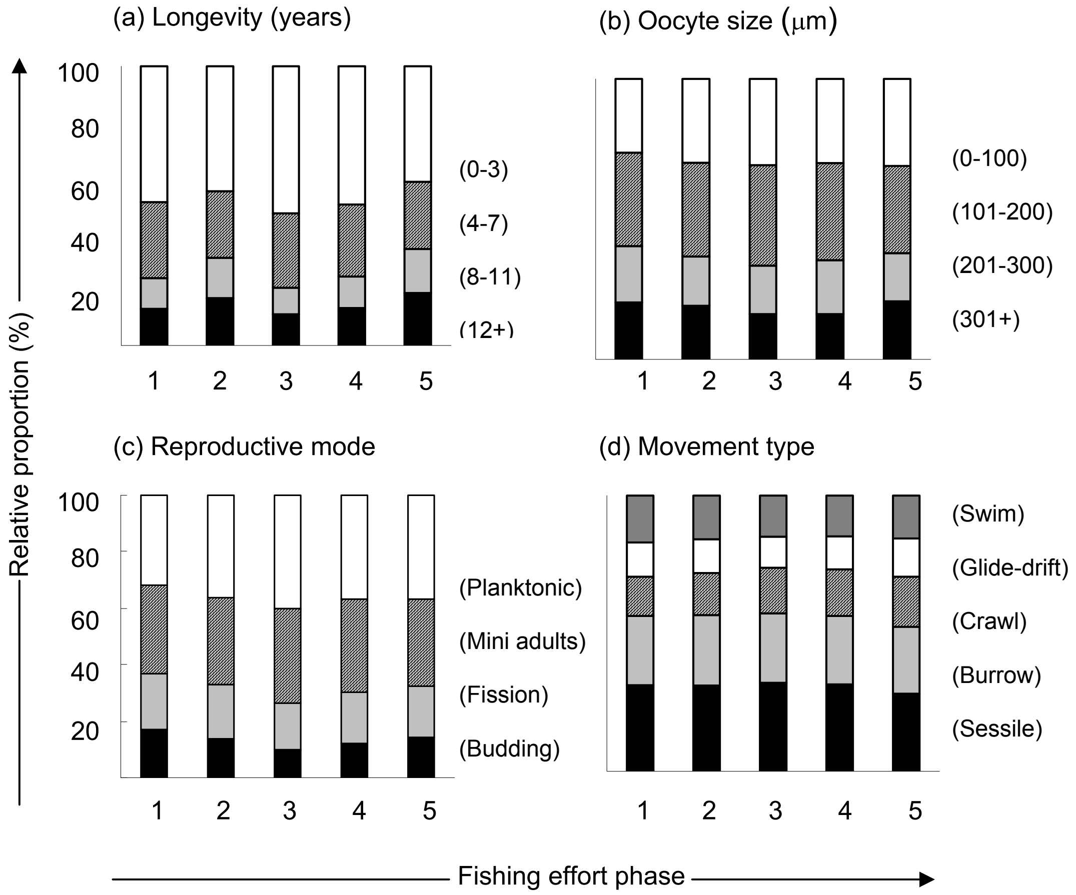


Figure 5.4. Comparison of selected biological trait composition during five levels of changing fishing effort on a north-eastern English coast benthic assemblage (Level one = initial low effort, Level two = initial moderate effort, Level three = high effort, Level four = subsequent moderate effort, Level five = subsequent low effort).

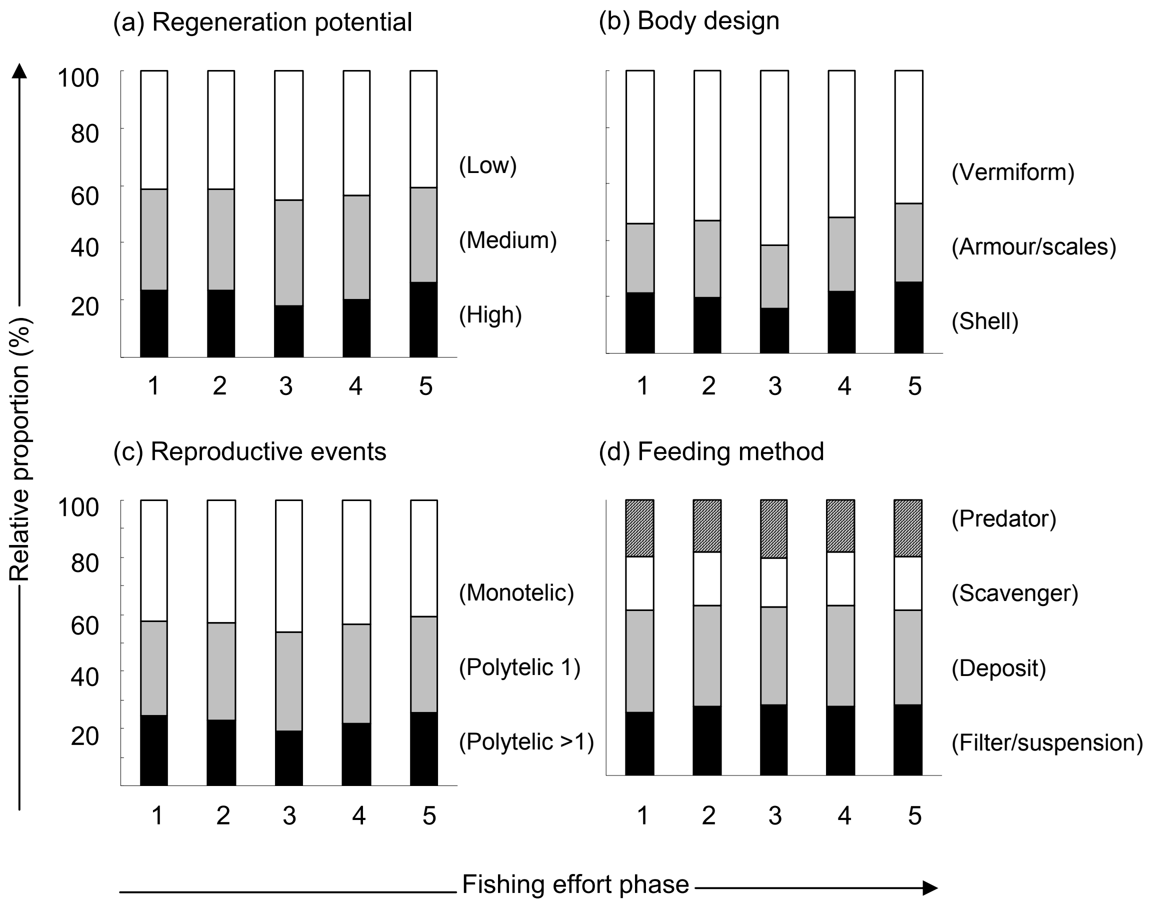


Figure 5.5. Comparison of selected biological trait composition during five levels of changing fishing effort on a north-eastern English benthic assemblage (Level one = initial low effort, Level two = initial moderate effort, Level three = high effort, Level four = subsequent moderate effort, Level five = subsequent low effort).

when fishing subsequently declined during phase five (Figures 5.4(b)-(c), 5.5(a)-(c)). The decrease in asexually budding organisms was the most marked, and this decrease was mirrored to a lesser degree by those organisms that reproduced asexually through fission (Figure 5.4(c)).

Shelled organisms and those exhibiting high regeneration potential increased to proportions in excess of that found during the initial low effort period, whereas organisms reproducing asexually by budding failed to regain the proportions observed during the early years of the study. No single taxon exhibited each of the five trait categories negatively impacted by fishing, although oligochaetes and nemerteans both showed medium to high affinity for polytelic reproduction, large oocytes and high regeneration potential.

Other organisms displaying trends related to fishing effort were long-lived (>12 years) and armoured/scaled animals (Figures 5.4(a) and 5.5(b)). These trait categories decreased within the assemblage between Phases one and three. However, they did not decrease gradually, and both categories showed a slight increase when effort initially rose, at the beginning of the 1980s. As effort reduced from high to low, their proportions increased beyond those observed during the initial low-effort period. Organisms that reproduced sexually with a short planktonic larval development phase, matured at 13-24 months and produced small oocytes also increased between Phases one and two, although unlike the long-lived and armoured/scaled animals, they did not subsequently decrease when fishing effort became high.

DISCUSSION

The biological trait composition of infaunal assemblages off the northeast English coast has shown a pattern of change in response to fishing pressure that has potential implications for the wider ecosystem and fisheries management. Some of these changes corresponded with current expectations about vulnerability of particular types of organism, whilst others did not.

Trait categories responding according to predictions were those associated with opportunistic life history strategies. Organisms maturing relatively early, producing small oocytes or exhibiting short pelagic development phases increased in frequency at the beginning of the 1980s, then showed less response to changing fishing effort. Species composition of the area was relatively stable through the 1970s, where population cycles were linked to the flux of organic matter to the benthos (Buchanan *et al.*, 1986; Buchanan & Moore, 1986; Frid *et al.*, 1996; Frid *et al.*, 1999a). This relationship broke down at the beginning of the 1980s, when the increase in fishing led to subtle changes in species composition (Lindley *et al.*, 1995; Frid *et al.*, 1999a). Opportunistic life history traits allowed the organisms to respond quickly to the initial increases in fishing effort, and to retain dominance in the assemblage when effort fluctuated in later years.

This dominance of opportunist traits may have led to an alternate state of functioning within this benthic assemblage. The increase in opportunistic traits co-incided with a reduction in evenness of trait distribution during high fishing, and trait composition during the later period of low effort, although similar to, did not return to that seen in the initial period of light fishing in the 1970s. The extent to which ecosystem functioning can resist fishing pressure and the forcing of alternate states is a question of much importance in marine ecology (Thrush & Dayton, 2002). However, the trait composition of the assemblage towards the end of the study appears to be situated somewhere between that of the initial low and moderate fishing years. There may be a time lag between the reduction of fishing pressure and the response of the less opportunistic biological traits, so recovery may be happening, but more slowly than the initial effects. It is too early to determine whether this system has entered an alternate state, although further monitoring of the site may yield an answer to this question.

As also predicted by life-history theory, the frequency of long-lived organisms decreased in response to increased fishing effort, then recovered once trawling declined. *Amphiura* spp. was the only taxon in the dataset to exhibit this trait category, so no other long-lived taxa were available to replace it. The contributions made by long-lived organisms to ecological functioning were depressed in times of high fishing pressure. Some biological characteristics may not be vital for the functioning of ecosystems and their loss may be of limited consequence. However, we do not currently know which characteristics are dispensable and the losses of which may lead to considerable ecosystem change (Snelgrove *et al.*, 1997). In light of this uncertainty, it is important to retain as many ecological roles as possible. Taxon redundancy ensures that these roles may continue to be expressed even if taxon changes occur, because other species exhibiting the same or similar traits would compensate for the loss (Chapin *et al.*, 1997).

This does not appear to be the case for the trait 'long lifespan'. However, the advantages of ecological redundancy are obvious if other traits expressed by *Amphiura* spp. are considered. *Amphiura* spp. are burrowing organisms. The burrowing activities of benthic fauna facilitate nutrient recycling, aerate sediments, create habitat complexity and influence hydrodynamics (Coleman & Williams, 2002; Reise, 2002). Reductions in *Amphiura* spp. abundance removed their contribution to these important ecological processes. However, many taxa in the assemblage performed some form of burrowing activities. The absence of any decrease in burrowing itself indicated that the reduction in *Amphiura* spp. was compensated for by other organisms exhibiting similar traits.

Using a subset of the infauna assemblage may limit the ability of the analysis to identify the responses of certain biological traits. As large taxa tend to be rare in benthic systems (Warwick & Clarke, 1996), it's likely that they were under-represented in the analysis. Large taxa are particularly vulnerable to fishing effects and they may have important roles in the functioning of the system. Although the individual roles played by these rare taxa may not affect functioning by themselves, their cumulative contribution may be enough to dampen the impact of fishing on traits expressed by only a single abundant taxon. This has implications for the way in which the analysis is interpreted. The reduction in long-lived organisms noted in the reduced dataset analysed here is not perhaps as important in terms of functioning as is implied by the analysis, because the gap left by *Amphiura* spp. may be filled by the cumulative contributions of other long-lived but rare taxa.

When species composition is analysed, the reduction of full fauna lists to a subset does not result in a loss of information (Gray *et al.*, 1988). However, because very few species carry the same combinations of biological characteristics, reducing datasets during biological traits analysis is more likely to distort conclusions. Ideally, the full fauna list would be used, but this would require information on the biological characteristics of a large number of species. Gaps in the natural history knowledge of many benthic infauna species would prevent much trait information from being coded and compromise the ability of the analysis to reveal any patterns in trait composition. This creates a trade-off between taxa and traits; either the number of species or the range of traits included must be reduced.

As these results show, a variety of traits are involved in species' responses to fishing pressure, and often not in the ways predicted. For example, Collie *et al.* (2000b) attributed a lack of response to fishing noted in *Abra* spp. to their small size. However, *Abra* spp. are also shelled organisms, and as evidenced here, this trait is negatively affected by fishing. Taxa with high powers of regeneration or asexual reproduction were predicted to respond positively, because recovery of damaged appendages allow organisms to survive the direct impact of trawls (Hill *et al.*, 1996; Bradshaw *et al.*, 2002) and the ability to reproduce regularly provides a survival advantage in disturbed systems (Grassle & Sanders, 1973). These traits, in fact, responded negatively; possibly because regular reproduction and regeneration allow organisms to survive initial disturbance events but increase their energy requirements, making them more vulnerable to competition (Grassle & Sanders, 1973, but see; Hall *et al.*, 1994) .

It is clear that our knowledge of the responses of different types of organism to fishing impacts, although expanding rapidly, is far from complete. As such, retaining a wide range of traits in analyses, even at the expense of the full species list, is important at this time because it helps provide a picture of ecosystem functioning. This, ultimately, may allow us to ask which characteristics are important in determining the responses of benthic taxa to fishing.

There were no apparent changes to the relative frequencies of feeding method and food choice traits in the present study. Increases of scavenging fish and epifauna have been found in areas subject to trawling disturbance (Hall-Spencer *et al.*, 1999; Rumohr & Kujawski, 2000) but there is little evidence of this response in opportunistic infaunal scavengers (Frid *et al.*, 2000a). Episodes of discard provision occur directly after trawling activity and mobile fish and epifauna often arrive at the trawl site very quickly (Kaiser & Spencer, 1996). This may reduce the opportunity for the smaller benthic infauna to utilise the extra food resources that become available (Frid *et al.*, 2000a). Hence, scavenging infauna may be largely unaffected by trawl discards.

If this is true, it is the combination of scavenging, location in the substrate and mobility that determines how a species responds to fishing. Combinations of characteristics affecting species vulnerability have been encountered in other studies. Bergmann and Hup (1992) found that large individuals of *Lanice* spp. (Malmgren) and some echinoid species were less vulnerable to trawling than small ones, because larger individuals built deeper tubes, into which they could escape. *Ophiura* spp. (Lamarck) lives in the upper layers of the sediments, where organisms are more exposed to physical disturbances (Hall *et al.*, 1994). Even so, this taxon can escape trawl impacts, probably because it is small enough to pass through the net (Bergmann & Hup, 1992).

Biological traits analysis considers the traits individually, so in this respect it would be difficult to use the technique in it's present form to determine species' sensitivities to fishing. The advantage of the approach is that, while it retains information on the species present in the assemblage, it enables the responses of traits themselves to be examined independently of the species expressing them. This can provide an indication of the functioning of the assemblage as a whole, and how it responds to fishing.

Despite previously noted changes to species composition in the study site (Frid *et al.*, 1999a), some traits linked directly to ecological processes, such as burrowing and feeding, remained relatively constant over the study period. Jennings *et al.* (2001b) also showed that trophic structure of a North Sea benthic assemblage was resistant to fishing pressure, even though species composition altered. The implications of this are that some aspects of functioning in benthic ecosystems may well be maintained in the presence of fishing, irrespective of the identities of species performing particular roles, with reservoirs of potential replacements for those fauna that are reduced. If this is the case, it means that the functions performed by benthic assemblages are more robust to disturbance than the fauna performing them.

The North Sea benthos has been fished intensively for over a century (Frid *et al.*, 2001), with rapid increases in effort occurring after the end of the Second World War (OSPAR Commission, 2000). This system is dominated by polychaetes, an occurrence associated with trawling-impacted ecosystems (Jennings *et al.*, 2001b). Given the dominance of vermiform taxa from the onset of the study, and the fishing history of the North Sea, it is likely that the system suffered some degree of impact on functioning before the 1970s. It is impossible to be sure what fishing-induced changes occurred in the system before the 1970s, or how these influenced the changes occurring afterwards. Biological traits analysis is a method new to marine ecology and it would be unwise at this time to apply the patterns emerging here to unfished systems. However, consistent patterns in the response of biological traits to human disturbance have been identified in freshwater invertebrate assemblages across Europe (Statzner *et al.*, 2001). The patterns emerging from this study, particularly those that are consistent across more than one taxa, are real biological results that have relevance to the study of benthic ecosystem functioning.

Biological traits analysis has made an important contribution towards elucidating the impacts of fishing on functioning in this western North Sea benthic infauna assemblage. The challenge now will be to determine how other infauna assemblages respond to fishing, and whether changes in their functioning will have wider effects on other ecosystem components such as meiofauna, megafauna and fish.

Chapter 6

The effects of human disturbance on ecological functioning in different intertidal habitats

ABSTRACT

Ecosystem approaches to marine resource management require information on the effects of anthropogenic activities on the structure and functioning of benthic communities. Impacts on ecological functioning have not been sufficiently addressed to-date, but recent advances in approaches to describing functioning are allowing these effects to be explored. In intertidal soft-sediments, invertebrate extraction is an important agent of human disturbance that can, even at low levels, affect assemblage structure. This study examines the effects of hand-raking, a technique commonly used to harvest the bivalve (*Cerastoderma edule* (Linnaeus)), on the ecological functioning of benthic assemblages in two intertidal habitats. Some assemblages were subjected to daily raking-disturbance for approximately one week, to examine initial responses to disturbance. Others were raked and then left undisturbed for a further week, to investigate subsequent effects. Ecological functioning at the muddy site was impacted. The frequency of, primarily, short lived fauna, deposit feeders, burrowers, gonochorists, brooders, benthic developers, flexible organisms and soft-bodied animals initially decreased, then recovered to levels in excess of those in non-disturbed assemblages. Tube-dwellers, in contrast, reduced in response to disturbance and did not recover. At the sandy site, ecological functioning was not impacted by the initial disturbance, but altered after raking ceased, with increases in flexible, soft-bodied, burrowing and free-living fauna and those with benthic larval development. The variety of traits impacted by raking in muddy assemblages suggests many resident taxa were physically affected, irrespective of their biological characteristics. Where these characteristics may be more important is in determining organisms' potential to recover after disturbance; with mobility, burrowing and tube-building habits important. Changes in ecological functioning in muddy assemblages may, potentially, have major consequences for marine ecological processes. Changes in trait composition at the sandy site, despite undetectable effects on taxon composition, indicate that functioning can be impacted, even in assemblages traditionally considered resilient. Future studies should seek to address human impacts on ecological functioning in these types of assemblage, and examine the magnitude of effects of changes in functioning on the rates of ecological processes.

INTRODUCTION

With the advent of an ecosystem approach to marine environmental management, the effects of anthropogenic activities on the structure and, especially, functioning of benthic assemblages are areas that require and are receiving increasing attention. Benthic environments are subject to several different types of human impact, including pollution, materials extraction and associated waste dumping, construction (e.g. oil rigs, wind farms and coastal defences) and the exploitation of target species.

In shallow subtidal soft sediment habitats, extraction of invertebrates for food purposes is common. These habitats are often fished commercially for bivalve molluscs using ship-towed hydraulic or toothed dredges. The dredges rake or slice through the top layers of the seabed, penetrating up to 30cm into substrates (Gaspar, 1994) and removing target animals and other organisms inhabiting the surface sediments. Studies have shown that dredge fishing affects the structure of benthic macrofauna assemblages, although the impacts may be short lived (Hall *et al.*, 1990; Eleftheriou & Robertson, 1992; Tuck *et al.*, 2000; Watling *et al.*, 2001; Chicharo *et al.*, 2002; Alves *et al.*, 2003) and less important than natural phenomena such as seasonal environmental changes (Alves *et al.*, 2003).

Intertidal sediments are also exploited to produce organisms for direct human consumption and to be used as bait by recreational or subsistence fishers. Bivalves such as cockles and clams are commonly harvested for human consumption (Brown & Wilson, 1997; Spencer *et al.*, 1998; Kaiser *et al.*, 2001), whilst some polychaetes, shrimps and clams are taken as bait (Olive *et al.*, 1993; Wynberg & Branch, 1997; Gutierrez *et al.*, 2004). These fisheries are prosecuted at both subsistence and commercial levels (Jackson & James, 1979; Cryer *et al.*, 1987; Olive *et al.*, 1993; Kaiser *et al.*, 2001), using hand-held equipment including rakes or suction pumps, tractor-towed mechanical dredges or boat-towed hydraulic dredges (Hall & Harding, 1997; Wynberg & Branch, 1997).

Hand gathering practices can have deleterious effects on both target and non-target organisms, although these effects appear to be short-lived in nature (Blake, 1979; Wynberg & Branch, 1997; Kaiser *et al.*, 2001). Mechanical extraction of intertidal animals has greater impacts on benthic assemblages than hand gathering (van den Heiligenberg, 1987), and although previous studies demonstrated repaid recovery from dredge impacts (Cotter *et al.*, 1997; Hall & Harding, 1997), recent evidence suggests this may not always be the case (Piersma *et al.*, 2001). In addition to the type of gear used, the impact of invertebrate extraction can vary depending on environmental conditions in the area exploited, with mud assemblages experiencing greater effects than those inhabiting sands (Emerson *et al.*, 1990; Ferns *et al.*, 2000).

The effects of intertidal harvesting can also vary between taxa. For example, Brown and Wilson (1997) showed that the polychaetes *Heteromastus filiformis* (Claparède), *Streblospio benedicti* (Webster & Benedict) and *Tharyx acutus* (Webster & Benedict) responded negatively to hand gathering activities, whilst oligochaetes, the gastropod *Hydrobia totteni* (Morrison) and the polychaetes *Scoloplos fragilis* (Verrill) and *Exogone hebes* (Webster & Benedict) were not affected. In Hiddink's (2003) study of the responses of selected species to suction dredging, negative effects were noted for *Mytilus edulis* (Linnaeus) and *Macoma balthica* (Linnaeus), but not *Hydrobia ulvae* (Pennant) or undersized (i.e. non-target) *Cerastoderma edule* (Linnaeus).

Species exhibit differing responses to anthropogenic disturbance because their response to environmental change is determined by the morphological, behavioural and life history characteristics that they possess. Robinson and Richardson (1998) showed that the speed with which exposed razor clams *Ensis arcuatus* (Jeffreys) could reburrow in sediments had a negative effect on their ability to survive suction dredging, whilst Emerson *et al.* (1990) found that, because *Mya arenaria* (Linnaeus) suffocated if they did not maintain siphon contact with overlying water, their ability to burrow upwards through sediment restricted their survival when buried under tailings resulting from clam digging.

These characteristics, or biological traits, also determine the contributions that individual species make towards the regulation of ecosystem processes (defined here as ecological functioning, see Chapter 4 and Naeem *et al.*, 1999). Burrowing abilities, for example, as well as determining species' responses to sediment disturbance, also determine their contributions towards benthic nutrient cycling (Biles *et al.*, 2002). It therefore follows that anthropogenic activities eliciting trait-specific species' responses may have consequent effects on ecological functioning.

Chapter 5 (Bremner *et al.*, 2004) provided evidence that anthropogenic disturbance, in the form of trawling, can impact on ecological functioning, through changes in the expression of traits across benthic assemblages. By monitoring a fishing ground over three decades, it showed that trawling led to long-term overall reductions in the frequency of long-lived organisms and those exhibiting asexual reproduction or high powers of regeneration. Some of the findings were predictable, based on current theory regarding the effects of fishing on benthos (e.g. reductions in long-lived organisms, see Kaiser *et al.*, 2000), whilst others appeared to be counter-intuitive; for example, scavenging fauna displayed little response to increased fishing (see Hall-Spencer *et al.*, 1999; Rumohr & Kujawski, 2000). It is clear that further study is required to elucidate the links between anthropogenic activities and ecological functioning.

One of the main problems with the study in Chapter 5 (Bremner *et al.*, 2004), and other descriptive studies, is the inability to assign causation to changes identified in the benthic assemblages. These types of study aim to identify changes in benthic assemblages that are co-incident with changes in disturbance intensity. This process can be difficult because the accurate measurement of fishing effort is often difficult (Jennings *et al.*, 2001b) and other anthropogenic activities and natural phenomena can affect benthic assemblages in similar ways to fishing, making it hard to attribute cause (Kaiser, 1998). Experimental studies, which can control anthropogenic disturbance regimes, can provide a useful addition to large-scale descriptive investigations of fishing impacts.

This study aimed to experimentally examine the effects of anthropogenic disturbance on ecological functioning in marine benthic habitats. In order to fully appreciate the impacts of anthropogenic activities on resident benthic assemblages, fishing effects studies should be carried out on a scale that is realistic to that of the actual fishery. Cockle fishing in intertidal habitats is often carried out on a local scale, which makes it appropriate for experimental study. Therefore, the specific aims of the study were to assess the response, in terms of initial impacts and subsequent effects, of mud (Seal Sands, England) and sand (Ballochmartin Bay, Scotland) assemblages to simulated hand-gathering of cockles.

METHODS

Experimental sites

The study was conducted at two intertidal sites in the Tees (northeast England) and Clyde (southwest Scotland) estuaries (Figure 6.1). Seal Sands (NZ 530 260), the Tees estuary site, is a sheltered mudflat situated in the lower estuary between the Conoco Phillips oil terminal and Hartlepool power station. Ballochmartin Bay (NS 182 570) is a sheltered sandy beach on the eastern coast of the Isle of Cumbrae, at the seaward end of the Firth of Clyde.

In the past, both estuaries have suffered from poor sediment quality related to industrial and domestic usage of the rivers (Hursthouse *et al.*, 1994; Balls *et al.*, 1997; Jones & Turki, 1997). No information is available on the levels or effects of sediment pollutants on the intertidal assemblages at Ballochmartin Bay, but there is evidence that sediment quality in the Firth of Clyde has improved in recent years (Hursthouse *et al.*, 1994). Historically, resident benthic assemblages at Seal Sands were negatively impacted by pollution (Gray, 1976), although improvements in environmental quality have prompted recovery (Hall *et al.*, 1996; Warwick *et al.*, 2002). Seal Sands was designated as a Site of Special Scientific Interest (SSSI) in 1983/84 and Ballochmartin Bay in 1985. Both sites currently receive low levels of direct human disturbance.

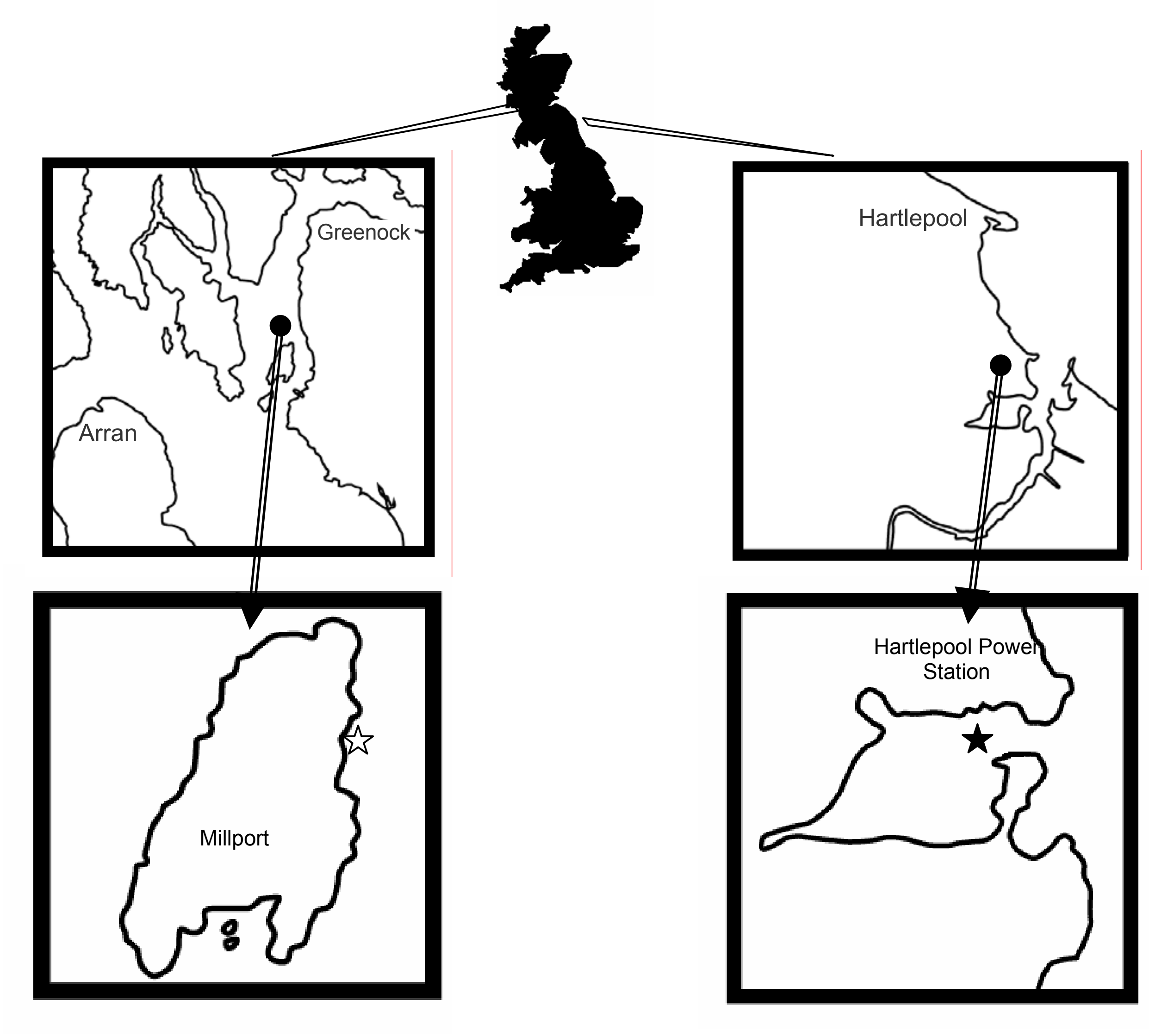


Figure 6.1 Intertidal sampling sites at Seal Sands (★) in the Tees estuary (northeast England) and Ballochmartin Bay (☆) in the Firth of Clyde (southwest Scotland).

Experimental design

A random block design was used to investigate the effects of hand-raking on macrobenthic assemblages at the two sites. Two blocks of 18m by 2m were marked out at each site. Each block contained five $4m^2$ plots, with a distance of 2m between plots. One randomly-selected plot from each block was sampled at the beginning of the experiment, to provide a description of baseline conditions. Two plots from each block were designated for the experimental treatments, the treatments being; (i) five (Seal Sands) or seven (Ballochmartin Bay) days of disturbance (initial impact), and (ii) five (Seal Sands) or seven (Ballochmartin Bay) days of disturbance followed by a further ten (Seal Sands) or six (Ballochmartin Bay) days where plots were left undisturbed (subsequent-effects). One further plot from each block served as a temporal control for the impact and one for the subsequent-effects treatments.

The experimental plots in each block were subjected to simulated cockle hand-gathering. They were completely raked over daily at low tide using a hand rake. Cockles retained by the rake teeth were removed from the plots. Baseline plots were sampled for fauna and sediment parameters on the first day of the experiments (immediately prior to the commencement of hand-raking), whilst the impact plots and their controls were sampled on days five (Seal Sands) or seven (Ballochmartin Bay) and subsequent-effects and their controls at the end of the experiment (days 15 and 13 respectively). Experiments were conducted between 3-17th April 2002 (Seal Sands) and 7-19th June 2003 (Ballochmartin Bay).

Sediment parameters

Two replicate cores of 15mm diameter by 70mm depth were taken from each plot for calculation of organic matter content. As sediments in the northeast of England contain high quantities of coal, traditional loss-on-ignition methods for determining organic matter are not suitable in these areas (Hyslop & Davies, 1996). Therefore, organic matter content was calculated using a modification of Johnson and Frid's (Johnson & Frid,

1995) and Hyslop and Davies' (Hyslop & Davies, 1996) hydrogen peroxide (H_2O_2) technique. Sediment samples were dried to constant weight at 60°C and 5g of sediment placed into 20ml of H_2O_2. The samples were left at room temperature until oxidation was complete and no bubbles could be seen on the surface. They were then washed over filter paper using distilled water, dried at 60°C and re-weighed to determine percentage organic matter.

Sediment grain size was analysed following Buchanan's (Buchanan, 1984) methods. At Ballochmartin Bay, two replicate cores of 15mm diameter by 70mm depth were taken from each plot, dried at 60°C and sieved through 500µm 250µm, 125µm and 63µm sieves. The sediments at Seal Sands were muddier and initial separation of the grains was required (Buchanan, 1984). Two cores of 100mm diameter by 80mm depth were removed from each plot. These were dried at 60°C, soaked overnight in 200ml of aqueous sodium hexametaphosphate $(NaPO_3)_6$ ($6.2gL^{-1}$), re-dried at 60°C and sieved through 500µm 250µm, 125µm and 63µm sieves (Spencer *et al.*, 1997). Grain size parameters were calculated using GRADISTAT v.4 (Blott & Pye, 2001).

Faunal sampling

Cylindrical plastic cores were used to take two samples from each plot. At Seal Sands, a 100mm diameter by 150mm depth core was placed flush to the sediment surface. At Ballochmartin Bay, a 220mm diameter by 335mm depth core was placed to a depth of approximately 250mm. The contents of the cores were fixed in 4% formalin with Rose Bengal. Macrofauna were separated from sediments by washing over a 500µm sieve, then preserved in formalin until processed. Macrofauna were sorted, identified to species where possible and counted.

Description of ecological functioning

Biological traits analysis was used to describe ecological functioning of the benthic assemblages (see Chapter 2, (Bremner *et al.*, 2003b) for a full description and justification of this approach). Ten biological traits were chosen for the analysis, reflecting life history (relative adult longevity, sexual differentiation, reproductive technique and larval development method), morphology (degree of flexibility and body design) and behaviour (relative adult mobility, movement, living habit and feeding type). Each trait was sub-divided into categories (Appendix 6(a)) and individual taxa coded for the extent to which they displayed the categories of each trait using fuzzy coding (Chevenet *et al.*, 1994). The scoring range of zero to 3 was adopted, with zero being no affinity to a trait category and 3 being high affinity. When no information on a particular trait was available for a taxon, zero values were entered for each trait category (Usseglio-Polatera *et al.*, 2000a). The table of trait scores is included as Appendix 6(b).

Trait category scores for each taxon present in a sample were weighted by the abundance of that taxon. These abundance-weighted scores were then summed over all taxa present in the sample, to provide a measure of the frequency of trait categories within that sample (Charvet *et al.*, 1998). The weighting procedure was repeated for each sample, resulting in a sample-by-trait table giving the total proportions of trait categories exhibited across the assemblages (biological trait composition).

Biological traits analysis requires a great deal of ecological information to be compiled for an, often, large number of taxa. This stage is time-intensive and information is often not available for all taxa, creating a trade-off between the number of traits and taxa included in the analysis. The solution to this trade-off is to reduce either the number of traits or taxa. As maximising the number of traits examined is an important factor in the ability of BTA to describe differences in ecological functioning (see Chapter 3), the removal of taxa that are rare, and hence make small individual contributions to overall trait frequencies, is the most pragmatic of the two available solutions (see Chapter 5, (Bremner *et al.*, 2004), for a discussion of the merits of removing rare taxa from datasets). Therefore, taxa occurring only once at each site were removed from both the taxon and trait-level analyses. Indeterminate crustaceans and bivalves were also removed from the analyses as their lack of identity prevented them from being coded for biological traits.

Statistical analysis

Initial comparisons of univariate and multivariate measures between baseline plots and impact/subsequent-effects controls were carried out to identify whether underlying natural temporal changes occurred at either site. Where natural temporal change was undetectable, baseline replicates were pooled with those from impact and subsequent-effects controls, and these plots were compared to impact and subsequent-effects treatments. If a temporal change was identified, this factor was accounted for in the statistical analysis used to compare the treatments.

Differences in the univariate measures total taxon abundance (N) and taxon and trait richness (S), diversity (Shannon's H') and evenness (Pielou's J') were compared using analysis of variance (ANOVA) or Kruskal-Wallis tests. Multivariate differences in taxon and biological trait composition were visualised by non-metric multidimensional scaling (nmMDS), using Bray Curtis similarity co-efficients and 4th root transformed taxon abundance or trait frequency data. (Clarke, 1993). Differences over time and subsequently between treatments were formally tested using analysis of similarities (ANOSIM). Where ANOSIM results were significant, similarity of percentages (SIMPER) analysis was used to identify the taxa or biological traits contributing most to these differences. Differences in mean abundance or frequency of selected taxa or traits identified by the SIMPER analysis were compared between treatments using ANOVA or Kruskal-Wallis tests. All analyses were carried out using the statistical packages MINITAB® v.14 (MINITAB® and the MINITAB logo® are registered trademarks of Minitab Inc) and PRIMER v.5.2.2 (PRIMER-E Ltd, Plymouth).

RESULTS

Seal Sands

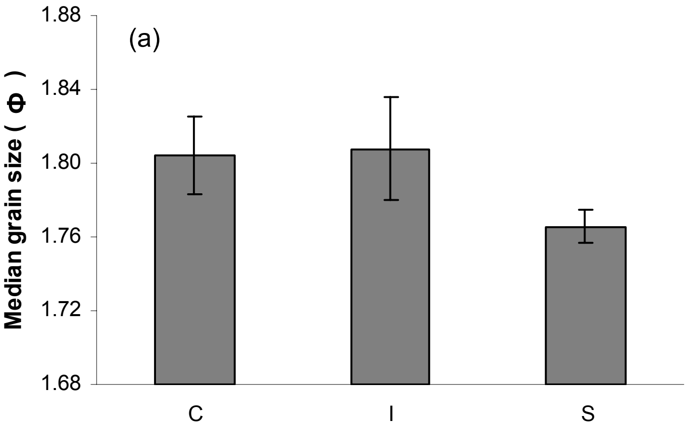
Sediments

Seal Sands sediments were moderately-well to well sorted fine to medium sands, with median grain size ranging from 1.78-1.89 Φ ($\bar{x}$ 1.83 ± 0.05 C.I.) and silt/clay contents of 1.49-4% ($\bar{x}$ 2.79 ± 1.10 C.I.). Organic matter content ranged between 1.17% and 3.36% ($\bar{x}$ 2.52% ± 0.94 C.I.). There was no significant change in sediment parameters between the baseline, impact control and subsequent-effects control plots, so replicates from these plots were pooled and compared to the impact and subsequent-effects treatments. Organic matter showed little variability between treatments and was not affected by the raking disturbance. However, median grain size increased in the subsequent-effects plots relative to impacts and controls (Kruskal Wallis; H = 8.44, d.f. = 2, $P<0.05$) and the silt/clay content was on average 55% and 36% lower respectively, although these differences were not significant (Figure 6.2).

Taxon analysis

Twenty six taxa in total were identified at Seal Sands, representing five different phyla (annelida, crustacea, mollusca, nematoda and nemertea). Six taxa occurred only once at the site (*Angulus tenuis* (da Costa), *Gammarus* spp. (Fabricius), *Liocarcinus* spp. (Stimpson), Nereidae., *Pholoe minuta* (Fabricius) and *Polydora quadrilobata* (Jacobi)) and consequently were not included in the analysis. Of the remaining twenty taxa, fifteen were found in the baseline plots, with harpacticoids, *Eteone longa* (Fabricius), *M. balthica*, *M. edulis* and *Nephtys* spp. only found in treatment plots or the temporal controls.

Taxon richness in the baseline assemblages ranged from 8-11 ($\bar{x}$ 9.75 taxa ± 1.47 C.I.) and total abundance from 485-1,592 ($\bar{x}$ 923.75 ± 461.93). The assemblages were heavily



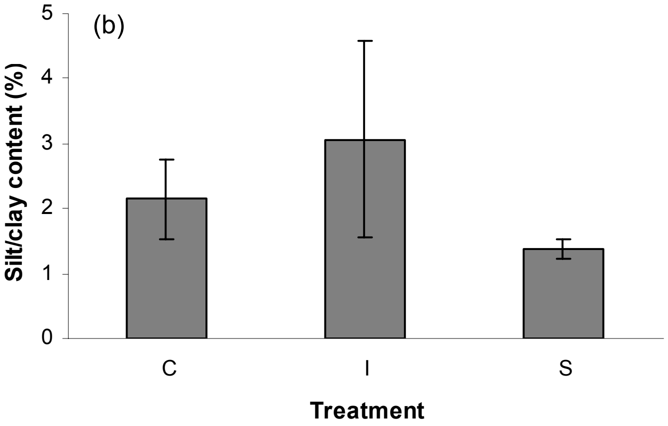


Figure 6.2. Differences in sediment (a) median grain size (Φ) and (b) silt/clay content (%), between impact (I), subsequent-effects (S) treatments and pooled controls (C) at Seal Sands. Values are presented as means (± 95% C.I). Median grain sizes differed significantly (Kruskal Wallis; H = 8.44, d.f. = 2, $p<0.05$) but silt/clay content did not.

dominated by the three most common taxa (Figure 6.3). These taxa; nematodes, oligochaetes and the tubeworm *Fabricia sabella* (Ehrenberg), were abundant within the baseline assemblages (Table 6.1), accounting for approximately 90% of total abundance. Cockles were found in two of the four baseline samples. Undersized and marketable size individuals were present in assemblages throughout the experiment, and on average were less abundant in the subsequent-effects treatment than controls, but more abundant in impact plots (Figure 6.4(a). However, they were not recovered in sufficient numbers for these differences to be analysed statistically.

None of the univariate community measures showed significant temporal changes in undisturbed conditions, so baseline and control replicates were pooled in order to assess treatment effects. Taxon richness varied little between the treatments (Figure 6.5(a)). Total abundance declined in impacted and increased in subsequent-effects plots compared to controls, however variability was high within both treatments and no significance could be attached to these changes (Figure 6.4(b)). Shannon diversity (H') and Pielou's evenness (J') were slightly, but non-significantly, higher in subsequent-effects than impacted or control assemblages (Figure 6.5(c) and (d)).

Taxon composition did not vary significantly in non-disturbed plots over the period of the experiment, and baselines were pooled with treatment controls. The taxon composition of control assemblages differed from that found in impact and subsequent-effects plots (ANOSIM Global R = 0.306, $P<0.05$). However, impact and subsequent-effects assemblages were both variable in composition and, although they separated from each other on the nmMDS plot (Figure 6.6), differences between these treatments were not significant at the taxon composition level.

SIMPER analysis indicated that several taxa exhibited consistent responses to raking disturbance, based on the results of the ANOSIM test (Table 6.1). *Manayunkia aestuarina* (Bourne), nematodes and oligochaetes were all lower on average in impact plots than in controls, and higher in subsequent-effects plots than controls, implying that all three initially reduced in response to raking disturbance, then increased over the

Table 6.1. SIMPER analysis of Seal Sands taxa contributing most to differences in composition between controls and impacts or subsequent-effects assemblages (average dissimilarity; controls v. impacts = 30.21, controls v. recovery = 30.41).

Taxon	Average abundance (a)	Average abundance (b)	Contribution to dissimilarity (%)	Cumulative contribution (%)
Control v Impact				
Fabricia sabella	114.75	103.75	10.77	10.77
Manayunkia aestuarina	84.75	63.75	8.96	19.73
Nematoda	257.75	196.50	8.64	28.37
Capitellidae	25.33	67.25	7.57	35.94
Hydrobia ulvae	6.58	0.50	7.23	43.17
Oligochaeta	291.50	263.75	6.43	49.60
Pygospio elegans	14.42	16.00	5.88	55.48
Control v Subsequent effects				
Capitellidae	25.33	110.00	9.80	9.80
Oligochaeta	291.50	342.75	8.90	18.70
Cirratulidae	0.75	13.50	8.41	27.11
Nematoda	257.75	414.25	8.17	35.28
Manayunkia aestuarina	84.75	87.50	8.06	43.34
Hydrobia ulvae	6.58	0.25	7.06	50.40
Pygospio elegans	14.42	4.75	6.74	57.14

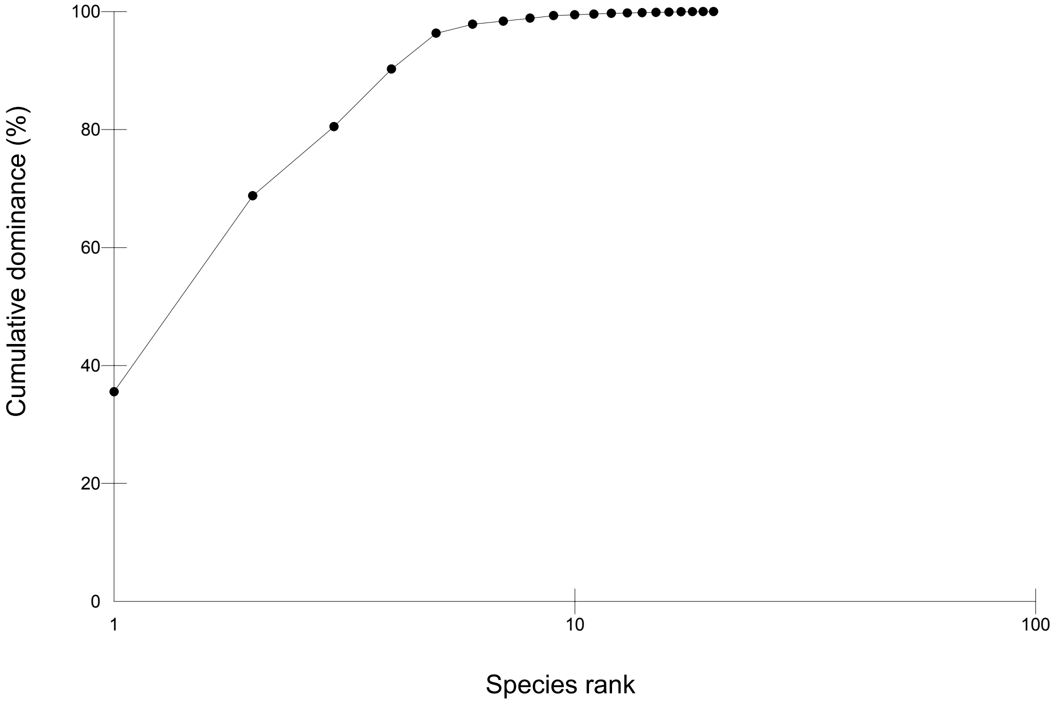
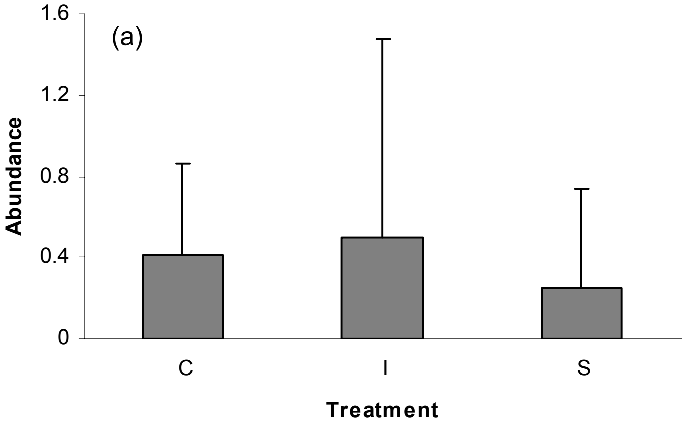


Figure 6.3. Cumulative dominance (% of total abundance) of taxa at Seal Sands before the commencement of hand-raking.



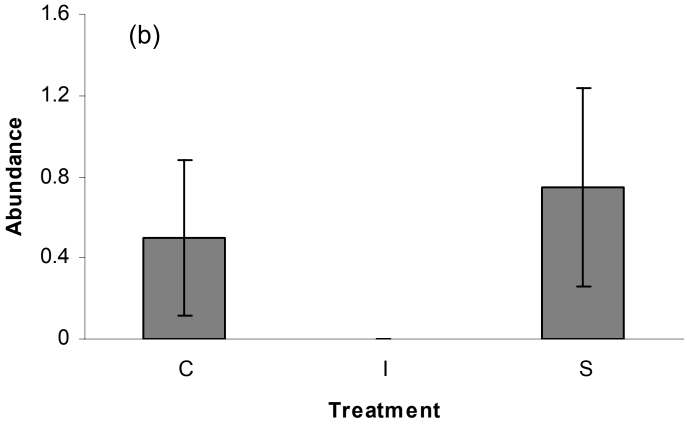


Figure 6.4. Differences in mean (± 95% C.I.) *Cerastoderma edule* abundance between impact (I), subsequent-effects (S) treatments and pooled controls (C) at (a) Seal Sands and (b) Ballochmartin Bay.

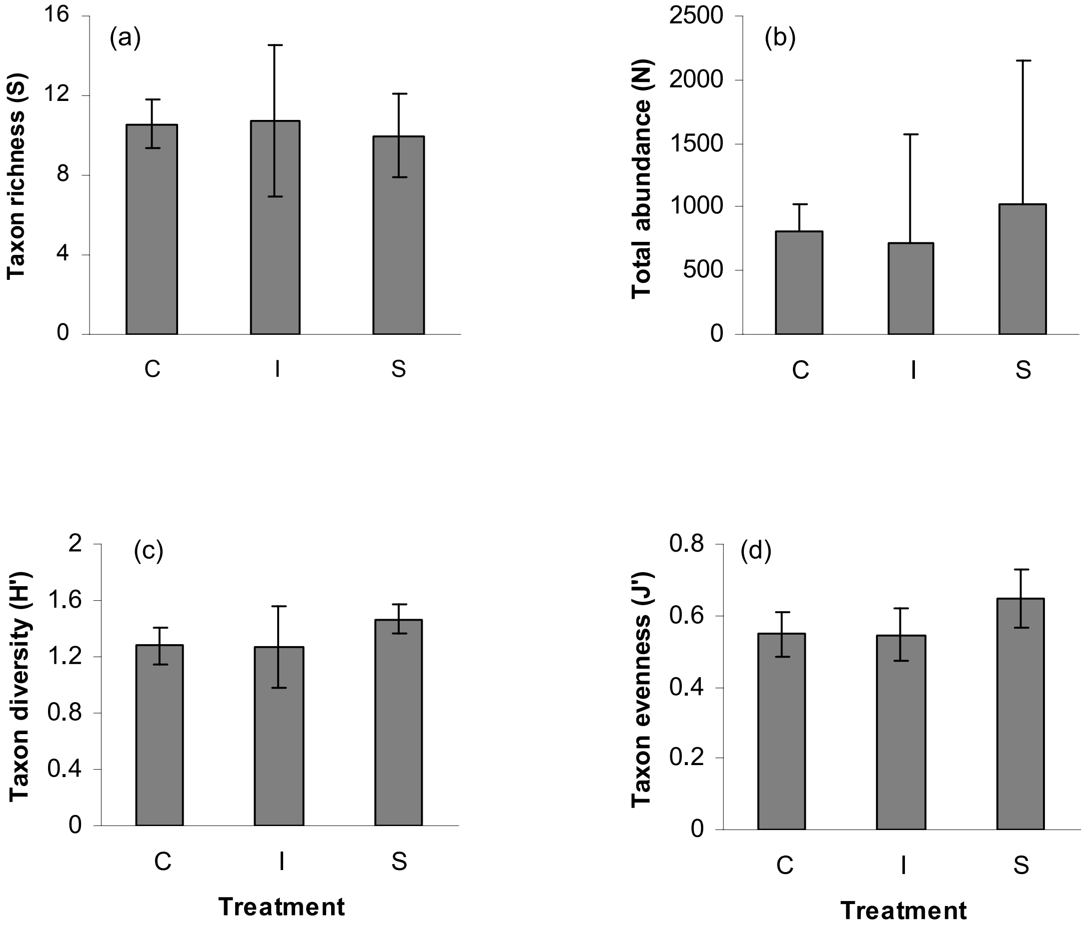


Figure 6.5. Differences in mean (± 95% C.I.) taxon (a) richness, (b) total abundance, (c) diversity and (d) evenness between impact (I), subsequent-effects (S) treatments and pooled controls (C) at Seal Sands. Differences were not significant with ANOVA/Kruskal-Wallis tests.

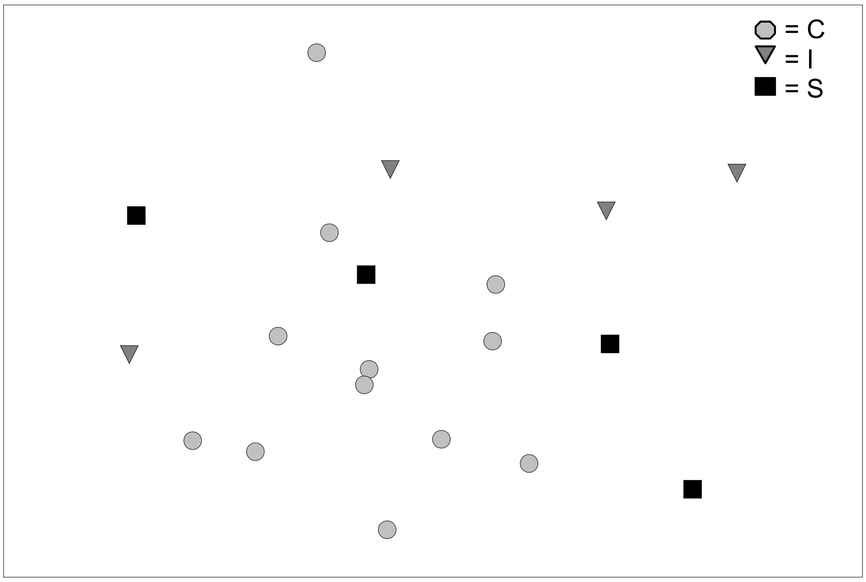


Figure 6.6. nmMDS ordination of taxon composition in impact (I), subsequent-effects (S) and control (C) assemblages at Seal Sands (stress = 0.19). Control assemblages were significantly different from impact and subsequent-effects treatments (ANOSIM Global R = 0.306, P<0.05).

subsequent period to abundances above that of control plots (Figure 6.7). Capitellids, in contrast, increased in response to hand-raking and continued to increase during the subsequent period, although these changes were non-significant.

Ecological functioning (biological traits analysis)

Each of the trait categories utilised in the study were represented at Seal Sands, with the exception of long-lifespan (12+ years). Between 34 and 36 (out of a total of 38) trait categories were represented ($\bar{x}$ 35 ± 0.8 C.I.) in baseline assemblages. These assemblages were not dominated by any one trait category (Figure 6.8), with the most common only accounting for 8.86% of total trait frequency (Table 6.2). Taxa with short lifespans, soft bodies or benthic larval development were common, as were those that burrowed, lived freely in sediments or deposit-fed and those with flexible bodies or separate sexes.

No temporal changes were noted for trait richness (S), diversity (H’) evenness (J’) or multivariate trait composition within the various control plots, and control replicates were pooled with baselines. Trait richness was variable within impact and subsequent-effects treatments (Figure 6.9(a)) and there was no significant difference between these and control plots. Both trait diversity and evenness exhibited no significant reductions between control and impact plots, and were higher for subsequent-effects assemblages than controls and impacts (Figures 6.9(b) and 6.9(c)).

Trait composition was similar across control assemblages (Figure 6.10). Trait composition in impact and subsequent-effects treatments was variable and some replicates grouped together with controls when viewed two-dimensionally. Trait composition in both treatments was distinct from that of control plots, although they were not different from each other (ANOSIM; Global R = 0.384, P<0.01).

Several traits exhibited similar responses to the treatments (Table 6.3). The traits ‘short lifespan’, ‘soft body’, ‘gonochorist’, ‘benthic larval development’, ‘reproduction by brooding', 'deposit feeding', 'movement by burrowing' and 'high flexibility' all reduced within the assemblages in response to hand-raking disturbance. The frequency of each trait was also higher in general within subsequent-effects plots than controls (Table 6.3). Some traits were important in determining differences between control and impact treatments but not between controls and the subsequent-effects treatment. These traits, 'tube-dwelling', 'moderate flexibility', 'low mobility' and 'filter/suspension feeding', however, all showed non-significant declines between controls, impact and subsequent-effects plots (Figure 6.11 (a)-(d)). Free-living and mobile fauna were not important in determining differences between controls and the impact treatment, but were key contributors to differences between controls and subsequent-effects plots (Table 6.3). These two traits decreased, on average, between control and impact plots, but increased in response to the cessation of raking (Figure 6.11 (d) and 6.11(e)). However these differences in mean frequency were not significant at the univariate level.

Ballochmartin Bay

Sediments

Sediments in Ballochmartin Bay were moderately to moderately-well sorted fine to medium sands. Median grain size ranged from 1.78-1.88 Φ ($\bar{x}$ 1.82 ± 0.05 C.I.) and silt/clay content from 0.35-0.7% ($\bar{x}$ 0.52 ± 0.15 C.I.). Sediments contained, on average, 3.02% (± 1.33 C.I.) organic matter. Sediment parameters did not vary significantly over time in non-disturbed plots. Furthermore, no significant changes in median grain size, silt/clay content or organic matter content occurred in either the impact or subsequent-effects plots relative to controls.

Table 6.2. Biological traits occurring most frequently in Seal Sands assemblages before the commencement of hand-raking disturbance.

Trait	Category	Frequency of occurrence ($\bar{x}$ ± 95% C.I.)	Mean % (± 95% C.I.)
Longevity (years)	0-3	2,769.75 (1,386.40)	8.86 (0.28)
Body design	Soft	2,733.00 (1,389.92)	8.71 (0.38)
Larval development	Benthic	2,714.00 (1,353.43)	8.70 (0.16)
Movement method	Burrowing	2,263.75 (755.98)	7.63 (1.18)
Feeding method	Deposit	2,134.00 (1,037.60)	6.87 (0.23)
Sexual differentiation	Gonochorist	1,984.50 (561.91)	6.26 (1.80)
Relative flexibility	High	1,978.00 (1,136.61)	6.98 (1.73)
Living habit	Free	1,957.75 (543.90)	6.79 (1.58)

Table 6.3. SIMPER analysis of biological traits contributing most to differences in composition between controls and impacts or subsequent-effects assemblages at Seal Sands (average dissimilarity; controls v. impacts = 16.37, controls v. subsequent-effects = 15.15).

Trait	Category	Direction of abundance change	Contribution to dissimilarity (%)	Cumulative contribution (%)
Control v Impact				
Sexual differentiation	Gonochorist	-	3.94	3.94
Living habit	Tube	-	3.79	7.73
Relative flexibility	Moderate	-	3.65	11.38
Longevity	0-3	-	3.59	14.97
Mobility	Low	-	3.57	18.54
Body design	Soft	-	3.57	22.11
Feeding method	Filter feeder	-	3.56	25.67
Larval development	Benthic	-	3.55	29.22
Relative flexibility	Low	-	3.54	32.76
Reproductive method	Brooder	-	3.28	36.04
Feeding method	Deposit feeder	-	3.24	39.28
Movement method	Burrowing	-	3.17	42.45
Movement method	Crawling	-	3.02	45.47
Relative flexibility	High	-	2.92	48.39
Relative mobility	None	-	2.89	51.28
Control v Subsequent effects				
Relative flexibility	High	+	3.79	3.79
Movement method	Burrowing	+	3.67	7.46
Living habit	Free-living	+	3.65	11.11
Body design	Soft	+	3.62	14.73
Longevity	0-3	+	3.61	18.34
Feeding method	Deposit feed	+	3.56	21.90
Larval development	Benthic	+	3.53	25.43
Relative mobility	High	+	3.35	28.78
Sexual differentiation	Synchronous hermaphrodite	+	3.24	32.02
Sexual differentiation	Gonochorist	+	3.06	35.08
Reproductive method	Brooder	+	3.02	38.10
Reproductive method	Eggs shed	+	2.96	41.06
Feeding method	Predator	+	2.92	43.98
Relative mobility	Moderate	+	2.89	46.87
Larval development	Pelagic	+	2.78	49.65
Body design	Shell	-	2.78	52.43

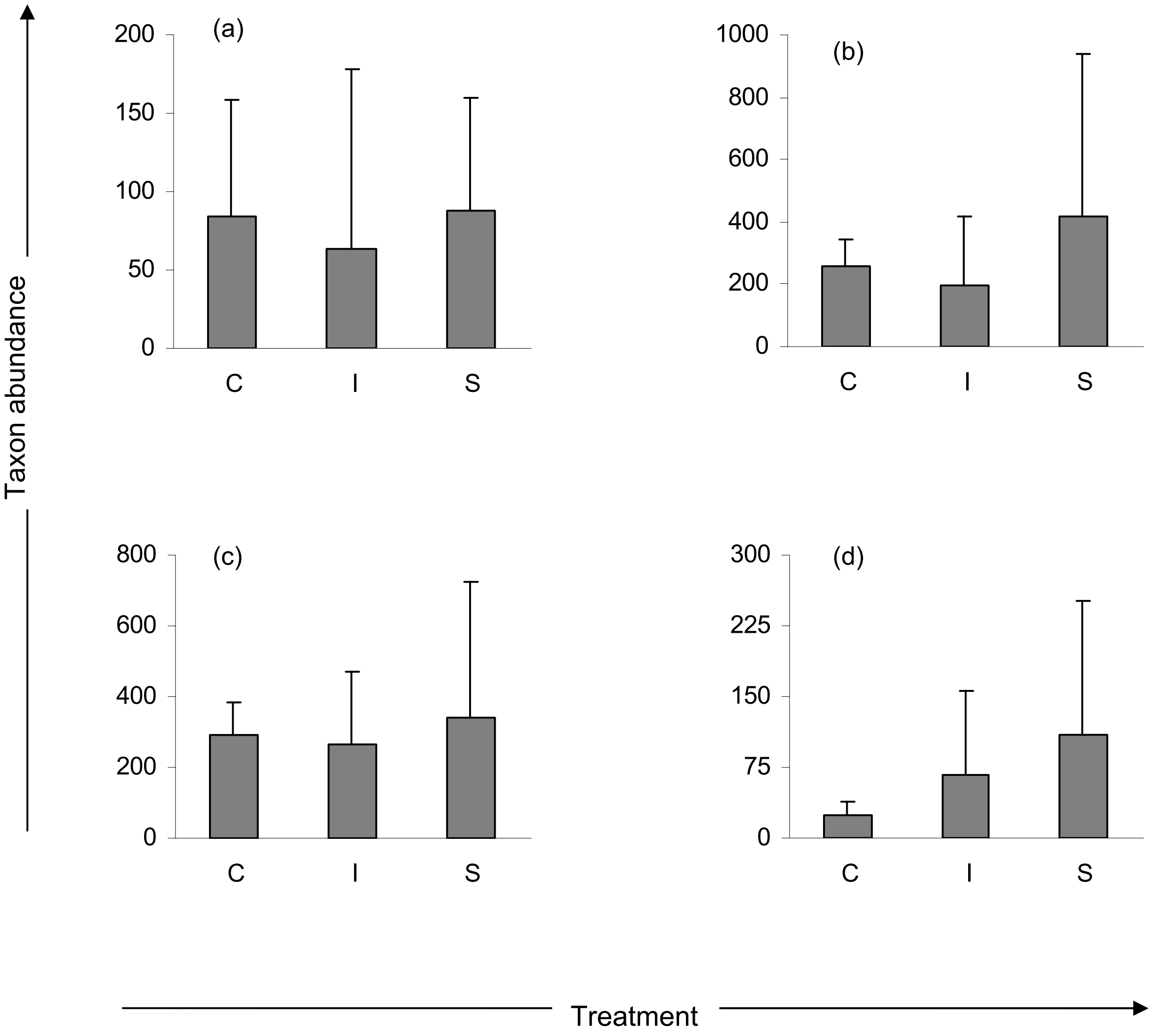


Figure 6.7. Differences in mean (± 95% C.I.) abundance of (a) *Manayunkia aestuarina*, (b) nematodes, (c) oligochaetes and (d) Capitellids, between control (C) assemblages and impact (I) or subsequent-effects (S) treatments at Seal Sands. The taxa were selected by SIMPER analysis as most important in determining differences between control and impact or subsequent-effects treatments. Differences were not significant with ANOVA/Kruskal-Wallis tests.

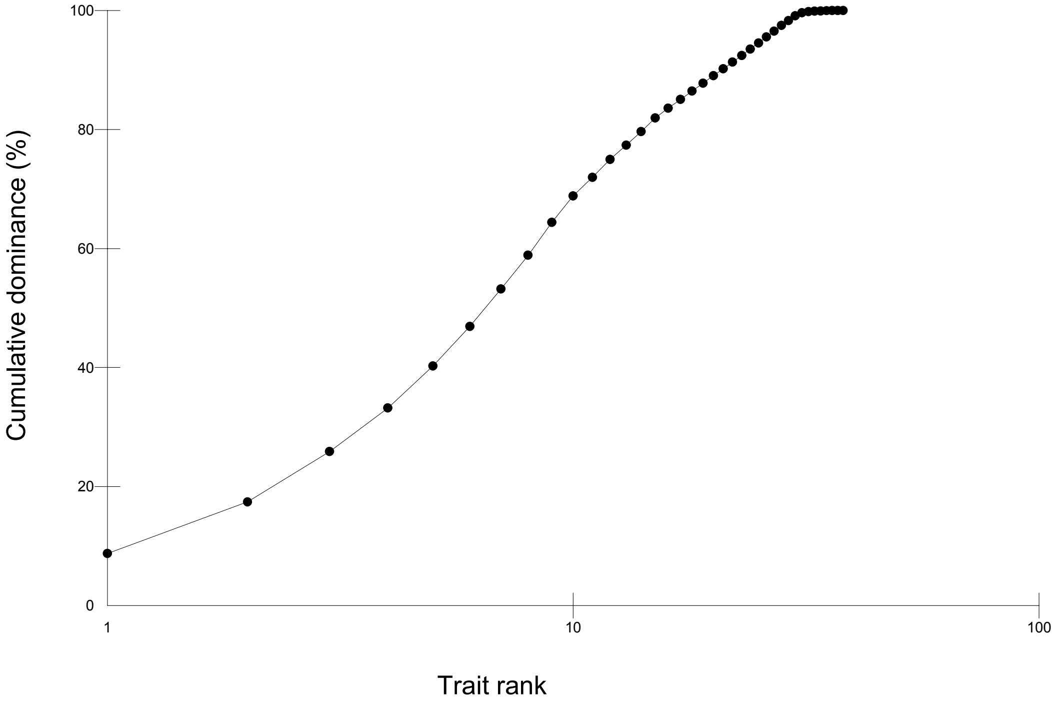


Figure 6.8. Cumulative dominance (% of total frequency) of biological traits at Seal Sands before the commencement of hand-raking.

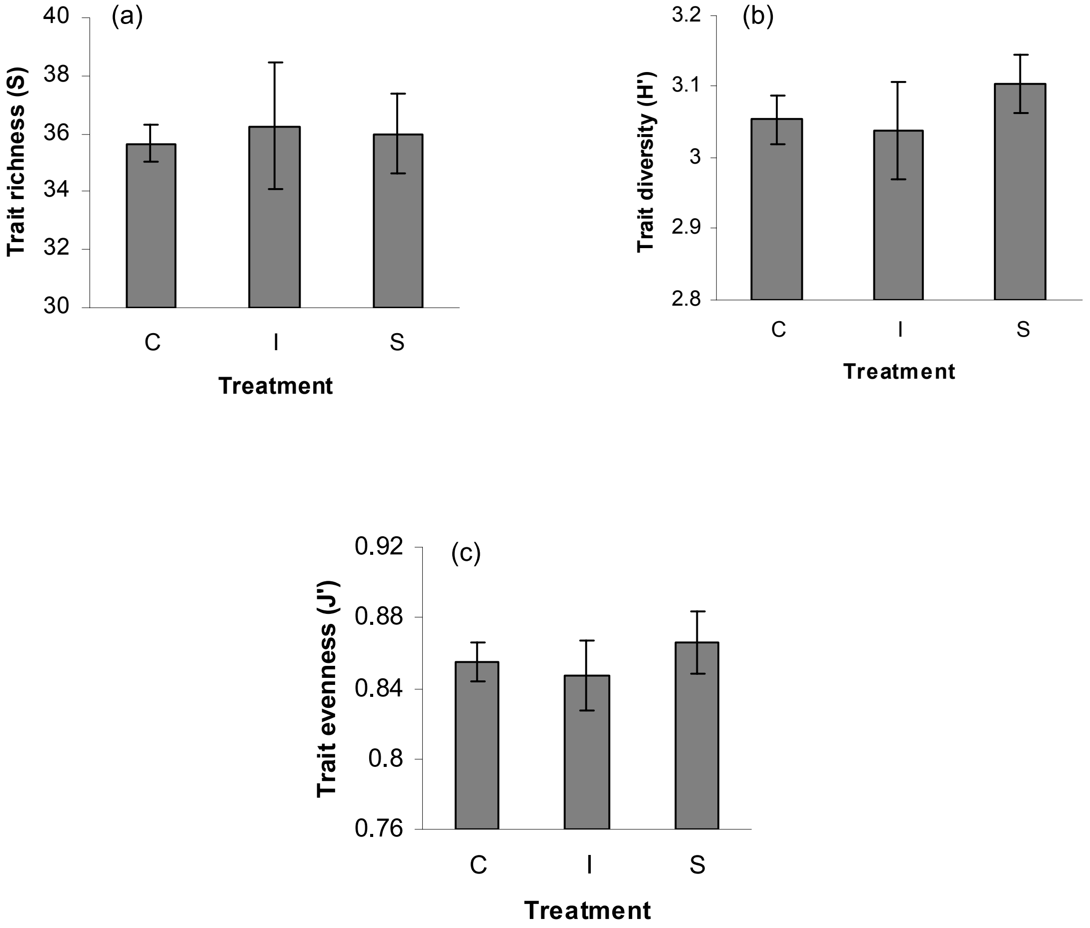


Figure 6.9. Differences in mean (± 95% C.I.) trait (a) richness, (b) diversity and (c) evenness between impact (I), subsequent-effects (S) treatments and pooled controls (C) at Seal Sands. Differences were not significant with ANOVA/Kruskal-Wallis tests.

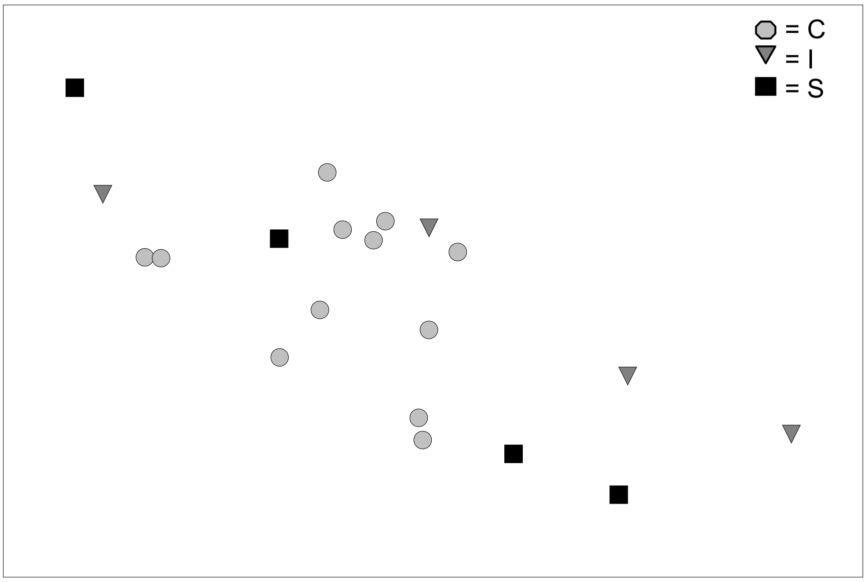


Figure 6.10. nmMDS ordination of biological trait composition in impact (I), subsequent-effects (S) and control (C) assemblages at Seal Sands (stress = 0.06). Control assemblages were significantly different from impact and subsequent-effects treatments (ANOSIM Global R = 0.384, P<0.01).

Taxon analysis

A total of forty taxa were recovered from Ballochmartin Bay plots, with seven different phyla represented (annelida, cnidaria, crustacea, mollusca, nematoda, nemertea and phoronida). Ten taxa were found only once at the site (four crustaceans, three polychaetes, two bivalves and a cnidarian) and were removed from the analysis. Of the remaining thirty taxa, seven were absent from baseline assemblages (*Bathyporeia* spp. (Lindström), *E. longa*, Harpacticoida, *Nephtys* spp., Sabellidae, Syllidae and *Travisia forbesii* (Johnston)).

Between thirteen and sixteen taxa were recovered from each baseline plot ($\bar{x}$ 14.5 ± 1.27 C.I.) and total taxon abundance in the plots ranged from 363-885 ($\bar{x}$ 671 ± 215.54 C.I.). Abundance was unevenly distributed between taxa (Figure 6.12), with the three most common taxa (oligochaetes, *Scoloplos armiger* (OF Müller) and nematodes) accounting for approximately 95% of total abundance. As at Seal Sands, undersized and marketable sized cockles were recovered from plots at the site. Decreases after raking were noticeable, and they appeared to increase during the subsequent-effects period (Figure 6.4(b)), but, again, they were not found frequently enough for abundance to be analysed.

There were no significant differences in univariate community measures between baseline plots and impact or subsequent-effects controls, so these were pooled in order to investigate the effects of the treatments. None of the univariate measures differed significantly between the treatments. However, taxon richness was reduced in impact and subsequent-effects plots relative to controls, whilst total abundance was lower in impact assemblages and higher (but very variable) in subsequent-effects plots (Figure 6.13(a)). There was little difference in diversity (H’) or evenness (J’) between the treatments (Figures 6.13(b) and 6.13(c)).

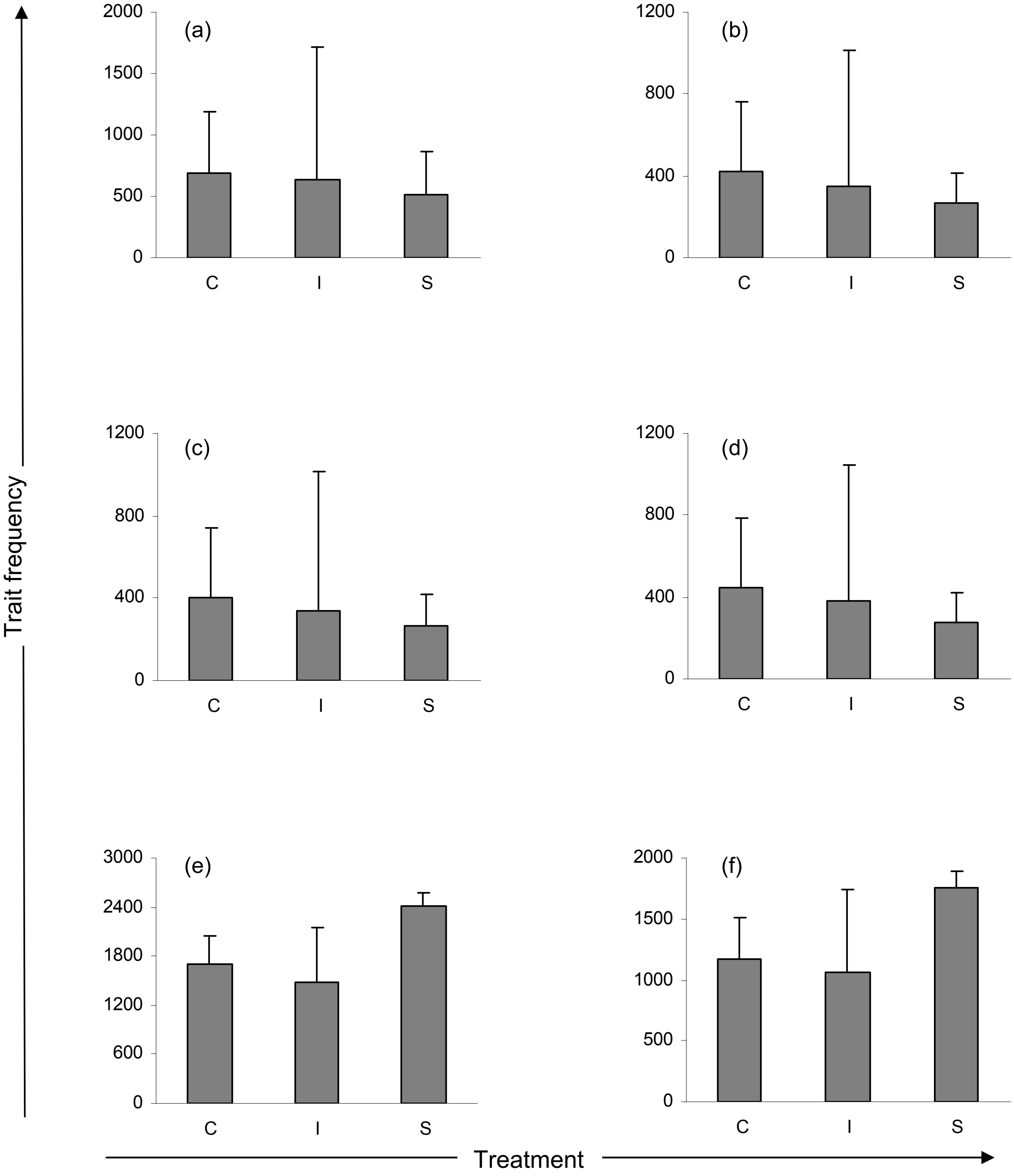


Figure 6.11. Mean (± 95% C.I.) frequency of selected traits identified from the SIMPER analysis as determining differences in biological trait composition between control and impact ((a)-(d)) or subsequent-effects ((e)-(f)) assemblages at Seal Sands. Traits presented are: (a) tube-dwelling, (b) moderate flexibility, (c) low mobility, (d) filter/suspension feeding, (e) free-living and (f) high mobility. Differences were not significant with ANOVA/Kruskal-Wallis tests.

Changes over time in the undisturbed plots were evident at the multivariate level, with significant differences in taxon composition between baseline conditions and both controls (ANOSIM; Global R = 0.356, $P<0.01$). Baseline assemblages were similar in their taxon composition, whilst impact and subsequent-effects control plots differed from baselines but not each other (Figure 6.14(a)). Nematodes were more abundant in both impact and subsequent-effects control plots than baselines, whilst nemerteans, oligochaetes, Spionidae, and *P. quadrilobata* were less frequent (Table 6.4).

As significant time effects were only apparent between baseline conditions and controls, not between the impact and subsequent-effects controls themselves (i.e. not apparent during the experiment), the time effect was accounted for by removing baselines from further multivariate analysis. Assemblages from impact and subsequent-effects plots were similar in their taxon composition to control plots and to each other (Figure 6.14(b)) and no significant disturbance effect was found.

Ecological functioning (biological traits analysis)

All of the trait categories included in the analysis were represented at Ballochmartin Bay, including longevity of 12+ years. Baseline conditions were similar to those at Seal Sands, with trait categories evenly represented in the assemblages (Figure 6.15) and short-lived, soft bodied, burrowing, free-living fauna with separate sexes, benthic larval development and deposit-feeding preferences common (Table 6.5). Most of the trait categories were expressed in each baseline assemblage ($\bar{x}$ trait richness 36.75 ± 0.96 C.I.).

No time effects were identified for trait richness (S), diversity (H’), evenness (J’) or trait composition. Therefore, replicates from baseline and all control plots were pooled for further analyses. No significant effects of raking disturbance were found for the univariate community measures, because variability within treatments was high. However, trait richness, diversity and evenness were all higher in the impact plots, on average, relative to controls and subsequent-effects assemblages (Figure 6.16).

Table 6.4. SIMPER analysis of Ballochmartin Bay taxa contributing most to differences in composition between controls and impacts or subsequent-effects assemblages (average dissimilarity; controls v. impacts = 30.73, controls v. subsequent-effects = 34.49).

Taxon	Average abundance (a)	Average abundance (b)	Contribution to dissimilarity (%)	Cumulative contribution (%)
Control v Impact				
Nemertea	2.00	0.00	7.94	7.94
Nematoda	160.00	423.37	7.53	15.47
Jassa marmorata	1.75	0.00	6.41	21.57
Crangon crangon	0.75	0.00	5.10	26.67
Polydora quadrilobata	6.50	1.00	5.03	31.70
Angulus tenuis	0.75	4.50	4.86	36.56
Amphipoda	2.00	3.50	4.52	41.08
Spionidae	1.50	0.50	4.51	45.59
Oligochaeta	283.75	133.25	4.50	50.09
Control v Subsequent effects				
Nematoda	160.00	444.25	7.72	7.72
Oligochaeta	283.75	104.25	6.84	14.78
Exogone hebes	3.25	0.50	6.32	21.10
Jassa marmorata	1.75	0.00	5.91	27.01
Crangon crangon	0.75	0.00	4.69	31.70
Polydora quadrilobata	6.50	1.50	4.56	36.26
Nemertea	2.00	1.00	4.31	40.57
Pygospio elegans	9.25	3.25	4.29	44.86
Spionidae	1.50	0.00	4.15	49.01
Corophium crassicorne	5.50	4.50	4.03	53.04

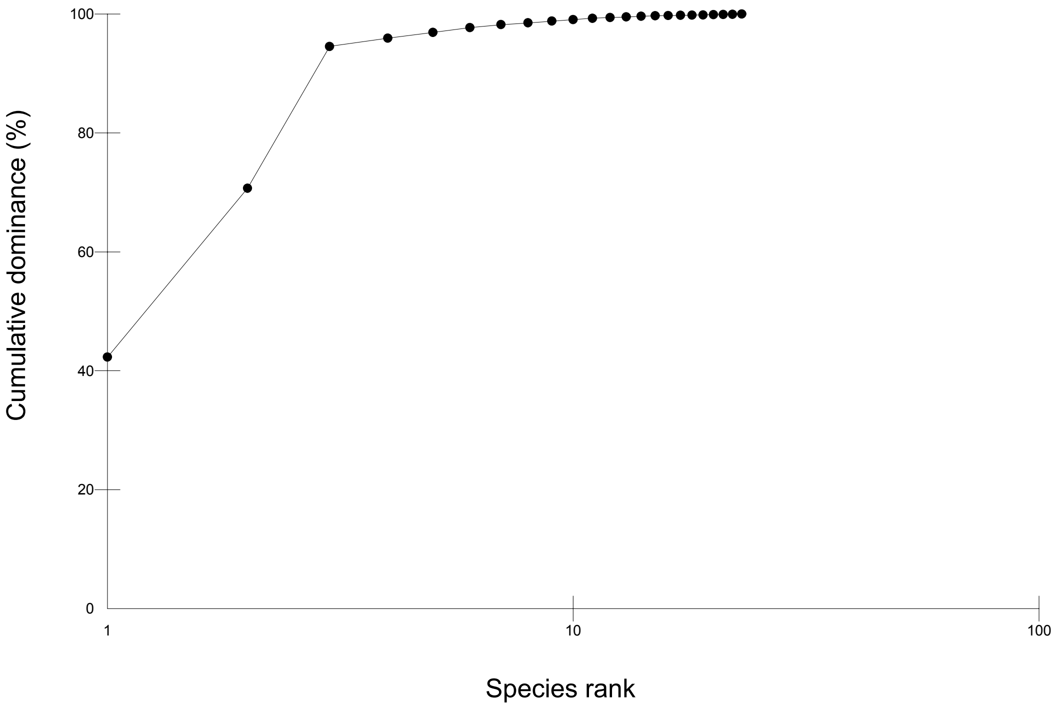


Figure 6.12. Cumulative dominance (% of total abundance) of taxa at Ballochmartin Bay before the commencement of hand-raking.

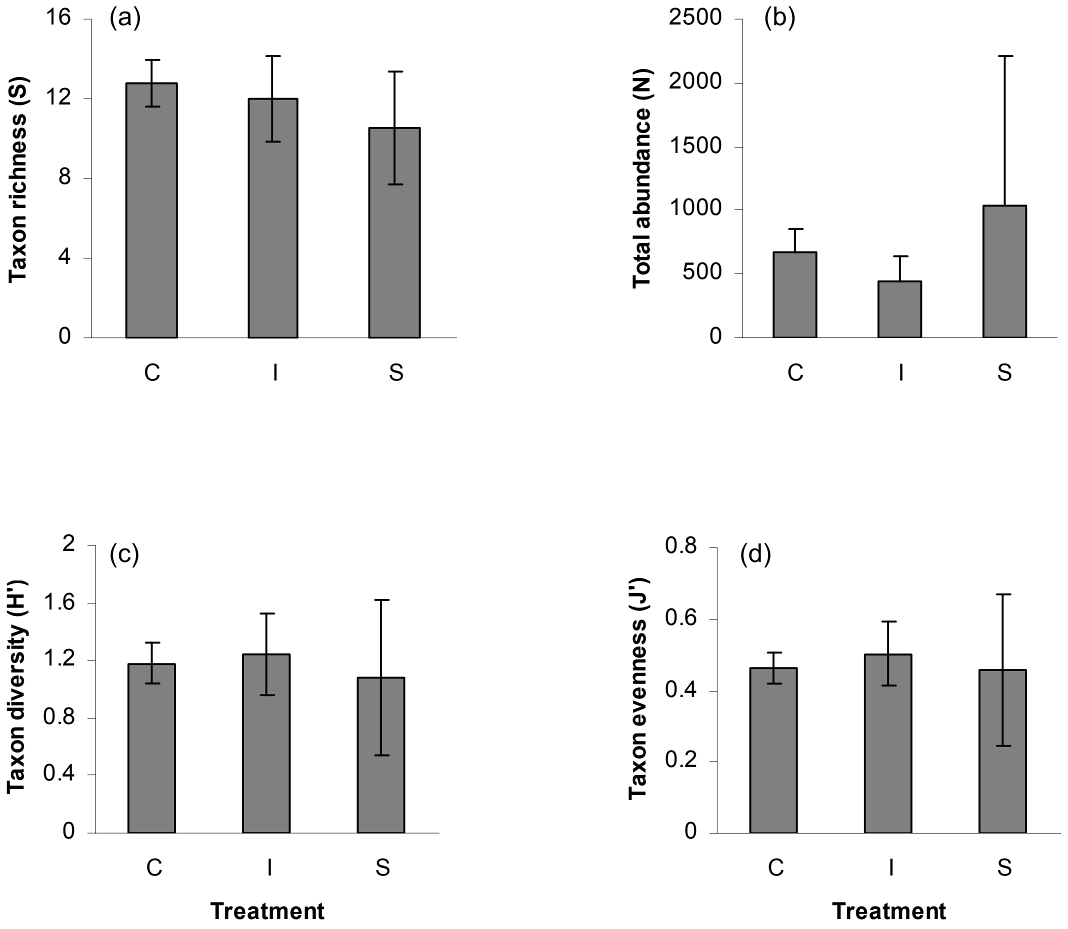


Figure 6.13. Differences in mean (± 95% C.I.) taxon (a) richness, (b) total abundance, (c) diversity and (d) evenness between impact (I), subsequent-effects (S) treatments and pooled controls (C) at Ballochmartin Bay. Differences were not significant with ANOVA/Kruskal-Wallis tests.

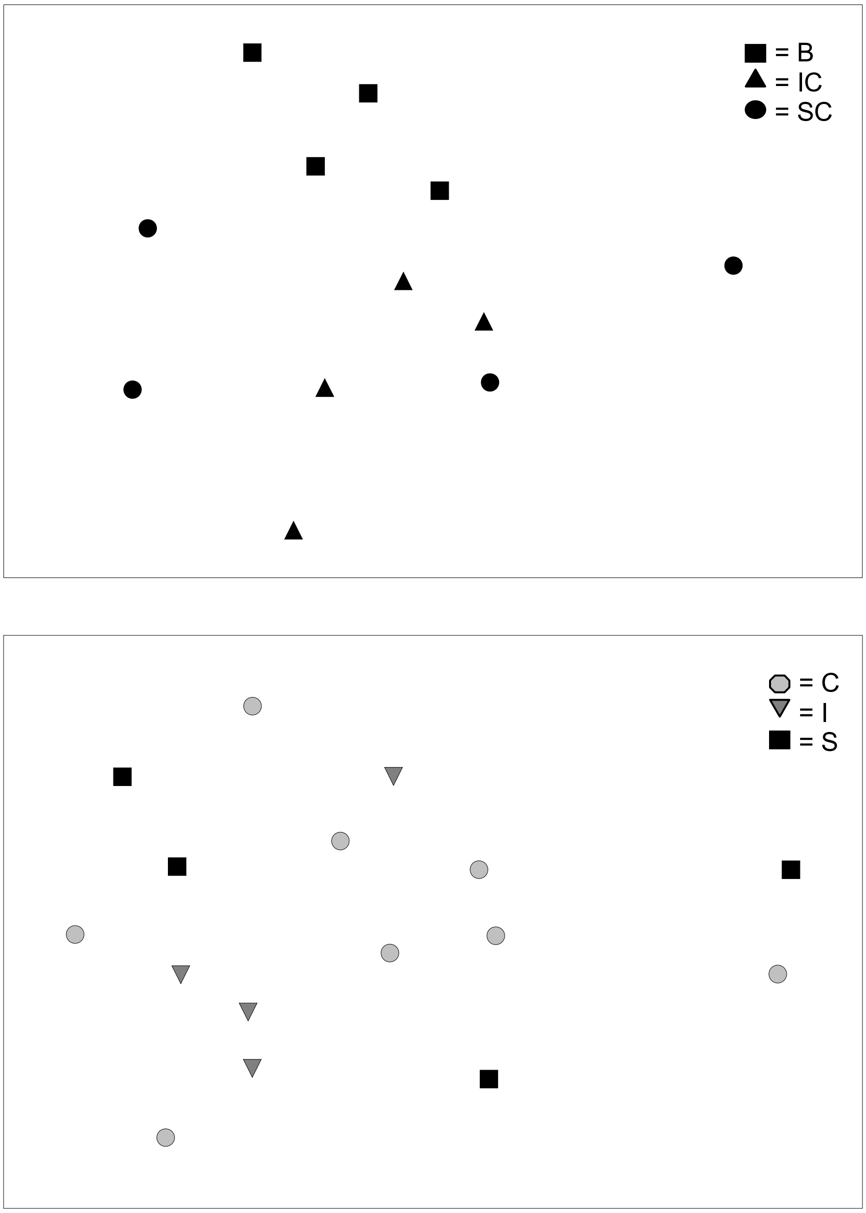


Figure 6.14. nmMDS ordinations of taxon composition in (a) non-disturbed plots over the study period (B = baseline assemblages, IC = controls for impact and SC = controls for subsequent-effects treatments) and (b) impact (I), subsequent-effects (S) and pooled control (C) assemblages at Ballochmartin Bay (stress = 0.13 and 0.15 respectively). Baseline assemblages were significantly different from controls (ANOSIM; Global R = 0.356, $p<0.01$), but there were no significant differences in taxon composition between treatments and controls.

There were no evident differences in trait composition between impact and control assemblages, which overlapped on the nmMDS plot (Figure 6.17). Assemblages in subsequent-effects plots were variable in their trait composition and although they were distinct from impact assemblages in the two-dimensional representation of trait composition, they were not significantly different. However, they were significantly different in composition from controls (ANOSIM; Global R = 0.260, P<0,05). A number of traits, primarily 'high flexibility', 'soft body form', 'benthic larval development', 'free-living' and 'burrowing', all increased in frequency in subsequent-effects assemblages relative to controls (Table 6.6).

DISCUSSION

Anthropogenic disturbance, in the form of cockle hand-raking, impacted ecological functioning in both sandy and muddy habitats. Assemblages in both habitats responded to raking-disturbance, although the nature of the response differed between the two. At Seal Sands, the muddier site, ecological functioning was impacted, both during the initial disturbance period and the subsequent undisturbed phase. Hand-raking changed trait composition through negative effects on a number of traits (primarily 'short lifespan', 'soft body', 'gonochorist', 'reproduction by brooding', 'benthic larval development', 'deposit feeding', 'movement by burrowing' and 'high flexibility'), which all consequently recovered to proportions in excess of control assemblages. These changes were concurrent with detectable alterations in taxon composition and changes to the sediments.

At Ballochmartin Bay, the sandy site, there was no detectable response during the week of raking disturbance, with little change in biological trait composition compared to control plots. However, trait composition was significantly altered during the subsequent phase, these changes in ecological functioning occurring despite no significant shift in taxon composition.

Table 6.5. Biological traits occurring most frequently in Ballochmartin Bay assemblages before the commencement of hand-raking disturbance.

Trait	Category	Frequency of occurrence ($\bar{x}$ ± 95% C.I.)	Mean % (± 95% C.I.)
Longevity	0-3	1,998.25 (644.25)	8.88 (0.10)
Body design	Soft	1,977.75 (649.42)	8.77 (0.07)
Larval development	Benthic	1,961.75 (647.60)	8.69 (0.12)
Movement method	Burrowing	1,945.50 (647.26)	8.61 (0.12)
Living habit	Free-living	1,929.75 (651.03)	8.52 (0.19)
Relative flexibility	High	1,922.25 (649.79)	8.49 (0.20)
Feeding method	Deposit feeder	1,799.75 (600.97)	8.00 (0.38)
Sexual differentiation	Gonochorist	1,160.25 (389.34)	5.20 (0.94)

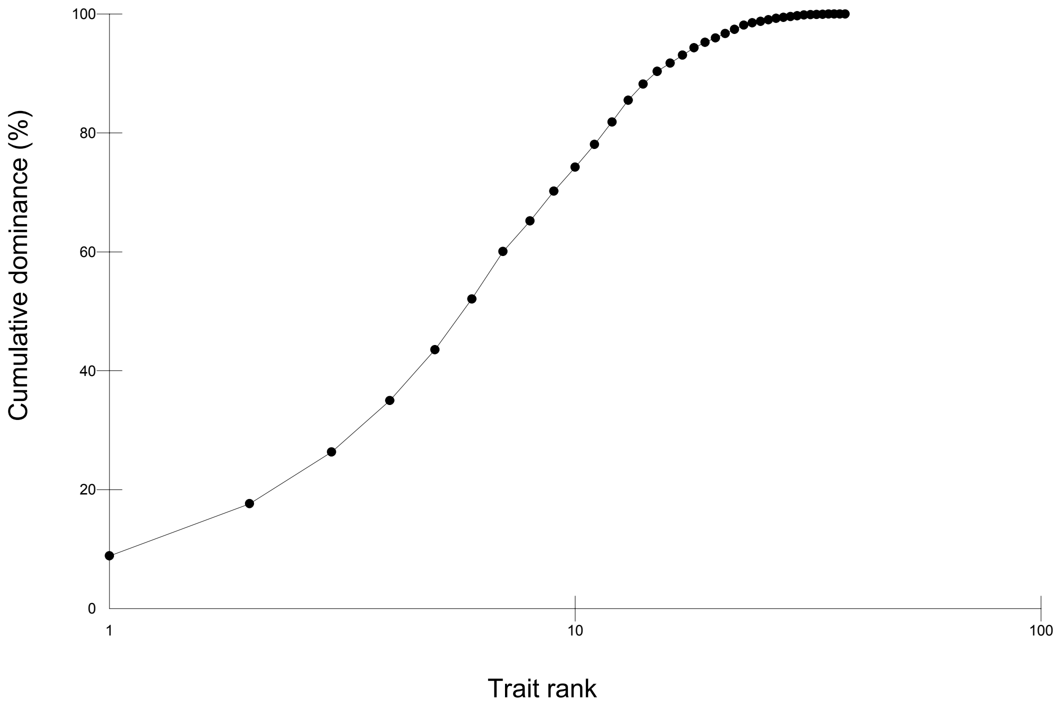


Figure 6.15. Cumulative dominance (% of total frequency) of biological traits at Ballochmartin Bay before the commencement of hand-raking.

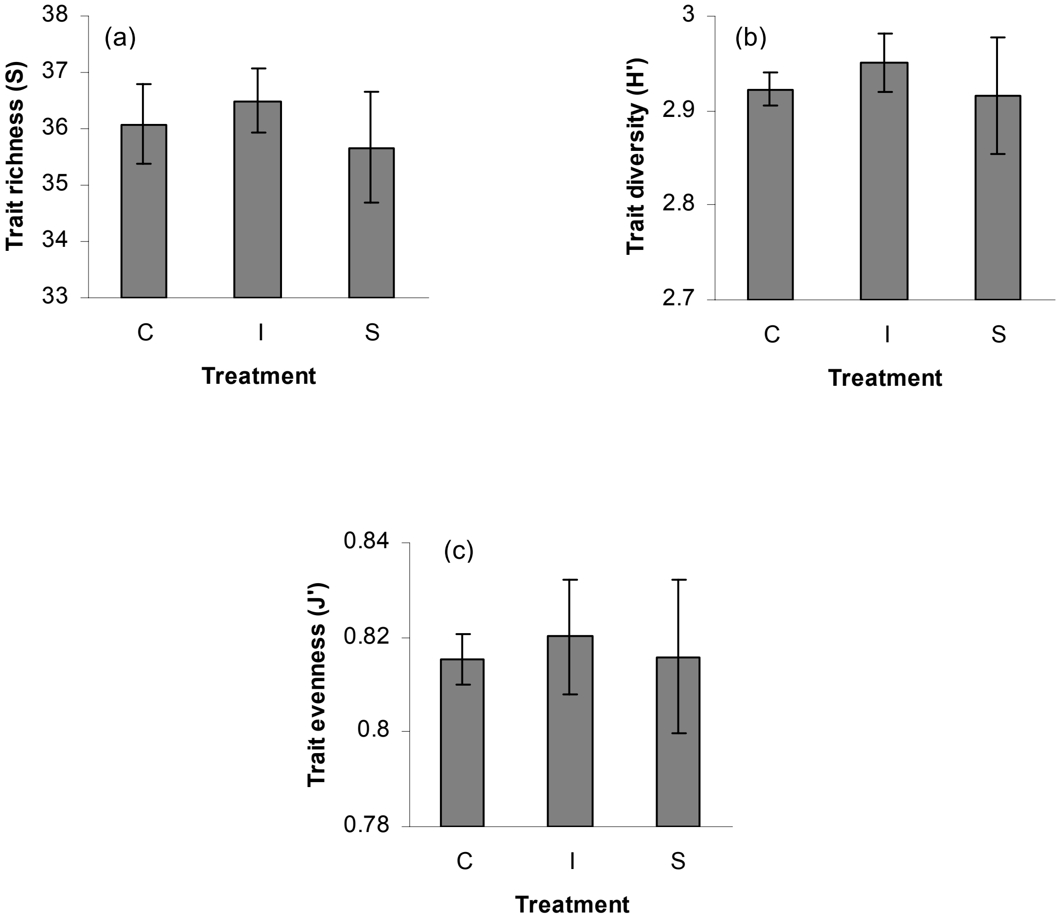


Figure 6.16. Differences in mean (± 95% C.I.) trait (a) richness, (b) diversity and (c) evenness between impact (I), subsequent-effects (S) treatments and pooled controls (C) at Ballochmartin Bay. Differences were not-significant with ANOVA/Kruskal-Wallis tests.

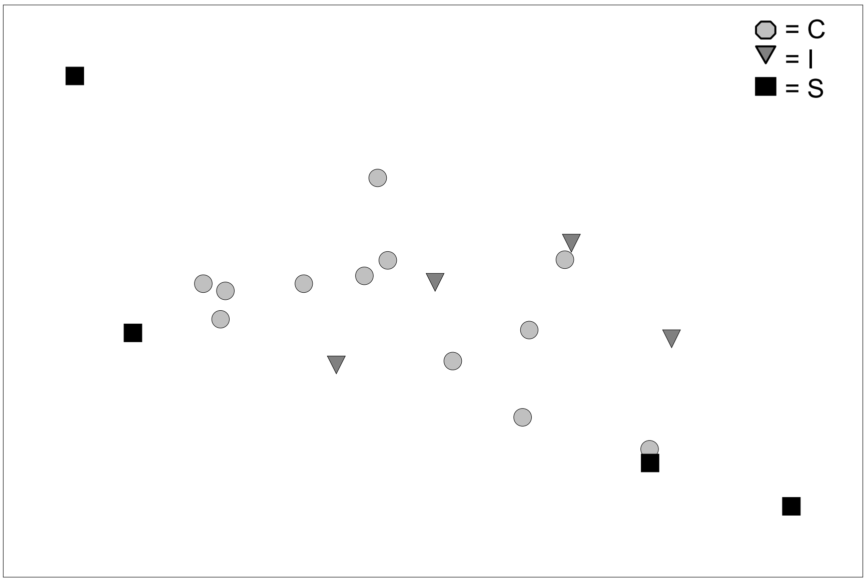


Figure 6.17. nmMDS ordination of biological trait composition in impact (I), subsequent-effects (S) and control (C) assemblages at Ballochmartin Bay (stress = 0.03). Control assemblages were significantly different from the subsequent-effects treatment (ANOSIM Global R = 0.260, $P<0.05$).

That individual taxa in sandy habitats exhibit less response to bivalve harvesting impacts than muddy habitats is consistent with other studies (Emerson *et al.*, 1990; Ferns *et al.*, 2000). However, although assemblages in these habitats are less vulnerable to anthropogenic disturbance in terms of taxon composition, the present study has shown that changes in ecological functioning do occur. Changes in functioning in the face of stability in taxon composition have also been documented in subtidal assemblages (see Chapter 2). The most likely explanation for such changes is that, at least in this system, some traits are expressed by several different taxa. Subtle changes in taxon abundance are not detected at the taxon composition level, but the cumulative contributions of these changes are noted when they are summed over shared traits. This implies that anthropogenic activities have the potential to alter ecological functioning, even in systems where response at the taxon level is not identified. If this is true, more investigation of anthropogenic impacts on functioning in these systems will be required to determine the extent of the effects.

Given the differences between treatments and controls at Seal Sands (the muddy site) it is perhaps surprising to note that no significant change in functioning between impact and subsequent-effects treatments could be identified. Changes between the treatments appeared to be consistent with differences between treatments and controls when individual traits were examined. For example, traits that reduced in impact plots and increased in subsequent-effects relative to controls, also increased on average between impact and subsequent-effects treatments (Figure 6.10).

The reason for this lack of significant change between the treatments seems to be high variability in trait composition within each (see Figure 6.9). Local variability in taxon composition and response to disturbance is well documented in soft-sediment communities (Hall *et al.*, 1994) and it seems this also occurs at the functional level.

Table 6.6. SIMPER analysis of biological traits contributing most to differences in composition between controls and subsequent-effects assemblages at Ballochmartin Bay (average dissimilarity; controls v. subsequent-effects = 16.27).

Trait	Category	Direction of abundance change	Contribution to dissimilarity (%)	Cumulative contribution (%)
Relative flexibility	High	+	4.31	4.30
Body design	Soft	+	4.30	8.61
Larval development	Benthic	+	4.25	12.86
Living habit	Free-living	+	4.24	17.10
Movement method	Burrowing	+	4.22	21.32
Longevity	0-3	+	4.20	25.52
Feeding method	Predator	+	4.07	29.59
Relative mobility	High	+	3.91	33.50
Reproductive method	Gonochorist	+	3.86	37.36
Feeding method	Deposit feeder	+	3.85	41.21
Reproductive method	Parthenogenesis	+	3.48	44.69
Sexual differentiation	Sequential hermaphrodite	+	3.45	48.14
Reproductive method	brooder	+	3.45	51.59

One method used to account for local-scale variability in environmental conditions and community composition is pooling of replicates at the base transect/plot level (Schoeman *et al.*, 2000; Kaiser *et al.*, 2001); an approach followed in the present study. Although this represents a form of sacrificial pseudo-replication (Hurlbert, 1984), the increased number of replicates provided can enhance the ability of the statistical analyses used to identify significant changes between treatments. The resulting high variability may be preventing even the conservative analytical procedures employed here from detecting the subtle changes occurring between the impact and subsequent-effects treatments.

The primary consequence of hand-raking at Seal Sands was a general reduction in the frequency of a number of traits. These traits included both those considered as opportunistic and those associated with vulnerability to disturbance. For instance, tube dwellers (vulnerable to physical disturbance, see (Collie *et al.*, 2000a)) decreased in response to raking, as did short-lived organisms (high mortality being an opportunistic trait (Grassle & Grassle, 1974). This suggests that many types of fauna were negatively impacted by the initial disturbance, irrespective of their biological characteristics. This is not surprising, as hand-raking removes surface sediments and creates mounds of ‘tailings’ at the edges of target areas. Fauna will be removed from plots along with the sediments and either exposed (to predators or washout by the incoming tide) or buried under tailings. Burial under sediments, in particular, can have lethal effects on infauna (Hewitt *et al.*, 2003, but see Chandrasekara & Frid, 1998).

There is little that infaunal organisms exposed to raking can do to prevent the initial removal from plots as, even if they are highly mobile relative to other members of the infaunal community, they must burrow downwards or horizontally through sediments in order to avoid the passage of the rake, and few organisms will be able to move quickly enough. Some types of mobile crawling or burrowing fauna may be resistant to disturbance in intertidal communities, but only through quick recolonisation after an isolated disturbance event (Savidge & Taghon, 1988). When disturbance events are as frequent as once per day these traits may be of little benefit, as even those fauna that have entered plots subsequent to the previous disturbance event will be removed by the next incident. Burrowing and high/moderate mobility fauna at Seal Sands were reduced by frequent raking disturbance, so it seems that these characteristics conferred no functional advantage for the fauna as long as disturbance was occurring frequently.

The characteristics exhibited by fauna at Seal Sands may be of more importance in determining patterns of recovery after the cessation of the disturbance. High mobility is a useful characteristic in terms of re-colonisation of impacted plots. Mobile organisms increased to levels in excess of those found in control assemblages after a post-raking period of ten days. The mobile fauna considered in this study moved by several means, including crawling, jumping, swimming/floating and burrowing. It has been suggested that macrofaunal recolonisation of disturbed areas is facilitated by transport through the water column in both shallow subtidal and intertidal communities (Hall *et al.*, 1990; Hall & Harding, 1997). Whilst 50% of the taxa recorded at Seal Sands exhibit some form of swimming/floating behaviour, the trait itself was not important in determining differences in functioning between controls and the subsequent-effects treatment. Burrowing, however, did increase. So, although the ability to swim or float provides a functional advantage to fauna recolonising areas after large-scale disturbance events, it is not as important on a small-scale as the ability to actively burrowing through sediments.

Whatever the causes of the relative changes in trait composition, the consequential changes in functioning will have implications for the regulation of ecological processes. Changes in the frequency of two traits, ‘tube-dwelling’ and ‘burrowing’, are of particular interest in this respect. Both traits were negatively impacted by raking disturbance at Seal Sands but, while burrowing fauna recovered after the cessation of disturbance, tube-dwellers continued to decline.

Tube-dwellers are important members of mud assemblages, with tube structures making clear contributions to functioning. At the sediment surface, tubes can alter water flow and increase sediment stability, permeability and shear strength (de Wilde, 1991; Meadows & Hariri, 1991; Meadows & Meadows, 1991; Bolam & Fernandes, 2002). Their presence allows increased bacterial colonisation of the sediment-water interface and affects faunal settlement and the regulation of macrofaunal community structure (Woodin, 1978; Gallagher *et al.*, 1983; de Wilde, 1991; Bolam & Fernandes, 2002; Callaway, 2003). Tube linings can act as molecular sieves, enforcing size-based regulation on the passage of particles into and out of the sediments and potentially facilitating the transformation of sediment toxins (Aller, 1983). Tube structures can also enhance bacterial populations within sediments by increasing the depth of oxygen penetration (de Wilde, 1991) and by providing materials for decomposition deeper in the sediments, where the organic matter present tends to be resistant to microbial degradation (Kristensen *et al.*, 1991).

Burrowing can alter sediment conditions through the re-suspension of fine particles into overlying waters, changes to the distribution of different-sized particles within sediments and increases in the oxygen and water contents (Rhoads, 1974; Meadows & Meadows, 1991; Constable, 1999). Burrowing activities also transport buried organic matter and nutrients to the sediment-water interface (Rhoads, 1974; Constable, 1999), stimulating benthic microflora and –fauna communities (Andersen & Kristensen, 1991; de Wilde, 1991) and hence decomposition processes.

The magnitude of the effects of these biological trait changes on ecological processes is uncertain. Predictions will always be confounded by the complex feedback loops that exist between macrofaunal activities and ecological processes (Giblin *et al.*, 1995; Biles *et al.*, 2003). Furthermore, taxa sharing traits such as burrowing or tube-dwelling can make variable contributions to ecological processes.

Burial of organic matter deposited by sedimentation is a very slow process, with only a few millimetres to centimetres covered per year (Andersen & Kristensen, 1991). Burial through the actions of burrowing fauna will greatly increase this rate. However, they will not all transport organic matter to the same extent, because burrowing species differ in their specific mode of burrowing and the depth to which they penetrate sediments (Constable, 1999; Widdicombe & Austen, 1999; Austen *et al.*, 2002). Tube production in some species can consume approximately 9% of carbon and 12% of nitrogen that is transported to the sediments (Kristensen *et al.*, 1991), so tubicolous species can make a significant contribution towards nutrient cycling. Yet species differ in the size and robustness of the tubes they produce, and also in their tube-irrigating activities (Woodin & Marinelli, 1991) and consequently, in their contributions towards ecological functioning.

There are two main issues that must be addressed before the implications of changes in trait composition for the regulation of ecological processes can be clarified. Firstly, the specific characteristics controlling organisms' contributions to ecological processes must be determined. For example, if the production of large tubes utilises more carbon than small tubes, it is the size of the tube, not the presence of a tube itself, that determines how much a tubicolous taxon contributes towards carbon cycling.

Secondly, descriptions of ecological functioning must incorporate more detailed trait information than is possible at present, particularly with respect to traits intricately linked to ecological processes, such as burrowing and tube-dwelling. As mentioned earlier in this paper, one of the major limitations of biological traits analysis is that it is constrained by the amount of taxon-specific information available. There is no point including detailed trait categories in the analysis if there is little information available on the expression of these categories across the taxa considered. However, although this currently makes it difficult to quantify the implications of changes in functioning, advances in research linking ecological processes to specific traits will, in time, enhance the precision of the approach.

Human-generated disturbance impacts on the ecological functioning of intertidal assemblages in both muddy and sandy habitats. Effects on functioning in muddy assemblages occur initially in response to frequent disturbance and, in both habitats, are detectable in assemblages after the disturbance ends. Changes in the relative frequency of biological traits, particularly burrowing and tube-dwelling characteristics, have important implications for the regulation of ecological processes, although the magnitude of their effects are not currently quantifiable.

Chapter 7

General discussion

This thesis has clearly demonstrated the utility of biological traits analysis for characterising aspects of ecological functioning in marine benthic communities. It has shown that the approach performs well in comparison to more traditional measures of ecological functioning (Chapter 2), displays the attributes of a good biomonitoring tool (it can be easily applied (Chapter 3), it is applicable to different geographical areas and habitat types (Chapters 2 and 4) and it is sensitive to and can identify the effects of anthropogenic activities (Chapters 5 and 6)) and provides useful information on the functioning of benthic assemblages. In addition, the findings presented in this thesis have raised some issues that are of both intellectual interest and practical importance for marine ecosystem ecology and management.

The ultimate purpose of ecosystem management is to maintain the 'goods and services' provided by marine ecosystems, with the former generally translating to the abundance of target species and the latter to maintaining the rates of ecological processes. We know that some anthropogenic activities can impact on receiving systems by altering the species richness, diversity or composition of local assemblages. The phenomenon is well documented in marine benthic systems, particularly in respect to anthropogenically-driven physical disturbances of the seabed such as fishing (Hutchings, 1990; Jennings & Kaiser, 1998; Johnson, 2002).

The need to conserve ecological processes, coupled with the occurrence of anthropogenically-driven changes in species abundances, prompts the question 'do changes in biodiversity lead to changes in ecological processes?', or, in other words, 'how does biodiversity relate to ecosystem functioning (actually ecosystem processes, see Raffaelli *et al.*, 2003)?'. Biodiversity and ecosystem 'functioning' is a well-established subject area in terrestrial circles, where much attention has been directed towards answering the question (see Tilman, 1999; Loreau *et al.*, 2001), but it is a very new field of study in the realm of marine ecology.

Initial marine research has documented complex relationships between species biodiversity and ecological processes, with changes in biodiversity causing process-changes in some situations but not others (Bolam *et al.*, 2002; Raffaelli *et al.*, 2003). This result adds weight to the assertion that the specific biological attributes exhibited by species are of more importance to the maintenance of ecological processes than simply species number itself (Bengtsson, 1998; Diaz & Cabido, 2001; Giller *et al.*, 2004), because these attributes determine the extent to which species contribute to ecological processes (in simple terms, all species are not equal in relation to ecological processes). A logical extension of this argument is that the biological attributes expressed *by an assemblage* (i.e. the sum total of attributes expressed by all component species) will determine how that assemblage contributes to ecological processes.

This, in turn, raises two further questions; (1) ‘do changes in the attributes expressed by an assemblage affect ecological processes?’ and on a more basic level, given that the same attribute can be expressed by a number of taxa, (2) ‘do changes in the species complement always lead to changes in the attributes expressed by an assemblage?’. The answer to the second question will clearly impact on the first as, if changes in the species complement do not lead to changes in the attributes expressed by assemblages, logic would suggest that the answer to the first question is of little practical importance for marine ecosystem management.

This thesis cannot directly address the first question as ecological processes have not been measured here, but the findings can contribute towards the second because BTA provides a measure of the attributes expressed by assemblages (biological trait composition). Chapters 2 and 4 provided evidence that, at least in some cases, changes in the species complement did not lead to changes in the biological trait composition of benthic assemblages in the southern North Sea, eastern Channel and Irish Sea regions. If this is a general phenomenon, it suggests that ecological processes will not always be affected by changes in species diversity, because these do not translate into changes in the attributes expressed by the assemblage.

However, extreme caution must be used in generalising these observations. Although some stability of trait composition in the face of changes in the species complement was documented in the thesis, it did not occur universally. In some cases, differences in species composition *did* translate into differences in trait composition. For example, in Chapter 2, megafauna assemblages off the north-eastern French coast (south of Boulogne, see Figures 2.2 and 2.7) were as variable when classified by their biological traits as they were when classified by species composition, and changes in the species complement of intertidal assemblages in a north-eastern English estuary resulted in changes in the attributes expressed by the assemblages (Chapter 6).

In theory, the attributes expressed by an assemblage remain stable when diversity changes because a given attribute will be expressed by several different species, so reductions or removals of one of these species will be compensated for by increases in one or more of the others (see Walker, 1992; Frost *et al.*, 1995; Naeem, 1998). Logic, however, dictates that a juncture will be reached where species change must impact on the attributes expressed by an assemblage. At some stage, if reductions in biodiversity are severe enough, all of the species expressing a given trait will be removed and compensation becomes impossible. This point is obvious. What is not clear is the stage at which more subtle changes in the species complement, such as changes in the relative proportions of component species, will lead to changes in the attributes expressed by assemblages.

This is not a trivial issue. Compensation is the mechanism by which stability in the biological attributes of assemblages is maintained. If we cannot determine the extent of compensation, we cannot determine when changes in the species complement will lead to changes in the attributes expressed by assemblages (question 2). This will, consequently, make it difficult to determine how anthropogenically-driven changes in the species complement will affect ecological processes. This thesis has provided evidence that the attributes expressed by benthic assemblages may sometimes remain stable in the face of changes in the species complement, but the extent of the phenomenon, and the mechanisms underlying it, although extremely important for ecosystem ecology and management, are far from clear and require appropriate quantification.

The changes in functioning documented in response to human impacts in Chapters 5 and 6 signal that ecosystem management needs to be applied at the level of ecological functioning as well as at the species level. Ecological functioning must be conserved in benthic assemblages if ecological processes are to be maintained. However, it would be extremely difficult to conserve ecological functioning in it's entirety without ceasing anthropogenic activities in the sea. As this is unlikely, priority may be given to identifying which aspects of functioning to preserve, or what actions to take to conserve as much functioning as possible. Clearly, ecosystem-based conservation should protect those aspects of functioning that have the strongest links to ecological processes.

In benthic assemblages, faunal attributes such as tube-dwelling, burrow-dwelling and burrowing have potentially important implications for the regulation of ecological processes (see Chapter 6). Protecting tube-dwelling, burrow-constructing and burrowing fauna should then, theoretically, make a large contribution towards maintaining the rates of ecological processes.

At the present time, the links between specific faunal activities and processes are, largely, based on theoretical predictions and many unknowns remain. For instance, although recent work has provided experimental evidence of the links between faunal activities and specific ecological processes (Biles *et al.*, 2002; Howe *et al.*, 2004; Lohrer *et al.*, 2004; Webb & Eyre, 2004a, b), the extent of the contributions these taxa make to processes is still unclear. Also, we do not know if all taxa sharing these traits have the same impact on processes, whether the degree to which taxa express a trait affects their contributions, or whether other traits expressed by the taxa also affect their involvement in the regulation of ecological processes. If we are to conserve functioning and, therefore, ecological processes we must have more information on how specific traits determine the maintenance of these ecological processes.

However, at a practical level, ecosystem management must operate in the absence of perfect knowledge and it is better to employ a cautionary strategy based on logic and theory than to apply none at all. Chapters 4 and 6 showed that, when the attributes expressed by assemblages were examined, the traits tube- and burrow-dwelling most often exhibited negative responses to fishing impacts. If the traits are fundamental to the regulation of ecological processes, these anthropogenically-mediated changes in functioning could have far-reaching consequences for marine ecosystems. Uncertainty over the importance of their role in process-regulation should not prevent these traits from being protected because, as shown in this thesis, this potentially crucial aspect of functioning is vulnerable to physical seabed disturbance.

Another option for preserving ecological functioning in the light of imperfect knowledge is to adopt one of the strategies used in conservation based on taxonomic identities. Here, communities are classified on the basis of their species composition, with community types that are rare within a given area being selected for protection. This is a conservative approach that protects communities which may otherwise be lost, even though the implications of their loss at the ecosystem level may be, as yet, unknown. An analogous strategy would be relatively simple to implement at the functional level, being conducted in much the same manner as at the taxonomic level, only using the biological attributes present in assemblages instead of species lists.

This approach has the advantage that it can be applied alongside species-level classification, which is essential as conservation must operate at both levels. These two approaches may well identify different communities for protection, as those communities that are designated as rare using species-level classifications may not be rare in terms of their functioning, or vice versa. Chapter 2 provides a good example of this situation. When biological trait composition was considered, a group of five assemblages was classified as rare throughout the southern North Sea and eastern Channel region (group 2, Figure 2.7). However, on the basis of species composition, these five assemblages were classified as common (Figure 2.2). This confirms that conservation focussed at the species level is not enough to protect ecological functioning in marine ecosystems. While protection of ecological functioning will add another level of complexity to ecosystem management strategies, it is necessary and can be fitted into the framework already in place for species and habitat conservation.

One requirement for successful ecosystem management that is currently lacking is consensus on terminology. Ecosystem investigation of this form incorporates different disciplines such as biology, chemistry and physical sciences and it is a relatively new area for many researchers, even in the comparatively advanced field of terrestrial ecosystem ecology. Ecologists from different research disciplines may use different terminology to refer to what may be, essentially, the same thing (see Emmerson & Huxham, 2002).

This thesis has followed Naeem *et al.* (1999) in defining ecological functioning as the maintenance and regulation of ecological processes. Other authors have defined *ecosystem* functioning as the 'processes occurring in a system' (Biles *et al.*, 2002), i.e. 'biogeochemical activities such as production, community respiration, decomposition, nutrient cycling or nutrient retention' (Naeem & Wright, 2003). Yet more authors define some of these 'activities', such as decomposition rates and nutrient cycling, as 'ecosystem properties' (Loreau *et al.*, 2001). These different terminologies are justifiable and understandable in what is an emerging field of interdisciplinary science. They do, however, create a great deal of confusion, and confusion in terminology can make it difficult to locate relevant information and share new findings and ideas in the inter-disciplinary arena. While these differences in terminology do not, and should not be allowed to, prevent the development of new research in marine ecosystems, consensus in terminology at some point in the near future would greatly aid understanding and the advancement of the field.

The focus of this thesis has been on developing biological traits analysis as a tool for describing ecological functioning of marine benthic assemblages, and investigating changes in functioning in response to both natural and anthropogenic factors. However, the work has also raised and contributed to our knowledge of some interesting ecological and management issues, such as the relationship between species and the attributes expressed by assemblages, the information required for conservation of functioning and, ultimately, ecological processes, and the need for, and strategies for implementation of, conservation of ecological functioning. The thesis has therefore both contributed to our understanding of biological traits analysis in ecosystem biomonitoring and opened up a number of interesting avenues for consideration and future research, with regards to the relationship between biodiversity, functioning and ecological processes.

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Appendices

Appendix 1(a). Biological trait variables and categories used to describe ecological functioning in the megabenthic assemblages of the southern North Sea and eastern Channel.

Trait code	Trait	Number	Category
S	Individual/colony size (relative weight)	1	Small
		2	Small-medium
		3	Medium
		4	Medium-large
		5	Large
L	Adult longevity (years)	1	<2
		2	2-5
		3	>5
R	Reproductive method	1	Asexual (budding)
		2	Sexual (broadcast spawn)
		3	Sexual (egg lay/brood - planktonic larvae)
		4	Sexual (egg lay/brood - mini-adults)
M	Relative adult mobility	1	None
		2	Low
		3	Medium
		4	High
A	Degree of attachment	1	None
		2	Temporary
		3	Permanent
H	Adult life habit	1	Sessile
		2	Swim
		3	Crawl
		4	Burrow
		5	Crevice-dweller
F	Body flexibility (^{o})	1	>45
		2	10-45
		3	<10
FO	Body form	1	Flat
		2	Mound
		3	Erect
FD	Feeding habit	1	Deposit
		2	Filter/suspension
		3	Scavenger/opportunist
		4	Predator

Appendix 1(b). Fuzzy-scored biological traits for 40 megabenthic taxa used in Chapter 2. Explanations of traits and categories are given in Appendix 1(a).

	S					L			R				M				A			H					F			FO			FD			
	1	2	3	4	5	1	2	3	1	2	3	4	1	2	3	4	1	2	3	1	2	3	4	5	1	2	3	1	2	3	1	2	3	4
Acanthocardia spp			1	2				3		3			2	1			3						3				3		3			3		
Aequipecten opercularis		1	2				1	2		3				3			3			3							3	3				3		
Alcyonidium diaphanum		2	2				3				3		3						3	3					3					3		3		
Alcyonium digitatum			1	1	2			3	1		3		3						3	3							3		1	2		3		
Aphrodita aculeata		1	2				2	1		3					3		3					2	1		3			2	1		1		2	
Ascidians	1	1	1	1			3		1	2			3					1	2	3						1	2		1	2		3		
Asteris rubens		1	1	1	1			3		3					3		3					3			3			3					2	2
Buccinum undatum			1	2				3				3			3		3					2	1				3		3		1		2	2
Cancer pagurus				1	2			3			3					3	3					1	1	1			3	1	2				2	1
Chaetopterus variopedatus		3					2	1		3				3				3					3			3		2		1		3		
Crepidula fornicata	1	2	1				2	1		3			2	1				1	2	3							3		3			3		
Crossaster papposus				1	2			3		3				2	1		3					3				3		3					1	2
Echinocardium cordatum			3					3		3				3			3						3				3		3		3			
Flustra foliacea			2	1			3				3		3						3	3					3					3		3		
Hinia reticulata	3							3			3			3			3					2	1				3		3		1		2	
Homarus gammarus					3			3			3					3	3					2		1			3		3				2	1
Hydroids		2	2			1	2		1	1	1		3						3	3					2	1				3		3		
Inachus spp	2	1						3			3			3			3					3					3	1	2				3	
Laevicardium crassum		3					1	2		3			2	1			3						3				3		3			3		
Liocarcinus depurator			2	1				3			3					3	3				1	2					3	1	2				2	1
Liocarcinus holsatus		1	2					3			3					3	3				1	2	1				3	1	2				2	1
Liocarcinus marmoreus		1	2					3			3					3	3				1	2	1				3	1	2				2	1
Macropodia spp	2	1						3			3			3			3					3					3	1	2				3	
Maja squinado					3			3			3					3	3					3					3		3				3	
Metridium senile			2	2			2	1	2	1	1			3				3		3						3			3			3		
Mytiilus edulis		1	2				1	2		3			3						3	3							3		3			3		
Necora puber			1	2				3			3					3	3				1	2		1			3	1	2				2	2
Ophiothrix fragilis	3							3		3				2	1		3			2		1		1			3	3			1	2		
Ophiura albida	3							3		3				3			3					2	1				3	3			1	1	1	
Ostrea edulis				3				3		2	1		3				2	1		3							3	3				3		
Pagurus bernhardus			1	2				3			3				2	1	3					3					3		3				3	
Pagurus prideaux		1	2					3			3				2	1	3					3					3		3				3	
Pecten maximus					3			3		3				3			3			3							3	3				3		
Pentapora foliacea				1	2		1	2			3		3						3	3							3		3			3		
Philine aperta	3						3			3				3			3					2	1			1	2	2	1				1	2
Psammechinus miliaris	2	2						3		3				3			3					2		1			3		3				3	
Sabellaria spinulosa			1	2			1	2		3			3						3	3							3		3			3		
Spatangus purpureus					3			3		3				3			3						3				3		3		3			
Sponges		1	1	1	1		1	2	2	1			3						3	3						1	2		2	1		3		
Urtica felina		1	2				3		2	1				3				3		3						3			3					3

Appendix 2(a). Biological trait variables and categories used to describe ecological functioning in the megabenthic assemblages of the southern North Sea and eastern English Channel. The first 9 traits were used in initial investigations, whilst the last 4 (shaded) were added for the purposes of later analyses.

Trait code	Trait	Number	Category
S	Individual/colony size (relative weight)	1	Small
		2	Small-medium
		3	Medium
		4	Medium-large
		5	Large
L	Adult longevity (years)	1	<2
		2	2-5
		3	>5
R	Reproductive method	1	Asexual (budding)
		2	Sexual (broadcast spawn)
		3	Sexual (egg lay/brood - planktonic larvae)
		4	Sexual (egg lay/brood - mini-adults)
M	Relative adult mobility	1	None
		2	Low
		3	Medium
		4	High
A	Degree of attachment	1	None
		2	Temporary
		3	Permanent
MV	Adult movement	1	Sessile
		2	Swim
		3	Crawl
		4	Burrow
F	Body flexibility (^{o})	1	>45
		2	10-45
		3	<10
FO	Body form	1	Flat
		2	Mound
		3	Erect
FD	Feeding habit	1	Deposit
		2	Filter/suspension
		3	Opportunist/scavenger
		4	Predator
SX	Sexual differentiation	1	Gonochoristic
		2	Synchronous hermaphrodite
		3	Sequential hermaphrodite
SC	Sociability	1	Solitary
		2	Gregarious
		3	Colonial
MI	Migration	1	Non-migratory
		2	Seasonal migration
		3	Life stage migration
H	Living habit	1	Tube-dweller
		2	Permanent burrow dweller
		3	Crevice dweller
		4	Free living

Appendix 2(b). Fuzzy-scored biological traits for benthic taxa used in Chpater 3. Explanations of traits and categories are given in Appendix 2(a).

	S					L			R				M				A			MV				F			FO			FD				SX			SC			MI			H			
	1	2	3	4	5	1	2	3	1	2	3	4	1	2	3	4	1	2	3	1	2	3	4	1	2	3	1	2	3	1	2	3	4	1	2	3	1	2	3	1	2	3	1	2	3	4
Acanthocardia spp			1	2				3		3			2	1			3						3			3		3			3			3				3		3						3
Aequipecten opercularis		1	2				1	2		3				3			3			3						3	3				3				3			3		3						3
Alcyonidium diaphanum		2	2				3				3		3						3	3				3					3		3				3			1	2	3						3
Alcyonium digitatum			1	1	2			3	1		3		3						3	3						3		1	2		3			3					3	3						3
Aphrodita aculeata		1	2				2	1		3					3		3					2	1	3			2	1		1		2		3			3			3						3
Ascidians	1	1	1	1			3		1	2			3					1	2	3					1	2		1	2		3				3		1	1	1	3					2	2
Asteris rubens		1	1	1	1			3		3					3		3					3		3			3					2	2	3			2	2		2	1					3
Buccinum undatum			1	2				3				3			3		3					2	1			3		3		1		2	2	3			2	1		2	2					3
Cancer pagurus				1	2			3			3					3	3					2	2			3	1	2				2	1	3			3				2	2			1	3
Chaetopterus variopedatus		3					2	1		3				3				3					3		3		2		1		3			3				3		3			3			
Crepidula fornicata	1	2	1				2	1		3			2	1				1	2	3						3		3			3					3		3		3						3
Crossaster papposus				1	2			3		3				2	1		3					3			3		3					1	2	3			3			3	1					3
Echinocardium cordatum			3					3		3				3			3						3			3		3		3				3				3			1	2		3		
Flustra foliacea			2	1			3				3		3						3	3				3					3		3				3			1	2	3						3
Hinia reticulata	3							3			3			3			3					2	1			3		3		1		2		3			3	1		3					3	
Homarus gammarus					3			3			3					3	3					3				3		3				2	1	3			3			1		2			3	
Hydroids		2	2			1	2		1	1	1		3						3	3				2	1				3		3			1	1	1	1	1	2	3					1	3
Inachus spp	2	1						3			3			3			3					3				3	1	2				3		3			2	2			3					3
Laevicardium crassum		3					1	2		3			2	1			3						3			3		3			3			3				3		3						3
Liocarcinus depurator			2	1				3			3					3	3				1	2				3	1	2				2	1	3			3	1			3					3
Liocarcinus holsatus		1	2					3			3					3	3				1	2	1			3	1	2				2	1	3			3	1			3					3
Liocarcinus marmoreus		1	2					3			3					3	3				1	2	1			3	1	2				2	1	3			3	1			3					3
Macropodia spp	2	1						3			3			3			3					3				3	1	2				3		3			2	2			3					3
Maja squinado					3			3			3					3	3					3				3		3				3		3			1	2			2	1				3
Metridium senile			2	2			2	1	2	1	1			3				3		3		1			3			3			3			3				2	1	3					2	2
Mytiilus edulis		1	2				1	2		3			3						3	3						3		3			3			3			1	3		3					2	2
Necora puber			1	2				3			3					3	3				1	2				3	1	2				2	2	3			3			2	1				3	1
Ophiothrix fragilis	3							3		3				2	1		3			2		1				3	3			1	2			3				3		3					2	2
Ophiura albida	3							3		3				3			3					2	1			3	3			1	1	1		3			1	2		3					1	3
Ostrea edulis				3				3		2	1		3				2	1		3						3	3				3					3		3		3						3
Pagurus bernhardus			1	2				3			3				2	1	3					3				3		3				3		3			2	1		3	1					3
Pagurus prideaux		1	2					3			3				2	1	3					3				3		3				3		3			3	1		3						3
Pecten maximus					3			3		3				3			3			3						3	3				3				3		1	3		3						3
Pentapora foliacea				1	2		1	2			3		3						3	3						3		3			3				3			1	2	3						3
Philine aperta	3						3			3				3			3					2	1		1	2	2	1				1	2		3		3			3						3
Psammechinus miliaris	2	2						3		3				3			3					3				3		3				3		3			1	2		3					3	
Sabellaria spinulosa			1	2			1	2		3			3						3	3						3		3			3			3			2	2		3			3		1	
Spatangus purpureus					3			3		3				3			3						3			3		3		3				3			1	2		3				3		
Sponges		1	1	1	1		1	2	2	1			3						3	3					1	2		2	1		3				3		1	1	1	3					2	2
Urticina felina		1	2				3		2	1				3				3		3		1			3			3					3	3			1	2		3					2	2

Appendix 3. Fuzzy-scored biological traits for benthic taxa used in Chpater 4. Explanations of traits and categories are given in Appendix 2(a).

	S					L			R				M				A			MV				F			FO			FD				SX			SC			MI			H			
	1	2	3	4	5	1	2	3	1	2	3	4	1	2	3	4	1	2	3	1	2	3	4	1	2	3	1	2	3	1	2	3	4	1	2	3	1	2	3	1	2	3	1	2	3	4
Acanthocardia spp			1	2				3		3			2	1			3						3			3		3			3			3				3		3						3
Aequipecten opercularis		1	2				1	2		3				3			3			3						3	3				3				3			3		3						3
Alcyonidium diaphanum		2	2			2	1				3		3						3	3				3					3		3				3			1	2	3						3
Alcyonium digitatum			1	1	2			3	1		3		3						3	3						3		1	2		3			3					3	3						3
Anseropoda placenta			1	2			3			3				1	2		3					2	1			3	3					3		3								3				3
Aphrodita aculeata		1	2				2	1		3					3		3					2	1	3			2	1		1		2		3			3			3						3
Archidoris pseudoargus			2	1			3				3			2	1		3					3			3		2	1					3		3		1	2		3					3	
Arctica islandica				1	2			3		3			1	2			3			1			2			3		3			3			3	1		1	3				3				3
Ascidians	1	1	1	1		1	2		1	2			3					1	2	3					1	2		1	2		3				3		1	1	1	3					2	2
Asterias rubens		1	1	1	1			3		3					3		3					3		3			3					2	2	3			2	2		2	1					3
Astropecten irregularis			2	1			2	1		3				1	2		3					2	1		3		3					3		3				3			3					3
Buccinum undatum			1	2				3				3			3		3					2	1			3		3		1		2	2	3			2	1		2	2					3
Cancer pagurus				1	2			3			3					3	3					2	2			3	1	2				2	1	3			3				2	2			1	3
Carcinus maenas			1	1	1		2	1			3					3	3				1	2				3	1	2				3		3			2	1			2	2			1	3
Crangon crangon	2	1				2	1				3				2	1	3				1	1	1		1	2	2	1				3		3		1	2	1			2	2				3
Crepidula fornicate	1	2	1				2	1		3			2	1				1	2	3						3		3			3					3		3		3						3
Crossaster papposus				1	2			3		3				2	1		3					3			3		3					1	2	3			3			3	1					3
Echinocardium cordatum			3					3		3				3			3						3			3		3		3				3				3			1	2		3		
Echinus esculentus				1	2			3		3					3		3					2				3		3				3		3			1	3		3					2	2
Eledone cirrhosa					3		3					3				3	3				2	1		3			2	1				3		3			1	3		1	1	1			2	1
Flustra foliacea			2	1			2	1			3		3						3	3				3					3		3				3			1	2	3						3
Homarus gammarus					3			3			3					3	3					3				3		3				2	1	3			3			1		2			3	
Hyas coarctatus	1	2				2	1				3				2	1	3					3				3	1	2				3		3											1	3
Hydroids		2	2			1	2		1	1	1		3						3	3				2	1				3		3			1	1	1	1	1	2	3					1	3
Inachus dorsettensis	2	1					3				3			3			3					3				3	1	2				3		3			2	2			3					3
Liocarcinus depurator			2	1			2	1			3					3	3				1	2				3	1	2				2	1	3			3	1			3					3
Liocarcinus holsatus		1	2				2	1			3					3	3				1	2	1			3	1	2				2	1	3			3	1			3					3
Luidia ciliaris					3		2	1		3					3		3					3			1	2	3					1	2	3			2	2		3						3
Macropodia rostrata	2	1					3				3			3			3					3				3	1	2				3		3			2	2			3					3
Maja squinado					3			3			3					3	3					3				3		3				3		3			1	2			2	1				3
Marthasterias glacialis					3		2	1		3					3		3					3		2	1		3					1	2	3				3		2	1					3
Metridium senile			2	2			2	1	2	1	1			3				3		3		1			3			3			3			3				2	1	3					2	2
Modiolus modiolus				1	2			3		3			3						3	3						3		3			3			3	1		1	3		3					1	3
Mytilus edulis		1	2				1	2		3			3						3	3						3		3			3			3			1	3		3					2	2
Necora puber			1	2			2	1			3					3	3				1	2				3	1	2				2	2	3			3			2	1				3	1
Nephrops norvegicus				1	2		2	1			3				1	2	3					1	2		1	2	2	1				3		3			1	3		3				3		1
Neptunea antique				1	2			3				3			3		3					3				3		3				3		3						2	2					3
Ophiothrix fragilis	3						2	1		3				2	1		3			2		1				3	3			1	2			3				3		3					2	2
Ophiura albida	3						2	1		3				3			3					2	1			3	3			1	1	1		3			1	2		3					1	3

Appendix 3 (continued). Fuzzy-scored biological traits for benthic taxa used in Chpater 4. Explanations of traits and categories are given in Appendix 2(a).

	S					L			R				M				A			MV				F			FO			FD				SX			SC			MI			H			
	1	2	3	4	5	1	2	3	1	2	3	4	1	2	3	4	1	2	3	1	2	3	4	1	2	3	1	2	3	1	2	3	4	1	2	3	1	2	3	1	2	3	1	2	3	4
Ophiura ophiura	1	2					2	1		3				2	1		3					2	1			3	3			1		2		3				3		3						3
Ostrea edulis				3				3			3		3				2	1		3						3	3				3					3		3		3						3
Pagurus bernhardus			1	2				3			3				2	1	3					3				3		3				3		3			2	1		3	1					3
Pagurus prideauxi		1	2					3			3				2	1	3					3				3		3				3		3			3	1		3						3
Pandalus montagui	2	1				2	1				3				2	1	3				2	2			1	2	2	1				3		2		2	1	3			3	1			1	3
Pecten maximus					3			3		3				3			3			3						3	3				3				3		1	3		3						3
Pentopora				1	2		1	2			3		3						3	3						3		3			3				3			1	2	3						3
Philine aperta	3						3			3				3			3					2	1		1	2	2	1				1	2		3		3			3						3
Psammechinus miliaris	2	2						3		3				3			3					3				3		3				3		3			1	2		3					3	
Sabellaria spinulosa			1	2			1	2		3			3						3	3						3		3			3			3			2	2		3			3		1	
Spatangus purpureus					3			3		3				3			3						3			3		3		3				3			1	2		3				3		
Sponges		1	1	1	1		1	2	2	1			3						3	3					1	2		2	1		3				3		1	1	1	3					2	2

Appendix 4. Fuzzy-scored biological traits for 15 macrobenthic taxa used in Chapter 5. Explanations of traits and categories are given in Table 5.1.

	S					L				D			R				RE			AM				E				RS				DR		
	1	2	3	4	5	1	2	3	4	1	2	3	1	2	3	4	1	2	3	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3
Abra	3					3	1				3				3		1	1	1	3	1			3				1	3	3	1	2	3	
Amphiura			1	2	2	2	2	1	2			3			3		1	2	1		1	3	2	3					3	2		1	3	
Chaetozone	3					3				3				1	1	3	3				3			1	3			2	1	1	2	1	1	1
Glycera	1	2	2	2	1	1	3			3					3		3				1	1	3		3					2	2	1	3	
Harpinia	3					3						3				3	1	1	1		3							1	1	1	1		2	2
Heteromastus		1	1	2		3				3					3	1	3	1			3	1		1	1			3	1	1	2		3	
Levinsenia	3					3				3						3	3	1		3	1				3					2	3		3	
Lumbrineris	1	2	1	1	3	2	2			3						3	3					3		1	3	2		1	3	2	1		3	
Nemertea	1	2	1	1	3	3				3				1	1	2	2	1	2	2	2						3	2	2	2	1	1	3	2
Oligochaeta	3	2	1	1		3	1			3			2	2		3	1	1	3	2	1	2				2	3	2	2	1	1	1	2	2
Ophelina	1	3				3				3					3		2	2		3	1			3				3			2	2	2	
Paramphinome	3									3																								
Praxillella	1	3	1	1		1	1			3			1	1	1	3		3							2	2		2			3	2	2	
Prionospio	3	1				3				3					3		3	1			1	3	1	1	3				3	3	1		3	
Spiophanes		3				3				3					3		3	1			3	1			3			2	2	2	1	2	3	

	DP			MV					M				AP			SL				H				FD				FT					RP		
	1	2	3	1	2	3	4	5	1	2	3	4	1	2	3	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	5	1	2	3
Abra		2	3	1	2		1		2	2			3	2		3	1				1		3	1	3					2	2		3		
Amphiura		2	3		2	1			1	3					3	3	2	1			2		2	2	2			1		1	1				3
Chaetozone	3	1		2	2				2	1			3	1		3				1	1		3		3					2		2	3	2	
Glycera		3	1		2			2				3	3			1	2	3	1		3	1				1	3	3	1				3	1	
Harpinia	3					2		1		1	2	1				3				2			2		1	2			2	1					
Heteromastus	1	3		3	1				2	1					3	1	1	3	1	1	3	1		1	2					2	1	1	3	1	
Levinsenia	3			3					3							3	2						3		3					3			3	1	
Lumbrineris	3				3						2	1	3			3	1	1		1	2		2		2	1	1	2	1	1		1	3	1	
Nemertea	3	1	1		1	1	1	2				3		2	2	3	1	1	1	3	1	1	1	1		2	2	1	1	1				1	3
Oligochaeta	3				3			1				3		1	3	3	2	1					3		3		1			1		2		2	2
Ophelina		2	2	3	2				1	1	2	1			3	1	3				2		3		3					2		2	3	1	
Paramphinome						3				3	1					3	1	1					3		3		2	2		3			3	1	
Praxillella	3	1		3	1				3	1			1	1	1	1	2	2		3			1		3					3				3	
Prionospio		1	3	3					3				2		2	2	1	3	1	3	1		1		3					3			2	2	
Spiophanes		3	1	3	1				3	1			3			2	2	1		3			1		3					3			2	2	

Appendix 5:

Bremner, J., Rogers, S.I. & Frid, C.L.J. (2003) Assessing marine ecosystem health: the long term effects of fishing on functional biodiversity in North Sea benthos. *Aquatic Ecosystem Health and Management.* **6**(2) 131-137

Appendix 6(a). Biological trait variables and categories used to describe ecological functioning in intertidal infauna assemblages in the Tees and Clyde estuaries.

Trait code	Trait	Number	Category
L	Longevity (years)	1	0-3
		2	4-7
		3	8-11
		4	12+
SX	Sexual differentiation	1	Gonochorist
		2	Synchronous hermaphrodite
		3	Sequential hermaphrodite
R	Reproductive method	1	Asexual: budding
		2	Asexual: fission
		3	Asexual: parthenogenesis
		4	Sexual: brood
		5	Sexual: eggs shed
LD	Larval development	1	Benthic
		2	Pelagic
D	Body design	1	Soft
		2	Hard – exoskeleton
		3	Hard – shell
F	Relative flexibility	1	Low
		2	Moderate
		3	High
M	Relative mobility	1	None
		2	Low
		3	Moderate
		4	High
MV	Movement method	1	Sessile
		2	Burrow
		3	Bore
		4	Crawl
		5	Jump
		6	Swim/float
H	Living habit	1	Tube
		2	Burrow/gallery
		3	Crevice/fissure
		4	Free
FD	Feeding method	1	Filter/suspension
		2	Deposit
		3	Scavenger
		4	Predator

Appendix 6(b). Fuzzy-scored biological traits for benthic taxa used in Chpater 6. Explanations of traits and categories are given in Appendix 6(a).

	L				SX			R					LD		D			F			M				MV						H				FD			
	1	2	3	4	1	2	3	1	2	3	4	5	1	2	1	2	3	1	2	3	1	2	3	4	1	2	3	4	5	6	1	2	3	4	1	2	3	4
Amphipoda	3				3						3		3			3			3				2	2		2		2	1	2	2	1		1	1	1	1	1
Angulus tenuis	3				3							3		3			3	3					3			3								3	2	1		
Arenicola marina	1	3	2		3							3	3		3					3	2	1			2	1				1		3				3		
Bathyporeia spp.	3				3						3		3			3			3				2	2		2				1				3		3		
Capitellidae	3				3		1				2	2	2	2	3					3			1	2		3					1	1		1		3		
Cerastoderma edulis	1	2			3							3		3			3	3					3	1		3		1						3	3			
Cirratulidae	2	2	1		3	1			1	1	1	1	3	1	3					3	2	1	1		3	2				1		1	2	2		3		
Corophium crassicorne	3				3						3		3			3			3				1	3		2		1		2	3				2	2		
Corophium volutator	3				3						3		3			3			3				1	3		2		1		2	3				2	2		
Crangon crangon	3	1			3		1				3			3		3		2	1				1	3		1		1		1				3			3	
Eteone longa	3	1			3						1	3		3	3					3				3		2		1		1		1		3			1	2
Exogone hebes					3		1				3		3		3					3				3				3		1	3					1	1	1
Fabricia sabella	3				3						3		3		3			2	2		1	2			1	1		1						3	2	2		
Fabulina fabula	3				3							3		3			3	3					3			3								3	2	1		
Harpaticoidea	3				3						3		3			3		2	1				2	1		1		1		1				3	1	3		
Hydrobia ulvae	3				3							3	2	2			3	3					3			1		2		2	3					3		
Jassa marmorata	3				3						3		3			3			3				1	3				2		2				3	3	1		
Macoma balthica	1	3	3	1	3							3		3			3	3					3	1		2		1			3				2	2		
Manayunkia aestuarina	3				3						3		3		3			2	2		1	2			1	1		1					2	2	2	2		
Mytilus edulis	2	2	2	1	3							3		3			3	3			3				3									3	3			
Nematoda	3				3		1			1	1	2	3		3					3			1	2		3		1	1		1		2	2		2	1	2
Nemertea	3				3	1			1		1	3	3	1	3					3			1	2		2		2		1		1		2			2	2
Nephtys spp.		3	1	1	3							3		3	3					3				3		2				2	1	2		2			1	2
Nereidae	3	1			3						1	2	1	2	3					3			1	3		2				2				3	1	1		3
Oligochaeta	3	1				3		1	1		2		3		3					3			1	2		3				1	3					3		1
Phoronis spp.					1	2		1	3		2	2	1	3	3			3			3	1			3	2	1						1	3	3			
Phyllodoce spp.					3							3		3	3					3				3				3			2		1				1	3
Poecilochaetus serpens												3		3	3			2	2			2	2			3					3				2	2		
Polydora quadrilobata	3				3						3			3	3			3				2	2			2		2			3				2	1		
Pygospio elegans	3				3				1		3		1	2	3			3			3				3						3			1	2	2		
Sabellidae	3	1			3				1		2	2	2	2	3			2	2		1	2			1	1	1	1						3	2	2		
Scoloplos armiger	3	1			3							3	3		3					3			2	1		3					3	1		1		3		
Spionidae	3				3				1		2	3	1	3	3			3	1		1	1	1		1	1	1			1	1		1	3	1	2		
Syllidae					3	1	2		1		2	2	3	1	3					3				3				3		1				3				3
Travisia forbesii															3				2	1			1	2		3										3		