Causes and consequences of variability in marine benthos

Thesis submitted in accordance
with the requirements of the
University of Liverpool for the
degree of Doctor in Philosophy

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March 2016

ABSTRACT

The last two decades have seen a shift of emphasis in ecology; from a focus on the drivers of biodiversity change toward a consideration for its effects on ecosystem functioning. Ecosystem functioning is affected by individual species (i.e. species with functionally dominant biological traits), but can also be influenced by other factors, such as interspecific interactions. Current evidence suggests that biotic influence over marine ecosystem functioning is largely underpinned by the effects of individual species. However, there are indications that this might not constitute a complete understanding of the link between marine biodiversity and ecosystem function (BEF). For this thesis, I applied our current understanding of marine BEF relationships (i.e. the causal link between particular biological traits and particular ecological functions) to long-term benthic community time series and investigated the causes of ecological change and its consequences for ecosystem functioning. A shift in the taxonomic composition of the species assemblage was explained by underlying variation in extrinsic drivers. However, the long-term conservation of trait composition suggests that functioning can be sustained in the face of environmental and ecological change. Experiments conducted to test BEF relationships in intertidal marine benthos reaffirmed the functional importance of the biological traits of species, but also showed that interactions among species can influence the delivery of ecological functions in various ways, including facilitation (i.e. function delivery is enhanced) and antagonism (i.e. function delivery is reduced). The results suggest that biotic influence over marine ecosystem functioning is more complex than previously suggested, and that the impacts of biodiversity change (e.g. species extinctions or shifts in species densities) could be either exacerbated or mitigated depending on the composition of the affected assemblage and the ecological function considered. To produce more realistic results, future indirect assessments of ecosystem functioning would benefit from incorporating interactions among species as well as their biological traits.

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Chapter 1

General Introduction

The causes of biodiversity change: a long-standing question in ecology

The composition of biological assemblages is variable over space and time (Tilman & Kareiva 1997; Gaston & Blackburn 2006; Magurran et al. 2010). Understanding the causes of this variation has long been a central goal of ecology (Levin 1992). To achieve this goal requires that cause-effect relationships between proposed drivers and biotic responses are experimentally demonstrated (Hairston 1989). However, long-term and broad-scale surveys are also required to assess the degree to which proposed drivers can explain compositional change in natural assemblages (Goldsmith 1991; Magurran et al. 2010).

Ecological datasets extend back as far as the field of ecology itself, and have shed light on the dynamics of biota ranging from phytoplankton to birds (Magurran et al. 2010). Addressing the causes of long-term ecological change, however, remains a challenge to this day. Biological assemblages typically exhibit high amplitude and high-frequency (short-term, e.g. seasonal) temporal fluctuations, thus producing both ‘noisy’ and autocorrelated time series and potentially obscuring long-term ecological trends (Rohani et al. 2004). Moreover, assemblages can experience changes to species composition simply as a result of drift (Dornelas et al. 2014), thus potentially resulting in long-term trends in biota that are independent of changes to external forcing (i.e. a ‘random walk’). Extrinsic factors that are postulated to impact biological assemblages may also be correlated with each other, thus making it difficult to identify the drivers of systematic long-term ecological change.

In the modern era, characterised by human dominance over the natural world, it is essential to improve our understanding of the drivers of ecological change so that we can mitigate anthropogenic impacts. Rates of extinction are currently high in both terrestrial and aquatic ecosystems (Sala et al. 2000; Sala & Knowlton 2006), and there are suggestions that a 6th mass extinction could be underway (Barnosky et al. 2011). Climate change and other phenomena linked to anthropogenic greenhouse gas emissions pose a threat to global biodiversity (Walther et al. 2002; Hoegh-Guldberg & Bruno 2010), while similar threats are posed by disturbances that occur locally (e.g. fishing and eutrophication) but are pervasive world-wide (Jennings & Kaiser 1998; McKinnon & Taylor 2012). These drivers, possibly acting in combination, have already had impacts on biodiversity and will continue to do so into the future. Disentangling their roles requires that we consider the mechanisms through which they are expected to act (and interact) on ecosystems and test these hypotheses with appropriate models.

The consequences of biodiversity change: development of an ecological field

Inspired by ongoing human transformation of the natural world and the elevated global extinction rate (Wilson 1988; Myers 1990), ecologists in the mid-1990s began to consider the effects of changes to biodiversity on the functioning of ecosystems (i.e. how they produce biomass, retain nutrients, decompose organic material and deliver other functions that form the basis of ecosystem service provision). The first experiments in the field of biodiversity and ecosystem functioning (BEF; Schulze & Mooney 1993) sought to establish whether the level and stability of function delivery varied in relation to species richness (Naeem et al. 1994; Tilman & Downing 1994; Tilman et al. 1996). Their results showed that various aspects of functioning were impaired as species were lost from communities. The publication of these papers was, however, quickly followed by others which questioned the generality of their findings and the mechanisms through which BEF relationships could emerge (e.g. Aarssen 1997; Grime 1997; Huston 1997).

Two broad categories were defined to represent the ways through which biota can influence the level of function delivery: *identity* effects and *complementarity* effects (Loreau 2010). Identity effects are said to occur when individual species, with particular biological traits (i.e. life history, morphological or behavioural characteristics), have a dominant effect on functioning. In such instances, changes to the composition of assemblages (with or without changes to species richness) can alter functioning via the loss or gain of functionally dominant species. The second category, complementarity effects, are said to occur when function delivery by an assemblage exceeds predictions based on the performances of the individual constituent species. Two mechanisms were proposed to explain how complementarity could arise: *facilitation* (i.e. positive species interactions) and *niche partitioning* (i.e. the ability of different species to utilise different sections of the available niche space). Research conducted within terrestrial plant assemblages following the pioneering BEF experiments pointed to the importance of individual species (with particular biological traits) but also implied a level of complementarity among species (e.g. Hooper & Vitousek 1997; Tilman et al. 1997; Hector et al. 1999).

More recent analyses have attempted to partition the degree to which the two categories of mechanisms contribute to BEF relationships. In an analysis of biomass production across multiple terrestrial plant experiments, Loreau & Hector (2001) found that the identity effect was on average approximately zero, whereas the complementarity effect was positive overall. Their results suggest that while individual species can have positive (or negative) effects on ecosystem functioning, niche differentiation or facilitation among species may tend to enhance function delivery in diverse species assemblages. Subsequent studies reaffirmed the generality of complementarity and found that its effect on functioning increases over time (Cardinale et al 2007; Reich et al. 2012) and in heterogeneous environments (Wacker et al. 2008). These results point to the importance of maintaining diverse biological assemblages as a means of securing a high level of function delivery.

While the evidence for complementarity has been accumulating, the two mechanisms commonly proposed to explain complementarity have been empirically demonstrated. Experiments conducted within laboratory microcosms have shown biota to influence functioning through interspecific facilitation (Cardinale et al. 2002; Tiunov & Scheu 2005) and niche partitioning (Cardinale 2011). Interspecific antagonism (i.e. negative species interactions) has also emerged as a mechanism through which increasing biological diversity can reduce function delivery (Polley et al. 2003; Jousset et al. 2011). Recent evidence suggests that niche partitioning contributes to the patterns of complementarity observed in long-term field experiments (Zuppinger-Dingley et al. 2014). However, little is known about the degree to which facilitative and antagonistic interactions among species contribute to BEF relationships.

Paralleling the theoretical developments regarding the effect of biodiversity on the level of function delivery, various hypotheses have also been proposed to explain how biodiversity could influence the stability of ecosystem functioning. A general feature of these hypotheses is the prerequisite for functional redundancy (Walker 1992). Functional redundancy is said to occur when an assemblage contains multiple species that contribute to the same ecological functions (i.e. they share the particular biological traits that drive these functions). Therefore, if a species is lost from the system, then its contribution to functioning can potentially be compensated for by the remaining redundant species. High biodiversity begets high functional redundancy, which in turn begets a greater capacity to buffer changes to functioning in the event of a population collapse or extinction (Naeem & Li 1997; Naeem 1998).

The main mechanisms proposed to explain how biodiversity can influence functional stability pertain to the different ways through which compensation among redundant species can occur (Loreau & de Mazancourt 2013). One of these mechanisms is the *insurance effect* (Yachi & Loreau 1999), whereby different species exhibit asynchronous population fluctuations under variable environmental conditions (i.e. they do not share the particular traits that control biotic response to perturbations). In other words, as the densities of some species decrease, the densities of other species increase and substitute for their functional roles. The number of redundant species and the degree to which they differ in their responses to environmental change therefore determine the stability of function delivery. If there are many redundant species with diverse response traits then functioning will likely remain stable, whereas if there are few redundant species with similar response traits then functioning will be destabilised by environmental fluctuations.

Studies of biomass production in grasslands have showed that functional stability tends to increase in diverse species assemblages as a result of population asynchrony (Tilman et al. 2006; Isbell et al. 2009; Hector et al. 2010). Effects relating to *complementarity* (i.e. an increase in the level, but not variance, of function delivery) were also detected in their analyses, as was an effect resulting simply from the statistical averaging of (correlated or uncorrelated) population fluctuations. These results suggest that conserving diverse species assemblages will promote stability in ecosystem functioning; however, little is known about stability in functions other than biomass production in temporally variable assemblages.

The abovementioned BEF studies, and various others that form the foundations of the BEF field (see Loreau et al. 2001; Hooper et al. 2005), consist mainly of experiments conducted within terrestrial ecosystems. Experiments conducted using freshwater and marine benthic assemblages have been relatively uncommon, and with aquatic biodiversity rapidly changing (Dudgeon et al. 2006; Sala & Knowlton 2006) this continues to be an area in need of much research attention. The seafloor, in particular, is the world’s most extensive habitat, plays a major role in global carbon and nutrient cycling, and is subjected to multiple anthropogenic stressors (Snelgrove et al. 1999; Snelgrove et al. 2014). Hence, there is a particular need to assess both the drivers of biodiversity change in the marine benthos and the impacts this has on ecosystem functioning.

BEF research conducted within marine ecosystems has focussed mainly on the level, rather than the stability, of function delivery. As was observed in terrestrial ecosystems, early experiments found identity effects to be an important determinant of marine ecosystem functioning, with a role of complex interspecific interactions and a degree of complementarity also implied (Duffy et al. 2001, 2003; Emmerson et al. 2001; O'Connor and Crowe 2005). A number of subsequent studies, which focussed on nutrient cycling by marine macroinfaunal assemblages, reaffirmed the importance of individual species (Norling et al. 2007; Godbold et al. 2009a,b; Godbold et al. 2011) and showed that the level of function delivery varies with respect to changes in their densities (e.g. Ieno et al. 2006; Braeckman et al. 2010). Despite consistent and dominant complementarity effects being reported for experiments using freshwater macroinfauna (e.g. Mermillod-Blondin et al. 2003; Karlson et al. 2010; Caliman et al. 2011), a role of complementarity among marine macroinfauna has seen little support. Moreover, recent reviews indicate that identity effects tend to underpin BEF relationships across marine ecosystem components (Gamfeldt et al. 2015; Strong et al. 2015), which can be attributed to the biological traits of functionally dominant species (Stachowicz et al. 2007). These results suggest that marine species that exhibit functionally dominant traits need to be protected if high levels of function delivery are to be sustained.

Trait-based inferences of changes to ecosystem functioning

The experimental studies cited in this chapter have shed light on BEF relationships, their underlying mechanisms, and consequently how biodiversity conservation might be approached within a BEF context. Their utility can, however, also be extended by applying their findings to ecological survey data in order to make indirect inferences about potential changes to functioning. Given that the density and biological traits of species determine their contributions to function delivery (Chapin et al. 1997; Diaz & Cabido 2001), it is possible to make predictions about changes to functioning in spatially or temporally variable assemblages. This can be done on the premise that as the density of a species increases or decreases, the delivery of any functions driven by its biological traits will also increase or decrease, respectively. Multiple functions can therefore be considered simultaneously, providing that they can be linked (empirically or logically) to measurable traits (i.e. functional effect traits). This approach may provide a particularly good proxy for functioning when applied to marine biota, given the apparent dominance of species identity effects over complementarity effects within this particular ecosystem.

Various studies over the last 10-15 years have used trait composition to assess potential changes to functioning, many of which focussed on marine benthic ecosystems (e.g. Bremner et al. 2003; Hewitt et al. 2008; Caswell & Frid 2013). The authors have generally selected a suite of traits (e.g. body size, feeding mode, lifespan), based on the availability of information and the particular aspect of functioning being considered, and assumed that changes to trait composition imply potential changes to ecosystem functioning. Some recent studies have gone a step further and begun to link specific traits to specific functions (e.g. small and short-lived species promote high carbon turnover) in order to reconstruct patterns in ecosystem functioning over time (e.g. Frid 2011; Frid & Caswell 2015; Frid & Caswell 2016). Such approaches allow functional changes to be assessed based on the degree to which compositional change entails substitutions of taxa with the same traits (i.e. functioning is sustained), substitutions of taxa with different traits, or uncompensated population fluctuations (i.e. functioning changes in both of the latter cases). Their analyses suggest that functioning can be sustained despite compositional changes over various timescales, and that the degree to which functioning varies depends on the particular function considered. However, a focus on subsets of assemblages (e.g. dominant or temporally variable taxa) raises the possibility that excluded taxa could collectively compensate for, or amplify, changes to functioning implied by the taxa included in analyses.

In addition to the studies that have applied traits to assess potential changes to functioning, others have used traits to investigate the drivers of biodiversity change. This approach has been applied to ecological survey data to assess spatial and temporal variation in relation to fishing pressure (e.g. Bremner et al. 2005; Tillin et al. 2006; de Juan et al. 2007); organic matter input (e.g. Papageorgiou et al. 2009; Villnäs et al. 2011); temperature (Neumann & Kröncke 2011); pollution and salinity gradients (e.g. Oug et al. 2012; Darr et al. 2014) and other potential drivers. This approach improves on traditional analyses of taxonomic composition as particular biological traits determine the way in which species respond to particular changes to their environment (i.e. response traits). For example, theory and experiments indicate that large, sessile filter-feeders tend to be negatively affected by trawling, whereas small, mobile scavengers tend to respond positively (Jennings & Kaiser 1998). A consideration for the biological traits of species therefore allows researchers to propose hypotheses that are grounded in ecological theory and focus on the characteristics of species that are most relevant to the proposed drivers (or the drivers that are likely to be important given the characteristics of the species), consequently strengthening our ability to gain a mechanistic understanding of any observed relationships. Moreover, as the biological traits of species determine their response to environmental change and their influence over ecosystem functioning (Lavorel & Garnier 2002), trait-based approaches provide a tool through which to link the causes and consequences of variability in assemblage composition.

Real-world applicability of ecosystem functioning inferences

The research that followed the initial BEF experiments has shed much light on how biota influence ecosystem functioning, yet questions remain regarding the real-world applicability of results (e.g. Srivastava & Vellend 2005; Hillebrand & Matthiessen 2009; Strong et al. 2015). Randomly assembled communities have been used in most BEF experiments, including the long-term grassland experiments that form much of the foundations of the BEF field (Tilman et al. 2014). In nature, communities are not assembled at random, nor are they assembled instantaneously (i.e. in a manner akin to planting individuals into a cleared field plot or an enclosed environmental chamber). It has therefore been argued that results of such experiments may have little direct relevance in contexts other than biodiversity restoration (Srivastava & Vellend 2005). Moreover, species are not lost or gained from ecosystems at random, and the order of extinction (e.g. random *vs.* realistic) affects how ecosystem functioning is affected (Solan et al. 2004; Larsen et al. 2005; Bracken et al. 2008; Bracken & Low 2012). An emphasis on species loss in BEF research may also be questionable, given that the species richness of assemblages is experiencing little long-term change on average (Dornelas et al. 2014), whereas shifts in species densities are pervasive (Dirzo et al. 2014). More realistic biodiversity change scenarios should therefore be incorporated into experiments assessing biotic influence over ecosystem functioning.

An additional issue regarding the realism of BEF research is the environmental context in which experiments are conducted. Much of the work that has contributed to our mechanistic understanding of BEF relationships has been performed under controlled laboratory conditions (e.g. Cardinale et al. 2002; Tiunov & Scheu 2005; Cardinale 2011). For BEF studies conducted using marine organisms, the use of homogenous experimental microcosms has been particularly common, especially for those focussed on soft-sediment benthos (Gamfeldt et al. 2015). Such conditions are ideal for isolating biotic effects from any confounding influence of environmental heterogeneity. However, this raises questions about whether biotic effects are of any significance in natural ecosystems, where functioning might be primarily under the direct influence of environmental heterogeneity (Strong et al. 2015). With that said, the influence of complementarity on ecosystem functioning may be enhanced under levels of heterogeneity typical of natural ecosystems (Stachowicz et al. 2008; Wacker et al. 2008), and the nature of biotic interactions may vary with respect to environmental context (Tiunov & Scheu 2005; Maestre et al. 2010; Jousset et al. 2011). Moreover, the short-term experiments that have dominated the marine BEF field may be of insufficient duration to detect the effects of complementarity, which have been found in natural ecosystems to increase over time (Stachowicz et al. 2008). The behavioural traits that species express (e.g. feeding mode) can also depend on environmental context (Ólafsson 1986; Törnroos et al. 2015), which could affect the degree to which changes to functioning implied by microcosm experiments are applicable to natural ecosystems. Such issues have implications for our ability to use trait-based approaches to infer changes to ecosystem functioning and for our ability to use findings to successfully inform conservation.

Scope and overall aims of thesis

This chapter has covered a shift in emphasis in ecology; from a focus on the drivers of biodiversity change toward a consideration for its effects on ecosystem functioning. The preceding decades have contributed substantially to our understanding of both aspects of ecological variability. However, as highlighted above, there remain unresolved questions and thus opportunities to address some of the existing gaps in knowledge. The goal of this thesis was to take this opportunity, with a specific focus on the causes and consequences of variation in marine benthic community composition.

The main aims of this thesis were to:

1) Apply theoretical advances and experimental findings regarding the roles of biological traits in order to shed light on the drivers of long-term change in natural assemblages and determine the potential impacts on ecosystem functioning.
2) Formulate and test hypotheses – based on recent developments and current gaps in knowledge – in order to further our understanding of biotic influence over the functioning of ecosystems.

With these mains aims considered, this thesis can be conveniently divided into two main sections, with the first section focussed on aim 1) and the second section focussed on aim 2). Each section contains two chapters, and each of these chapters was written in the style of a manuscript to be submitted for academic publication.

For the first section (**Chapters 2 & 3**), long-term time series were used to investigate the causes of temporal change in marine macroinfaunal assemblages (Fig. 1.1, **Ch. 2**) and assess the consequences of this change for the delivery of multiple key ecological functions (Fig. 1.1, **Ch. 3**). Community dynamics were modelled over time in **Chapter 2** to test whether the observed patterns were explained by underlying patterns in sea temperature and pelagic primary production, which were postulated to act (and potentially interact) on biota via their roles in determining and sustaining metabolic demand, respectively (see Introduction in **Chapter 2** for a more thorough explanation of the rationale underlying these hypotheses). As temporal trends can occur in the absence of external forcing, the analysis focused on changes to temporal trends in species densities and accounted for temporal autocorrelation in the models. **Chapter 3** applied our understanding of how biological traits determine the functional contributions of species in order to infer whether functioning is variable in assemblages experiencing long-term compositional change – i.e. does trait composition change or is it conserved by density compensation among functionally redundant taxa? This analysis used datasets consisting of the whole community (with the exception of the rarest taxa) so as to avoid potentially over- or underestimating the degree of variation in functioning.

For the second section (**Chapters 4 & 5**), trait-specific predictions of species density-function relationships, such as those applied in **Chapter 3**, were experimentally tested and the influence of interspecific (and intraspecific) interactions on function delivery was assessed (Fig. 1.1, **Ch. 4** & **Ch. 5**). In **Chapter 4**, a natural assemblage was manipulated to simulate a realistic pattern of biodiversity change and then sampled over an extended period to test the hypothesis that the effects of interspecific facilitation on ecosystem functioning increase over time. Microcosm and field experiments were used in tandem in **Chapter 5** to test whether species density-function relationships are altered by interspecific interactions (i.e. facilitation and/or antagonism) and whether these effects are consistent across artificial and natural environmental contexts. Whereas most previous studies of biotic influence over ecosystem functioning have focussed on changes to species richness, both **Chapters 4** and **5** focussed on shifts in species densities.

The final chapter of this thesis, **Chapter 6**, synthesises the findings of **Chapters 2** to **5**. The implications of findings and the avenues for future research are also discussed.

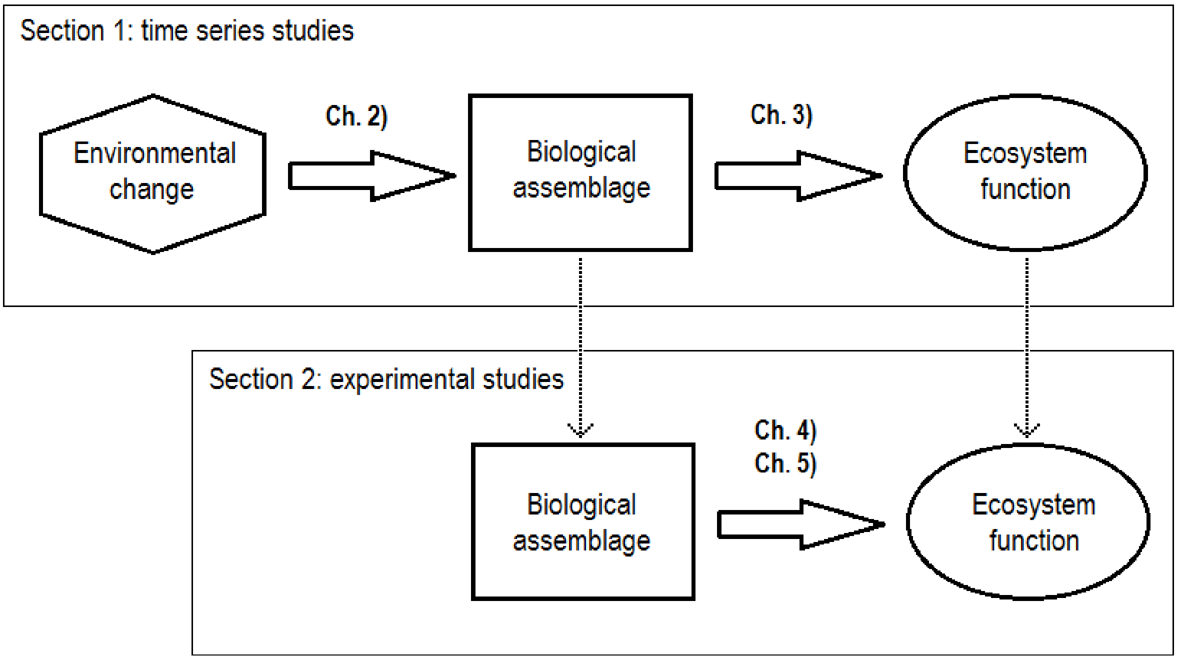

Fig. 1.1. The research focus of the chapters contained within this thesis and how they relate to each other. The first section uses long-term time series to assess the drivers of compositional change in benthic faunal assemblages **Chapter 2** (**Ch. 2**) and the consequences of this change for the delivery of ecosystem functions in **Chapter 3** (**Ch. 3**). The second section uses a field experiment in **Chapter 4** (**Ch. 4**) and a combination of microcosm and field experiments in **Chapter 5** (**Ch. 5**) to further investigate the influence that biological assemblages have over ecosystem functioning.

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Chapter 2

The roles of temperature and primary production in the long-term dynamics of benthic faunal composition

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ABSTRACT

Predicting the ecological consequences of environmental change requires that we can identify the drivers of long-term ecological variation. Biological assemblages can exhibit abrupt deviations from temporal trends, potentially resulting in irreversible shifts in species composition over short periods of time. Such dynamics are hypothesised to occur as gradual forcing eventually causes biological thresholds to be crossed, but could also be explained by biota simply tracking changes to their environment. Here, I modelled temporal variation in a North Sea benthic faunal assemblage over a 40-year period (1972–2012) to test for changes to temporal trends of biota and determine whether they could be explained by underlying patterns in sea temperature and primary production. These extrinsic factors were postulated to influence community dynamics through their roles in determining and sustaining the metabolic demands of organisms, respectively. A subset of mainly large and long-lived taxa (those loaded on the first principal component of taxa densities) exhibited two significant changes to their temporal trends, which culminated in a shift in assemblage composition. These changes were explained by an increase in pelagic primary production, and hence detrital food input to the seabed, but were unrelated to variation in sea temperature. A second subset of mainly small and short-lived taxa (those loaded on the second principal component) did not experience any significant changes to their temporal trends, as the enhanced pelagic primary production appeared to mitigate the impact of warming on these organisms. The results suggest that abrupt shifts in biological assemblages can occur as biota track underlying patterns in extrinsic factors, in this case primary production. Changes to the structure of ecosystems may therefore be predictable based on environmental change projections.

INTRODUCTION

Biodiversity is rapidly changing in an era of human dominance over the natural world (Steffen et al. 2007; Dornelas et al. 2014; McGill et al. 2015), putting species under increased risk of extinction and altering the functioning of ecosystems (Cardinale et al. 2012, Naeem et al. 2012; Dirzo et al. 2014). Predicting the impacts of environmental change requires that we identify the drivers of ecological variation. To this end, experiments are vital in demonstrating the effects of extrinsic factors (Hairston 1989; Stenseth et al. 2002). However, long-term monitoring is also required to track temporal variability in natural biological assemblages and assess whether potential drivers can explain the observed patterns (Dauvin 2010; Magurran et al. 2010). One pattern to recently emerge from long-term ecological datasets is the occurrence of abrupt deviations from temporal trends (Lees et al. 2006; Spencer et al. 2012); potentially resulting in irreversible shifts in species composition over short periods of time. The drivers of such community dynamics are not well understood. A common hypothesis is that abrupt ecological changes represent non-linear responses to gradual forcing, as biological thresholds are eventually crossed (Barnosky et al. 2012; Möllmann et al. 2015). An alternative explanation is that biota are tracking similar underlying patterns in extrinsic factors.

In attempting to understand the drivers of variation in species composition, a logical approach is to focus on the factors that are expected to exert the greatest ecological impacts. One of the most pertinent aspects of modern environmental change in this regard is the rise in global surface temperature associated with enhanced ‘greenhouse gas’ emissions (Hansen et al. 2006; Cook et al. 2013; Karl et al. 2015). Recent climate change has already had impacts on biological assemblages (Walther et al. 2002; Hoegh-Guldberg & Bruno 2010) and with global warming set to continue, severe impacts on biodiversity are predicted in the future (Bellard et al. 2012). Various other environmental changes are set to occur as a result of greenhouse gas emissions, including alterations to primary productivity (Chavez et al. 2011; Blanchard et al. 2012). Experiments indicate that such changes are likely to have their own ecological impacts (e.g. Walker et al. 2006; Wimp et al. 2010; Witt et al. 2011), but may also interact to exacerbate or ameliorate effects on biota (e.g. O’Connor et al. 2009; Castro et al. 2010; Hale et al. 2011).

Disentangling the roles of multiple extrinsic factors is one of the biggest challenges faced by those tasked with predicting the ecological impacts of environmental change (Stenseth et al. 2002). Selecting the appropriate analyses to achieve this goal is aided by consideration for the mechanisms through which potential drivers are expected to act (and interact). Increasing primary production is likely to lead to greater food availability for consumers, which can fuel population growth (Silby & Hone 2002). Small increases in temperature, on the other hand, can substantially increase metabolic rate and, thus, food requirements (Gillooly et al. 2001; Brown et al. 2004). Primary production and temperature may therefore drive community dynamics via their roles in sustaining and determining the metabolic demands of organisms, respectively. Moreover, it is plausible that these factors will interact in their effects on consumers, and that interactions will be either positive or negative. For example, a species may only decline in density in response to warming if there are insufficient food resources available to sustain the associated increase in its metabolic demand (negative interaction); or a species that responds positively to warming might require that there are plentiful food resources to fuel population growth (positive interaction). These interactions could exacerbate or mitigate changes to the temporal trends of consumers. For example, if temperature and primary production increase simultaneously, then a positive interaction could induce an abrupt shift in species composition, whereas a negative interaction could act to prevent such a shift from occurring.

Here, I study the existence and causes of changes to temporal trends in a North Sea benthic faunal assemblage using a 40-year time series. Specifically, the aims are to determine 1) whether changes to temporal trends occur, and 2) whether these changes are explained by underlying variation in sea surface temperature (SST) and pelagic primary production (hence detrital food input to the seabed); or whether other mechanisms such as different extrinsic drivers or the crossing of biological thresholds are implied. The North Sea experienced abrupt increases in SST and pelagic primary production in the late 1980s (Reid et al. 2001; Reid & Edwards 2001; Beaugrand 2004), with cold winters occurring both before (in the late 1970s; Reid & Edwards 2001) and, to a lesser degree, after this period (in the mid-1990s; Kröncke et al. 2013). The North Sea over the last 40 years is therefore an ideal model ecosystem within which to address these questions. I test for the above postulated interactions between extrinsic factors in the analyses. I also test whether these factors interact with season, as the effect of changing food input may differ between the period following summer growth and the period after winter die-offs, and this effect may in turn depend on whether the system is subjected to warm summers, cold winters, or mild conditions in either season.

MATERIALS AND METHODS

Benthic community time series

Dove Station M1 sits under 55 m of water in predominantly sandy sediment, 10.5 km east of the Northumberland coast in NE England (55° 04′ N, 01° 20′ W). The station is located away from local river discharges and outside the main grounds of a *Nephrops* trawl fishery. Temporal patterns in the benthos at M1 do not appear to be influenced by the level of fishing activity in the local area (Frid et al. 1999).

Macroinfauna (animals living within the sediment that are large enough to be seen with the naked eye) have been sampled biannually at M1 in March/April (spring) and September/October (autumn) since September 1972. Data are missing only for the springs of 1998 and 2004 and the autumns of 1987 and 1991, as weather conditions and/or operational constraints prevented sampling on these occasions. Samples were collected using van Veen grabs (0.1 m^2), sieved over 0.5 mm mesh and fixed with 4% buffered formalin. Retained fauna were identified to the lowest possible taxonomic level and enumerated. Sampling methods are described in detail in Buchanan & Warwick (1974). Since 1980 a total of 5 grabs have been collected on each sampling occasion; however, sampling effort ranged from 10 to 20 grabs up to this point. Here, I use all data available from autumn 1972 to autumn 2012.

Time series of potential extrinsic drivers

Pelagic primary production in the area of the study site (Area C2, central-western North Sea; see http://www.sahfos.ac.uk/cpr-data/standard-areas.aspx) was indexed using the Phytoplankton Colour Index (PCI) (Reid et al. 1998). PCI is based on the ‘greenness’ recorded on the silk of the continuous plankton recorder. The scale by which greenness is measured is calibrated using acetone-based measures of phytoplankton biomass. PCI has been used as a proxy for detrital food input to the seabed in previous analyses of benthic community dynamics at Dove Station M1 (e.g. Buchanan 1993; Frid et al. 2009a) and elsewhere (e.g. Frid et al. 2009b). Here, I took the mean PCI over 12-month periods starting at two different points in the annual cycle (January-December and July-June) to create estimates of detrital flux that could be matched to the macroinfaunal assemblage sampled in the spring and autumn of each year (see *Data Analysis* section below). The mean of these data over the preceding 5 years was also used to indicate the amount of detritus that had been made available to the benthos over a longer temporal scale.

Sea surface temperature (SST) records were obtained from three sampling stations located on the northeast coast of England, in Blyth (55° 8′ N, 1° 32′ W), Redcar (54° 38′ N, 1° 5′ W) and Scarborough (54° 17' N, 0° 22' W). The data were downloaded from the Coastal Temperature Network maintained by Cefas. Currents that carry cool water from the Atlantic into the northern North Sea flow down the northeast coast of the Great Britain toward Flamborough Head (Lee & Ramster 1981), passing over each of these stations and Dove Station M1. The temperature records at all three stations are therefore considered here to be indicative of the hydrothermal conditions experienced at the study site. None of these individual datasets formed complete time series over the entire study period. Monthly means were therefore averaged across all stations for which there were available data. Aggregate figures for December, January and February were then averaged to give a value for mean winter temperature each year. Likewise, figures for June, July and August were averaged to give mean summer temperatures. This produced a complete time series for winter and summer temperatures over the entire study period. These data were then standardised to temperature anomalies (i.e. standard deviations from the season-specific mean) to indicate temperature variability relative to the average conditions in the relevant season.

Data analysis

At each sampling occasion, taxa abundances were mean-averaged across all replicate samples and standardised to the number of individuals per square metre. Taxa that occurred at a density of ≥ 10 individuals per square metre in any year of the time series (in spring or autumn) were retained in the community dataset. Taxa that only ever occurred at densities of less than 10 individuals per square metre (one individual per grab) were excluded, as their abundances will not have been reliably estimated. Using this approach, over 98% of total abundance was represented in each year of the analysed data.

Principal components (PCs) were used to describe the main patterns of temporal variation in faunal composition (see Jolliffe 2002). PCs were derived from the correlation matrix of $\ln(x + 1)$ transformed taxa abundances. When community data were missing (i.e. benthic samples were not collected), PCs were estimated by taking the mean of the PC scores of the preceding and following years for the appropriate season. For this analysis I considered only PCs 1 and 2, which accounted for 16.2% and 9.4% of variation, respectively. All other PCs accounted for ≤ 6% of variation.

Generalized Additive Mixed Models (GAMMs; Wood 2006, section 6.6) were used to model temporal variation in PCs 1 and 2. In GAMMs, part of the linear predictor is specified in terms of ‘smoothed’ covariates, with the shape of the trend estimated via penalised regression splines (Lin & Zhang 1999). Here, time (i.e. the year of the time series; + 0.25 for spring samples and + 0.75 for autumn samples) was treated as a smoothed covariate to avoid making assumptions about the particular form of the relationship between PCs and time. The initial additive mixed model took the form:

$$y_{i,j} = \beta_{0,j} + f_{1,j}s(time_i) + f_{2,j}(season_i) + \varepsilon_{i,j},$$

where $y_{i,j}$ is the value of the *j*th principal component ($j = 1,2$) at time *i*, $f_{1,j}s(time_i)$ is the smoothed time function, $f_{2,j}(season_i)$ is the season in which sampling was conducted (spring *vs.* autumn) and $\varepsilon_{i,j}$ is a residual error, assumed to be normally distributed with zero mean and temporal autocorrelation described by a first-order continuous-time autoregressive (CAR(1)) model (Pinheiro & Bates 2000, section 5.3). GAMMs were fitted using the **mgcv** package in R (version 3.2.2; R Core Development Team). Smoothing was performed using restricted maximum-likelihood (REML) estimation (Harville 1977), which is preferable to other smoothing parameters as it tends to avoid severe ‘undersmoothing’ (Wood 2015).

To test for changes to the temporal trends of PCs 1 and 2, 95% confidence intervals for second derivatives (i.e. significant changes to the rate of change) were estimated by simulation following a modified version of the method in Orr et al. (2015) for confidence intervals on first derivatives (described below). For high-dimensional data, such as the dataset used in this study, the first principal component is expected to show a trend (i.e. a significant first derivative) even where each component is simply a random walk (Bookstein 2013). Focus was therefore placed only on changes to the temporal trend, as the trend itself is of little interest when investigating the causes of ecological change.

Random samples were drawn from the posterior distribution of smoothed time coefficients and multiplied by the linear predictor matrix to simulate the temporal trend. Second derivatives were estimated numerically by finite differences (Davis and Polonsky, 1965, section 25.3.23) with increments of 1×10^{-5} years around each point on a grid of 200 equally-spaced time points. Simultaneous 95% confidence intervals for these second derivatives were obtained from the 0.025- and 0.975-quantiles of 10,000 such simulations. Fitted values of PCs 1 and 2 were plotted against time, and periods during which the second derivative was significantly positive were highlighted in red, whereas periods during which the second derivative was significantly negative were highlighted in blue. With principal components the sign is arbitrary, but once the sign is fixed, this also fixes the definitions of positive and negative second derivatives.

To investigate the drivers of community dynamics, the initial models for PCs 1 and 2 were modified to include pelagic primary production and standardised SST as (non-smoothed) covariates. The maximum life-span and body length of taxa loaded on PCs 1 and 2 were compiled to determine the temporal scales over which phytoplankton biomass would be integrated when matched to each principal component of taxa densities. Small and short-lived opportunistic taxa are likely to respond to short-term fluctuations in primary production through rapid reproduction and recruitment (Gooday et al. 1990), whereas large and long-lived taxa, whose population growth rates are highly influenced by adult survival (Stearns 1992), are likely to respond to variation in primary production over longer temporal scales. The maximum lifespans and body lengths of taxa were taken from Marine Species Identification Portal (http://species-identification.org/) and MarLIN’s biological trait catalogue (http://www.marlin.ac.uk/biotic/biotic.php), with additional literature review and expert consultation used to corroborate and fill in gaps in information. When longevity information was unavailable, we assumed that body size was indicative of whether a taxon’s population dynamics are likely to be driven mainly by short-term recruitment (i.e. small-bodied) or long-term adult survival (i.e. large bodied).

As PC 1 was loaded mainly with large and long-lived taxa (see *PC 1* section of Results and Table 2.1), faunal data were matched to phytoplankton biomass data that were averaged over the preceding 5 years, with a 3-month time-lag to allow time for phytoplankton in suspension toward the end of this period to settle on the seabed and be made available to the benthos (e.g. fauna sampled in spring 1980 was matched to mean phytoplankton biomass from January 1975 to December 1979). As PC 2 was loaded mainly with small and short-lived taxa (see *PC 2* section of Results and Table 2.2), faunal data were matched to phytoplankton biomass data averaged over a 12 month period, with a 9-month time-lag applied to allow recently recruited individuals to reach the size necessary to be retained on the 0.5 mm mesh (e.g. fauna sampled in autumn 1980 was matched to mean phytoplankton biomass from January 1979 to December 1979). For both PCs, the assemblages sampled in spring and autumn were matched to the standardised SST of the previous winter and the previous summer, respectively.

Table 2.1. The top ten taxa with positive loadings (above dashed line) and the top ten taxa with negative loadings (below dashed line) on the first principal component of the macroinfaunal assemblage at Dove Station M1 from 1972 to 2012. Phyla are in brackets. Maximum body length and maximum lifespan of each taxon are shown, along with the mean values (± standard error) across positively- and negatively loaded taxa. In cases where maximum lengths of taxa were reported as a range, I used the midpoint when calculating the overall mean and standard error.

Taxon	PC loading	Max. length (mm)	Max. lifespan (years)
Arctica islandica (Mollusca)	0.160	120	500
Saccoglossus horsti (Hemichordata)	0.157	200	-
Parexogone hebes (Annelida)	0.156	10	2
Cerebratulus spp. (Nemertea)	0.153	100–1000	-
Glyphohesione klatti (Annelida)	0.150	13	5
Tubulanus polymorphus (Nemertea)	0.149	750	-
Trichobranchus spp. (Annelida)	0.139	20–35	-
Araphura brevimanus (Arthropoda)	0.126	3	1
Golfingia spp. (Sipuncula)	0.126	100–300	-
Platyhelminthes	0.126	1–600	-
Laonome kroyeri (Annelida)	-0.096	50	-
Lucinoma borealis (Mollusca)	-0.097	40	-
Cerianthus lloydii (Cnidaria)	-0.098	150	20
Polycirrus medusa (Annelida)	-0.098	70	10
Glossobalanus marginatus (Hemichordata)	-0.099	80	-
Phyllodocidae (Annelida)	-0.103	10–500	-
Kellia suborbicularis (Mollusca)	-0.120	10	-
Sphaerodoropsis minuta (Annelida)	-0.120	6	-
Chaetozone caputesocis (Annelida)	-0.121	17	3
Magelona spp. (Annelida)	-0.135	40–170	5
Mean (± SE)		148 (± 44)	68 (± 62)

As it was postulated *a priori* that the effects of temperature and primary production might interact in their effects on biota, and that their effects may differ with respect to season, these terms were added into the initial model as a three-way interaction with the season term:

$$y_{i,j} = \beta_{0,j} + f_{1,j}s(time_i) + f_{2,j}(season_i) * f_{3,j}(PCI_i) * f_{4,j}(SST_i) + \varepsilon_{i,j}$$

where $f_{3,j}(PCI_i)$ is an estimate of pelagic primary production in the area of the study site (and a proxy for detrital input to the seabed) and $f_{4,j}(SST_i)$ is standardised sea surface temperature.

Table 2.2. The top ten taxa with positive loadings (above dashed line) and the top ten taxa with negative loadings (below dashed line) on the second principal component of the macroinfaunal assemblage at Dove Station M1 from 1972 to 2012. Phyla are in brackets. Maximum body length and maximum lifespan of each taxon are shown, along with the mean values (± standard error) across positively- and negatively-loaded taxa. In cases where maximum lengths of taxa were reported as a range, I used the midpoint when calculating the overall mean and standard error.

Taxon	PC loading	Max. length (mm)	Max. lifespan (years)
Pholoe inornata (Annelida)	0.172	8	4
Spiophanes bombyx (Annelida)	0.162	60	2
Phoronis muelleri (Phoronida)	0.159	120	1
Ophelina acuminata (Annelida)	0.159	60	3
Gattyana cirrhosa (Annelida)	0.158	50	4
Phaxas pellucidus (Mollusca)	0.156	40	-
Levinsenia gracilis (Annelida)	0.156	25	2
Ampharete spp. (Annelida)	0.155	12–50	3–5
Acanthocardia echinata (Mollusca)	0.147	75	20
Poecilochaetus serpens (Annelida)	0.142	55	2
Thracia phaseolina (Mollusca)	-0.056	38	10
Laonice spp. (Annelida)	-0.058	60–120	1–3
Pseudocuma longicorne (Arthropoda)	-0.058	4	2
Ophiura spp. (Echinodermata)	-0.059	8–35	3–6
Retusa umbilicata (Mollusca)	-0.070	4	2
Thyasira biplicata (Mollusca)	-0.070	8	3
Ophelina cylindricaudata (Annelida)	-0.078	19	3
Paramphinome jeffreysii (Annelida)	-0.086	15	1
Aphelochaeta spp. (Annelida)	-0.091	10–15	-
Vitreolina philippi (Mollusca)	-0.096	8	-
Mean (± SE)		37 (± 7)	4 (± 1)

Wald-like tests (implemented using the `anova.gam` function) were used to approximate the statistical significance of each model term, conditional on the smoothing parameter estimates (Wood 2013). The resulting *p*-values are better justified than those derived from multi-model comparisons and have close to the correct distribution under the null, providing that the smoothing parameters are not poorly identified (Wood 2015). All non-significant interactions were removed from the models to reduce model complexity and free up degrees of freedom. Terms were considered to be statistically significant at $p < 0.05$.

Final models, with all statistically significant terms retained within the linear predictor matrix, were then tested for significant second derivatives in the smoothed time term in the same way as described above for the initial models. Fitted values of PCs 1 and 2 were plotted against time, with significantly positive and negative second derivatives highlighted in red and blue, respectively. If significant second derivatives identified in the initial models were not identified in the final models, then it was inferred that there was no reason to postulate additional mechanisms (e.g. other extrinsic factors or the crossing of biological thresholds) to explain changes to the temporal trend observed in the initial model.

Finally, the total number of species within the assemblage (species richness) and total abundance were plotted over time and then correlated against PCs 1 and 2 to assess the degree to which patterns in the subsets of taxa loaded on the principal components are indicative of variation in the diversity and density of the whole assemblage.

RESULTS

PC 1

The taxa with the top ten most positive and top ten most negative loadings on PC 1 consisted of representatives from eight phyla in total: seven phyla were among taxa with the most positive loadings and four were among taxa with the most negative loadings (Table 2.1). Many of these taxa were large and long-lived: twelve out of twenty could reach a body length of over 40 mm and nine could reach over 100 mm; five out of the eight taxa for which longevity information was available have a maximum lifespan of five or more years (Table 2.1). The species with the highest loading on PC 1 was the bivalve mollusc *Arctica islandica*, which can live for over 500 years and reach 120 mm in length (Table 2.1).

The densities of taxa loaded on PC 1 varied significantly over time (Table 2.3). In the initial model (i.e. the model containing only the (smoothed) time and season terms as explanatory variables) the temporal trend for PC 1 was positive at the onset of the time series and experienced a significant positive second derivative (a positive change to the rate of change) from 1987 to 1989, followed by a significant negative second derivative from 1993 to 1997 (Fig. 2.1a, solid line). These changes to the temporal trend culminated in a compositional shift from negatively-loaded to positively-loaded taxa (see Table 2.1). No further significant second derivatives occurred (Fig. 2.1a, solid line).

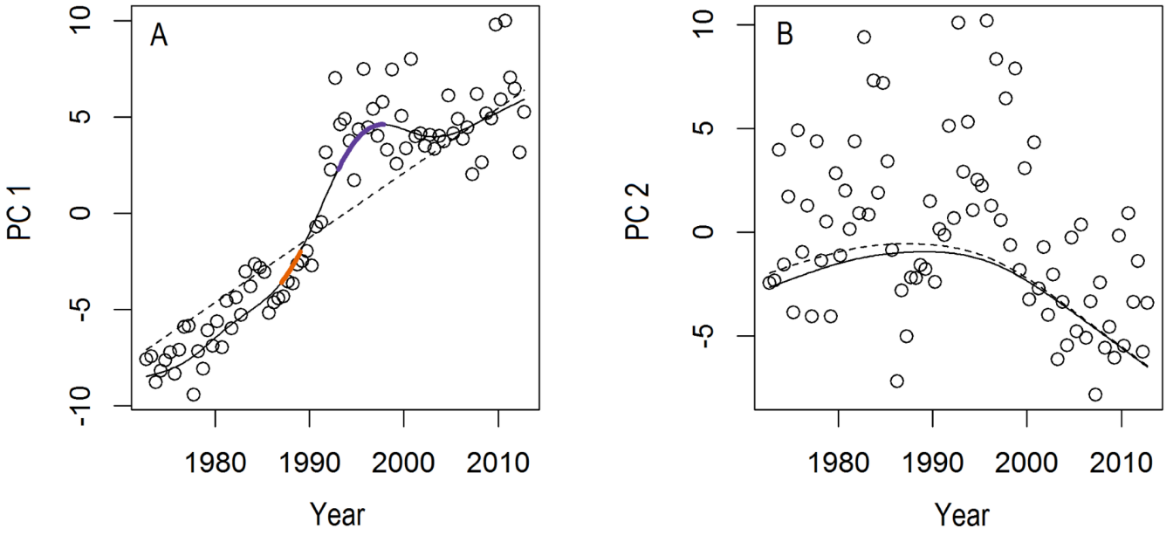

Fig. 2.1. Variation in (A) the first principal component and (B) the second principal component of taxa densities within the macroinfaunal assemblage at Dove Station M1 over (smoothed) time. Solid lines represent the relationships in the initial models (including only (smoothed) time and season terms) and the dashed lines represents the relationships in the final models, which included extrinsic drivers (i.e. pelagic primary production (PCI) and standardised sea surface temperature (SST; standard deviations from the seasonal mean)) that were significantly related (p < 0.05) to the principal components (including any significant interactions among extrinsic drivers and season) as terms in the linear predictor matrix. Periods during which second derivatives were significantly positive (i.e. changing toward positive PC scores; assessed with respect to 95% confidence intervals) are highlighted in red. Periods during which second derivatives were significantly negative (i.e. changing toward negative PC scores; assessed with respect to 95% confidence intervals) are highlighted in blue.

Temporal variation in the densities of taxa loaded on PC 1 was not significantly related to standardised SST, but was significantly related to pelagic primary production (PCI)*Season (Table 2.3). The relationship with pelagic primary production (averaged over the preceding 5 years) was positive in both seasons, but the slope was steeper in autumn (Fig. 2.2, solid line) than in spring (Fig. 2.2, dashed line). In other words, taxa with positive loadings tended to increase in density when pelagic primary production was high, and taxa with negative loadings tended to increase in density when pelagic primary production was low, but the increase was greater following the summer growth period than following the winter die-off.

The densities of taxa loaded on PC 1 closely tracked variation in pelagic primary production (averaged over the preceding 5 years) from the mid-1980s to the mid-1990s (Fig. 2.3a,c), which was the period during which both significant second derivatives occurred (Fig. 2.1a, solid line). In the final model (which included PCI*Season along with the (smoothed) time term) there were no significant second derivatives and the temporal trend was consistently positive and linear (Fig. 2.1a, dashed line), indicating that underlying variation in pelagic primary production explained the changes to the temporal trend of taxa loaded on PC 1.

Table 2.3. Generalized additive mixed model (GAMM) output showing variation in the first two principal components (PCs 1 & 2) of macroinfaunal taxa densities at Dove Station M1 from 1972 to 2012. Relationships between the PCs and pelagic primary production (PCI; averaged over the preceding 5 years (with a 3-month time-lag) for PC 1 and over 12 months (with a 9-month time-lag) for PC 2), standardised sea surface temperature (SST; standard deviations from the seasonal mean) and season (i.e. spring *vs*. autumn) are shown. All possible two-way and three-way interactions were tested. Non-significant interactions were removed. Significant *p*-values (< 0.05) are in bold.

	PC 1			PC 2		
Source	d.f.	*F*	*p*	d.f.	*F*	*p*
(Smoothed) Time	1	57.83	**< 0.0001**	1	4.27	**0.0469**
PCI	1	16.49	**0.0001**	1	0.85	0.3590
SST	1	1.85	0.1775	1	6.99	**0.0100**
Season	1	25.98	**< 0.0001**	1	198.17	**< 0.0001**
PCI*SST	-	-	-	1	4.77	**0.0322**
PCI*Season	1	35.72	**< 0.0001**	-	-	-
SST*Season	-	-	-	-	-	-
PCI*SST*Season	-	-	-	-	-	-

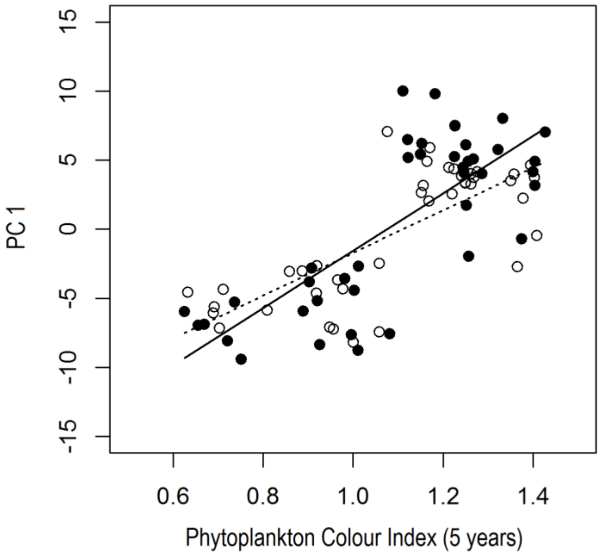

Fig. 2.2. Variation in the first principal component (PC 1) of macroinfaunal taxa densities at Dove station M1 from 1972 to 2012 in relation to pelagic primary production (Phytoplankton Colour Index; averaged over the preceding 5 years (with a 3-month time-lag)). Points for spring are hollow (dashed line) and points for autumn are solid (solid line).

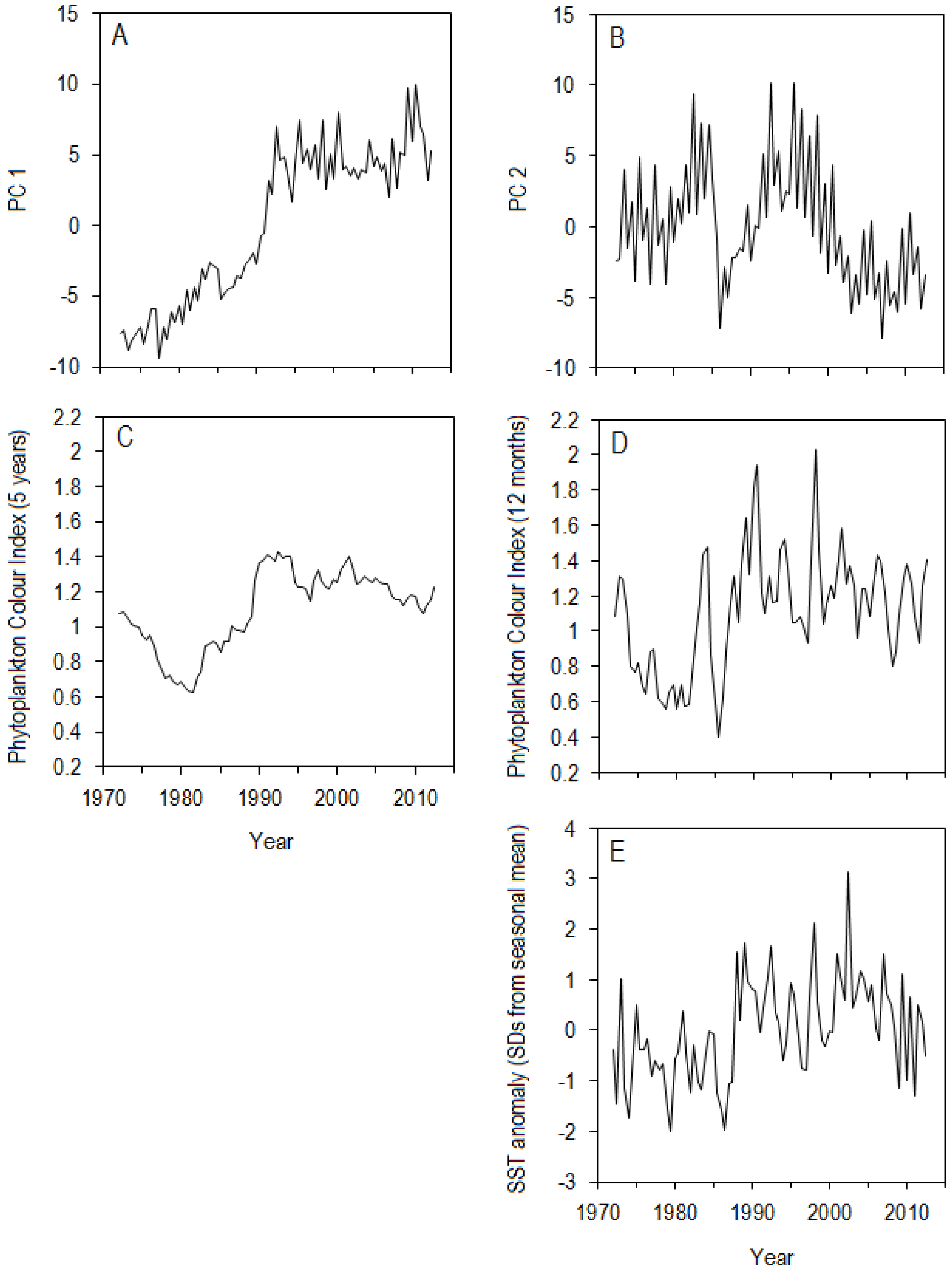

Fig. 2.3. Temporal variation in: (A) the first principal component and (B) the second principal component of macroinfaunal taxa densities at Dove Station M1; (C) pelagic primary production (Phytoplankton Colour Index) averaged over the preceding 5 years; (D) pelagic primary production averaged over 12 months; and (E) standardised sea surface temperature (SST anomalies; standard deviations from the seasonal mean). For (C), pelagic primary production was lagged by 3 months from the end of the 5-year period to the points marked on the graph. For (D), pelagic primary production was lagged by 9 months from the end of the 12 month period to the points marked on the graph.

The species richness of the assemblage abruptly declined in the mid-1980s and then increased following this period (Fig. 2.4a) as the shift from taxa negatively-loaded to taxa positively-loaded on PC 1 occurred. Whichever subset of taxa loaded on PC 1 were abundant at a particular period of time, an increase in their densities tended to be associated with an increase in species richness; however, this relationship was stronger when the densities of positively-loaded taxa increased (i.e. positive PC scores became more positive) than when the densities of negatively-loaded taxa increased (i.e. negative PC scores became more negative) (Fig. 2.4c).

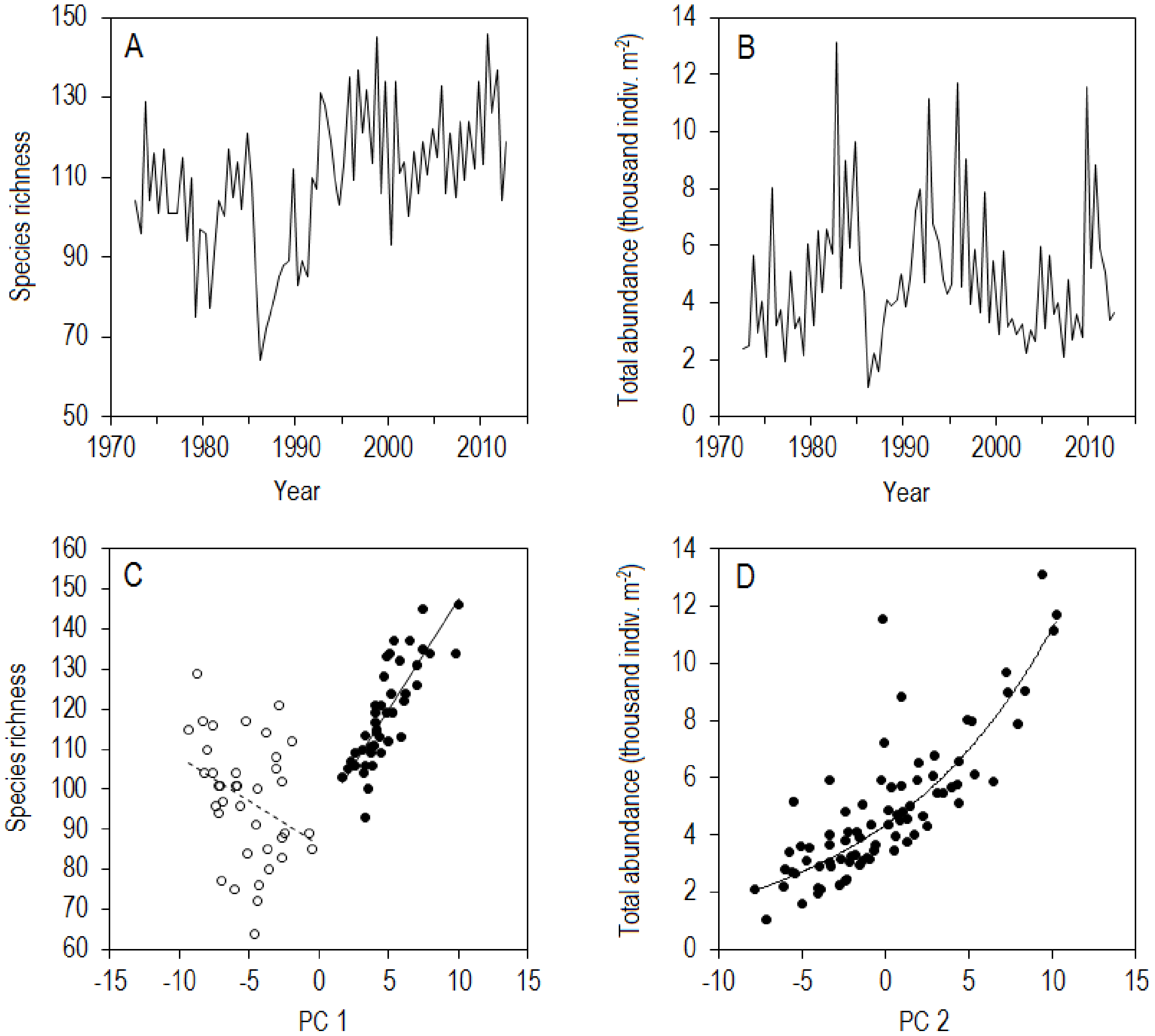

Fig. 2.4. Temporal variation in (A) the total number of species (species richness) and (B) the total number of individuals per m^2 (total abundance) in the macroinfaunal assemblage at Dove Station M1. The relationship between species richness and PC 1 (negative PC scores = hollow points, linear regression: $R^2 = 0.11$; positive PC scores = solid points, linear regression: $R^2 = 0.68$) is shown in (C). The relationship between total abundance and PC 2 (linear regression performed on ln-transformed total abundance: $R^2 = 0.67$) is shown in (D).

PC 2

For PC 2, the top ten taxa with positive loadings and top ten taxa with negative loadings together consisted mainly of annelids (11) and molluscs (6) (Table 2.2). Three other phyla each had one representative (Table 2.2). In contrast to PC 1, the taxa loaded on PC 2 were mainly small and short-lived: eight could reach over 40 mm and only two could reach over 100 mm; eleven out of the seventeen taxa for which longevity information was available have a maximum lifespan of 1–3 years (Table 2.2). The species with the most positive and most negative loadings both had a maximum body length of less than 10 mm (Table 2.2).

The densities of taxa loaded on PC 2 varied significantly over time (Table 2.3). The temporal trend for PC 2 was initially slightly positive and gradually became more negative (Fig. 2.1b), resulting in a long-term increase in the densities of negatively-loaded taxa and decrease in the densities of positively loaded taxa (see Table 2.2). There were, however, no significant second derivatives (i.e. changes to the temporal trend) in the initial model (i.e. the model containing only the (smoothed) time and season terms as explanatory variables; Fig. 2.1b, solid line).

Seasonal variation in the densities of taxa loaded on PC 2 was significant and marked (Table 2.3; Fig. 2.3b), with positively-loaded taxa experiencing a relative increase in autumn and negatively-loaded taxa experiencing a relative increase in spring. PC 2 varied significantly in relation to a negative interaction between pelagic primary production (averaged over 12 months) and standardised SST (PCI*SST; Table 2.3). Warming was associated with an increase in the densities of positively-loaded taxa and a decrease in the densities of negatively-loaded taxa; however, this effect became weaker as the level of pelagic primary production increased (Fig. 2.5).

Both pelagic primary production (averaged over 12 months) and standardised SST abruptly increased in the mid-late 1980s (Fig. 2.3d, e). However, the combined effect of these drivers on the densities of taxa loaded on PC 2 appears to have been small, as the (smoothed) time effect was similar in models with and without their inclusion (Fig. 2.1b).

As with species richness, the total abundance of the assemblage abruptly declined in the mid-1980s (Fig. 2.4b). Patterns in total abundance were generally similar to those observed for taxa loaded on PC 2 (Fig. 2.3b) and correlation revealed a close relationship between these variables; species richness increased exponentially with increasing densities of taxa positively loaded on PC 2 (Fig. 2.4d).

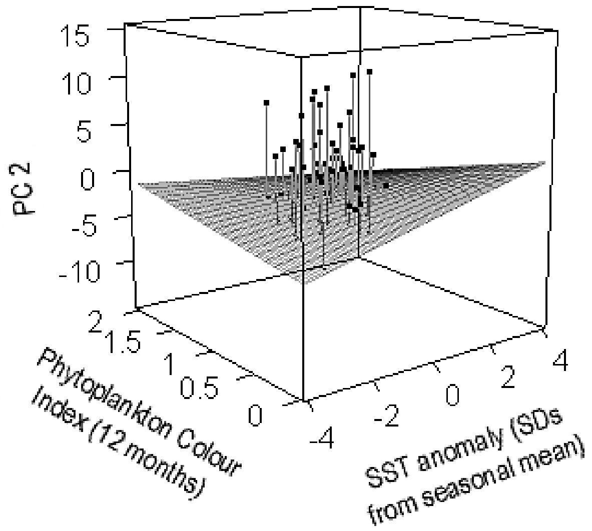

Fig. 2.5. Variation in the second principal component (PC 2) of macroinfaunal taxa densities at Dove Station M1 from 1972 to 2012 in relation to pelagic primary production (Phytoplankton Colour Index; averaged over 12 months (with a 9-month time-lag) and standardised sea surface temperature (SST anomalies; standard deviations from the seasonal mean). The 3D surface is based on the predicted values from a model containing each term and their interaction. 'Season' was set to "spring". The points represent the actual observations and the lines connecting the points to the 3D surface represent the residuals.

DISCUSSION

While abrupt shifts in ecosystems are now well-documented (see Möllmann et al. 2015), their causes are poorly understood. The main aim of this study was to test for changes to the temporal trends of biota in a natural ecosystem and determine whether they could be explained by underlying patterns in primary production and temperature. Changes to the temporal trend were identified for a subset of a benthic faunal assemblage (the taxa loaded on the first principal component) and resulted in a shift in species composition. These changes were explained by variation in pelagic primary production and, hence, detrital food input to the seabed. In contrast, taxa loaded on the second principal component of the assemblage did not experience any significant alterations to their temporal trend, but did show significant long-term change in relation to pelagic primary production and SST.

The onset of the shift in the taxa loaded on PC 1 occurred during a prolonged positive phase of the North Atlantic Oscillation Index (NAOI), during which Atlantic inflow to the North Sea, SST and pelagic primary production all increased (Beaugrand 2004). Various other biological components abruptly changed in their composition during this period, from phytoplankton (Reid et al. 1998) through to zooplankton (Beaugrand et al. 2002) and fish (Reid et al 2001; Beaugrand et al. 2003). The present study may therefore reveal within the benthic component of the ecosystem a signal of a multi-trophic level regime shift. Indeed, previous studies have reported local alterations to the density and diversity of the North Sea benthos during this period, and have attributed their results to climate variability (e.g. Kröncke et al. 1998; Kröncke 2011; Kröncke et al. 2013). Analyses conducted here build on these findings by explicitly demonstrating changes to the temporal trends of biota and providing some indication of the relative importance of different extrinsic factors in driving their dynamics.

The apparent role of pelagic primary production in driving the compositional shift is consistent with other studies that show detrital input to be an important driver of faunal assemblages (Moore et al. 2004), including those focused on the benthos (e.g. Levinton & Kelaher 2004; Ruhl & Smith 2004; Walther & Whiles 2011; Weigel et al. 2015). Previous analyses of the dataset used in this study suggest that the seabed was a food-limited environment prior to the increase in pelagic primary production in the mid-late 1980s (Buchanan 1993; Frid et al. 1996). As such, the taxa that subsequently increased in density (those positively loaded on PC 1) may have been able to utilise the enhanced food input to increase survival and/or reproduction (Silby & Hone 2002), whereas the taxa that decreased in density may have gained a competitive advantage when food supply was low (see Ruhl & Smith 2004). That the relationship between PC 1 and pelagic primary production was more positive in autumn than in spring (Fig. 2.2) suggests that the effect of changes to detrital input is weakened over winter, possibly because species that are abundant under a particular level of detrital input experience a degree of density-dependent mortality during this period of the year.

Regarding the dynamics of taxa loaded on PC 2, the negative interaction between pelagic primary production (averaged over 12 months) and standardised SST suggests that the effect of warming on these organisms was mitigated by an increase in food input. Experiments have shown that metabolism and food consumption increase in animals when they are subjected to higher temperatures (O'Connor et al. 2009; Carr & Bruno 2013; Seifert et al. 2014). It therefore follows that species densities may only be affected by warming when there are insufficient food resources available to sustain the associated increase in metabolic demand, as suggested by the results of this study. Another experiment found that the impact of warming on consumption rate was greater for a small species than for a large species of terrestrial beetle (Lang et al. 2012), reflecting a greater effect of temperature on the metabolism of the smaller species. This may explain why the mainly small taxa loaded on PC 2 experienced relatively little long-term variation in relation to a negative interaction between pelagic primary production and SST, whereas the mainly large taxa loaded on PC 1 responded only to changes in pelagic primary production and experienced a shift in species composition when the levels of both extrinsic factors increased.

A sensitivity of taxa loaded on PC 2 to environmental fluctuations is possibly reflected by their prominent seasonal variability. Some of the earliest analyses of the dataset used in this study reported that small, abundant species exhibited a marked seasonal cycle of summer population growth followed by winter die-off (Buchanan et al. 1978; Buchanan et al. 1986; Buchanan 1993; Frid et al. 1996). At different points during the first two decades of the time series, some of these populations (including taxa positively-loaded on PC 2, e.g. *Pholoe inornata* and *Levinsenia gracilis*) appeared to be affected by SST and/or pelagic primary production, which was also reflected in the total abundance of the assemblage (Buchanan et al. 1978; Buchanan et al. 1986; Buchanan 1993; Frid et al. 1996). These effects were mainly apparent in spring, possibly pointing to the importance of temperature and food input in determining winter survival. However, when the North Sea became warmer and more productive later in the time series, the apparent effect of these extrinsic drivers on the spring assemblage largely disappeared (Frid et al. 2009a). The novel analyses presented here suggest that a single mechanism, i.e. a mitigating effect of high primary productivity on the ecological impacts of changing SST, may explain these previous observations.

While correlative analyses such as the one conducted for this study cannot demonstrate causality, the results leave no reason to postulate alternative explanations for the observed community dynamics. The results are also consistent with theory and experimental findings. As such, there are reasons to be confident that the inferred mechanisms are valid. Pelagic primary production is under climatic influence (Behrenfield et al. 2006; Boyce et al. 2010; Blanchard et al. 2012) and is therefore likely to be affected by ongoing climate change. Future changes to North Sea pelagic primary production will allow us to scrutinize its apparent influence over the large and long-lived taxa studied here (i.e. those loaded on PC 1) and determine whether our interpretation remains viable. Likewise, if our interpretation is viable, then any future reductions in pelagic primary production should make the small and short-lived taxa (i.e. those loaded on PC 2) more responsive to temperature variation. Being able to explain long-term patterns in biological assemblages using proposed drivers is essential if we are to predict the impacts of future environmental change. The results of this study suggest that abrupt shifts in assemblages may, at least in some cases, be foreseeable based on projected changes to extrinsic factors.

ACKNOWLEDGEMENTS

Thanks must first go to Jack Buchanan, who started the time series used in this study. I also thank the masters and crew of the *RV Bernicia* and *RV Princess Royal*, Peter Garwood and staff at the Dove Marine Laboratory for their efforts in data collection.

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Chapter 3

Community variability and ecological functioning: 40 years of change in the North Sea benthos

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Published in *Marine Environmental Research* (2015), 107: 24–34.

ABSTRACT

Using established associations between species traits (life history, morphological and behavioural characteristics) and key ecological functions, I applied biological traits analysis (BTA) to investigate the consequences of 40 years of change in two North Sea benthic communities. Ecological functioning (trait composition) was found to be statistically indistinguishable across periods that differed significantly in taxonomic composition. A temporary alteration to functioning was, however, inferred at both sampling stations; coinciding with the North Sea regime shift of the 1980s. Trait composition recovered after one year at the station located inside the grounds of a trawl fishery, whereas the station located outside the main area of fishing activity underwent a six-year period of significantly altered, and temporally unstable, trait composition. A further alteration to functioning was inferred at the fished station, when the population of a newly established species rapidly increased in numbers. The results suggest that density compensation by characteristically similar (redundant) taxa acts to buffer changes to ecological functioning over time, but that functional stability is subject to aperiodic disruption due to substitutions of dissimilar taxa or uncompensated population fluctuations. The rate at which ecological functioning stabilises and recovers appears to be dependent on environmental context, e.g. disturbance regime.

INTRODUCTION

The composition of species assemblages varies temporally in response to natural and anthropogenic drivers (Gonzalez & Loreau 2009). Experimental evidence suggests that such changes to biodiversity can alter the functioning of ecosystems and the provision of ecosystem services to society (Hooper et al. 2005). However, long-term empirical studies on ecological functioning are rare, and the available data are derived mainly from assemblages that have had aspects of their biodiversity manipulated and maintained over time (Hector et al. 2010). Therefore, the impacts of long-term community variability on the functioning of natural ecosystems are yet to be discerned.

In lieu of empirical data, indirect methods can be used to assess how changes to biodiversity affect ecological functioning. Biotic control over ecosystem processes is largely determined by the abundance and functional characteristics (i.e. 'effect traits'; *sensu* Lavorel & Garnier 2002) of the constituent species (Chapin et al. 1997). Therefore, when taxonomic composition is altered, the associated change in effect trait composition can be used to predict changes in ecological functioning (Bremner 2008; Mouillot et al. 2011) and ecosystem service provision (Diaz et al. 2007).

It is recognised that where multiple species with shared effect traits coexist — i.e. there is functional redundancy (Walker 1992) — the impact of population loss on ecological functioning may be buffered by compensatory population growth of characteristically similar taxa (Naeem 1998). If such 'species substitutions' occur, then effect trait composition would experience little change over time despite alterations to taxonomic composition. However, the capacity for functional compensation depends on the extent to which characteristically similar taxa differ in their responses to environmental variability (Gonzalez & Loreau 2009). If similar taxa show similar responses, then effect trait composition will vary temporally due to uncompensated population fluctuations or substitutions of dissimilar taxa. It is currently unclear what effect long-term changes in taxonomic composition have on effect trait composition, or whether the degree of association between these two ecological properties varies over time.

In the central-western North Sea, two benthic stations (M1 & P) have been sampled annually for over 40 years. The composition of macroinfauna has changed over time at both stations in relation to multiple environmental factors. Shifts in community structure have been reported at M1 (Frid et al. 2009a; **Chapter 2**), with fluctuations in detrital input and sea temperature apparently destabilising the assemblage (Buchanan & Moore 1986; Buchanan 1993; **Chapter**

2). At P, temporal variability appears to have been influenced by heavy trawling activity during the 1980s; evidenced by patterns in taxa abundances (Frid et al. 1999; Frid et al. 2009b) and traits that determine species sensitivity to disturbance (i.e. 'response traits'; *sensu* Lavorel & Garnier 2002) (Bremner et al. 2003a; Bremner et al. 2005). A recent trait-based analysis, which focussed on the most temporally variable taxa, also suggests that functional delivery at the sites has varied over time; mainly due to changing aggregate density as characteristically dissimilar taxa fluctuated in synchrony (Frid 2011).

Here, temporal variability in the benthos at stations M1 and P was assessed using traditional analysis of taxonomic composition in tandem with biological traits analysis (BTA; Townsend & Hildrew 1994; Bremner et al. 2003b). For BTA, I focused on the composition of effect traits that link macroinfauna to the delivery of key ecological functions (see Tables 3.1 & 3.2). I aimed to: 1) identify years in which abrupt changes to taxonomic composition occurred, 2) compare changes in taxonomic and trait compositions in these years, and 3) assess patterns in taxonomic and trait compositions across periods divided by these years. I took concurrent changes in taxonomic and trait compositions to be indicative of either substitutions of characteristically dissimilar taxa or uncompensated population fluctuations. Changes to taxonomic composition alone were taken to imply functional compensation. If trait composition changed significantly across periods, I inferred the potential consequences for ecological functioning. An increase or decrease in the number of individuals exhibiting a modality was taken as evidence for potentially enhanced or reduced levels of associated functions, respectively.

Table 3.1. Life history, morphological and behavioural traits (and codes) used to describe the functional composition of macroinfauna at Dove stations M1 and P. Modalities represent the different categories that taxa can exhibit for each trait.

Trait (code)	Modalities
Lifespan (A)	< 1 yrs 1 - 2 yrs 3 - 10 yrs > 10 yrs
Maximum body length (B)	< 10 mm 10 - 29 mm 30 - 100 mm > 100 mm
Protective structure (C)	Tubiculous Shelled Unprotected
Mobility within sediment (D)	Sessile Limited Slow movement Free movement
Burrow ventilation mode (E)	Blind-ended burrow Open-ended burrow No ventilation
Sediment reworking mode (F)	Diffusive Upward conveyor Downward conveyor Regenerator Surficial modifier
Feeding mode (G)	Deposit Suspension Scavenger Predator Parasite
Life zone (H)	Surface Shallow (< 5 cm) Intermediate (5 - 10 cm) Deep (> 10 cm)
Epibenthic habitat modification (I)	Cast or mound Burrow ditch/hollow Emergent structure No modification

Table 3.2. Six ecological functions performed by macroinfaunal species and the trait modalities that drive them. References that demonstrate the links between traits and functions are numbered in superscript.

Ecological function	Trait	Modalities
Nutrient regeneration	Feeding mode	Deposit feeder[1], Suspension feeder[1]
	Sediment reworking mode	Upward conveyor[1], Regenerator[2]
	Burrow ventilation mode	Blind-ended[1, 3], Open-ended[1, 3, 4]
	Maximum body length	10-29 mm[5], 30-100 mm[5, 6], >100 mm
	Life zone	Intermediate[4], Deep[2]
	Mobility within sediment	Free movement[7, 8]
Carbon turnover	Maximum body length	< 10 mm[9]
	Lifespan	< 1 yrs
Carbon sequestration	Feeding mode	Suspension feeder[1]
	Sediment reworking mode	Downward conveyor[1]
	Protective structure	Shelled[10]
	Maximum body length	>100 mm[9]
	Lifespan	> 10 yrs
Food for fish	Maximum body length	10-29 mm, 30-100 mm, 100 mm
	Life zone	Surface, Shallow
	Protective structure	None
Reef-formation	Epibenthic habitat modification	Emergent structure
Sediment heterogeneity	Epibenthic habitat modification	Cast or mound, Burrow ditch/hollow

References: [1]Welsh (2003), [2]Norling et al. (2007), [3]Braeckman et al. (2010), [4]Mermillod-Blondin et al. (2004), [5]Thrush et al. (2006), [6]Norkko et al. (2013), [7]Day et al. (1989), [8]Solan et al. (2004), [9]Brown et al. (2004), [10]Lee et al. (2010)

MATERIALS AND METHODS

Study sites

Station M1 is located 10.5 km off the Northumberland coast (55°04’ N, 01°20’ W) and sits under 55m of water in predominantly sandy sediment with 20 % silt-clay content. Station P is located 18.5 km offshore (55°07' N, 01° 15' W) and is 80 m deep in sediment with > 50 % silt-clay content, around 20% of which is faecal pellets. Station P lies inside a *Nephrops* fishing ground while station M1 lies outside the main area of fishing activity (Fig. 3.1). Both stations are located away from local river discharges.

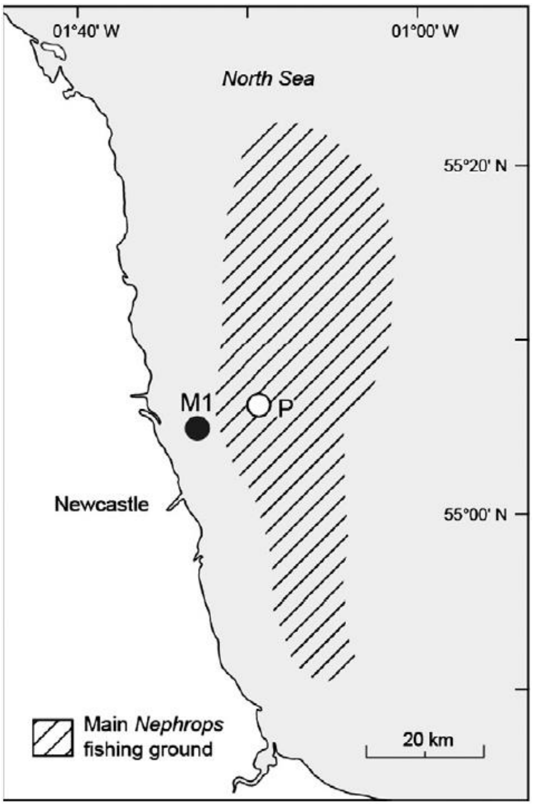

Fig. 3.1. Location of Dove stations M1 and P in relation to the grounds of a *Nephrops* fishery in the central-western North Sea.

Benthic community time series

Sampling of benthic macroinfauna began in January 1971 at P and September 1972 at M1. Subsequently data have been collected once a year in January/February at P and twice a year in March/April (spring) and September/October (autumn) at M1. In this study I consider two time series: one consisting of samples collected at M1 in spring and the other consisting of all samples collected at P. Data are missing for 1977 and 1998 at P and for 1998 and 2004 at M1, as weather conditions and/or operational constraints prevented sampling.

Samples were extracted using Van Veen grabs (0.1 m^2). Each sample was sieved over 0.5 mm mesh and the residue fixed with 4% buffered formalin. Organisms were identified to the lowest taxonomic level possible and enumerated. Sampling methods are described in detail in Buchanan & Warwick (1974). Information on sampling effort over time is provided in the Supplementary Material (Appendix 3.1).

Assembling community datasets

Taxonomic composition

Prior to collation of taxa abundance data, nomenclature was checked and updated, and synonymous taxa were merged under currently accepted names. Data were assembled at the lowest taxonomic level possible to minimise loss of information (over 70% of taxa in each time series were recorded at species level). Each year, population densities across all replicate samples were standardised to the number of individuals per square metre.

Previous trait analyses of the Dove benthic time series have used subsets of the community datasets, focussing either on dominant taxa (Bremner et al. 2003a; Bremner et al. 2005) or taxa that contributed most to temporal variation in community structure (Frid 2011). Here, taxa that made up $\geq$ 0.1% of total abundance over the entire time series, or occurred at a density of at least 10 individuals m^{-2} in a single year, were retained in the taxonomic dataset. Taxa that were consistently rare were removed (see Supplementary Material, Appendix 3.1). Using this approach at least 98% of total abundance was represented each year at both stations.

Trait composition

Nine biological traits were chosen for analysis; reflecting the life history, morphology and behaviour of taxa (Table 3.1). Traits were selected to cover a suite of characteristics that are empirically demonstrated or logically deduced to drive six key ecological functions (Table 3.2). As such, changes in the prevalence of these characteristics within communities imply changes to the potential levels of associated functions.

To represent species characteristics each trait was divided into modalities (categories; Table 3.1). For example, ‘feeding mode’ was divided into: deposit feeder, suspension feeder, predator, scavenger and parasite. Information on the modalities taxa exhibit was derived from the MarLIN open-access trait database (http://www.marlin.ac.uk/biotic/biotic.php) and a trait database compiled by staff from the Norsk Institutt for Vannforskning (NIVA). Literature searches and expert consultation were used to corroborate and fill in gaps in information. Where species-specific trait information was unavailable, modalities were inferred using well-studied, closely-related taxa.

All individuals retained in the taxonomic datasets were used to create trait datasets. Taxa were coded to represent their affinities to modalities within each trait, ranging from 0 to 1. For example, an obligate predator was coded 1 for predator and 0 for all other modalities within ‘feeding mode’, whereas a species that either deposit feeds or suspension feeds with equal probability was coded 0.5 for both of these modalities and 0 for all others. This ‘fuzzy coding’ procedure (Chevenet et al. 1994) accounts for phenotypic plasticity within species as well as phenotypic variability across species when using higher taxonomic levels. The annual abundance of each taxon was then multiplied by its affinity to the suite of trait modalities (across all nine traits), and the number of individuals exhibiting each modality was totalled across taxa. The resulting trait-by-year time series is analogous to the taxa-by-year time series, with densities of trait modalities replacing taxa abundances.

Data analysis

Taxa abundances were not transformed prior to analysis as I was interested in like-for-like changes in taxonomic and trait compositions, with all individuals accounted for. This approach assumes that contribution to function increases with population density and, therefore, that dominant taxa dominate function (see Grime 1998).

Line graphs of Bray-Curtis similarity to the preceding year were used to show year-to-year variability in taxonomic and trait compositions, which were compared to assess the degree of functional compensation. Additional line graphs of year-to-year percentage change in the total number of species (species richness), total abundance, and the densities of the ten dominant taxa were used to distinguish between substitutions of dissimilar taxa and uncompensated population fluctuations when trait composition showed a high degree of change. If data were missing for a year, then values the following year were calculated with respect to two years prior; e.g. 1999 against 1997.

The time series were divided into periods of stability and instability. ‘Break points’, that mark the start of a new period, were assigned to years in which there was an abrupt change to taxonomic composition (< 60% similarity to the preceding year) that was preceded or followed by ≥ 5 consecutive years of relatively-low temporal variability (each year showing ≥ 60% similarity to the preceding year). Non-metric multidimensional scaling (nMDS) ordinations were used to assess temporal variation in taxonomic and trait compositions. Statistical analyses of changes to taxonomic composition across periods were performed using ANOSIM in PRIMER v6 (Primer-E Ltd, Plymouth, UK). The same approach was applied to trait composition for BTA (Bremner et al. 2005; Neumann & Kröncke 2011). A significant difference was taken as $p < 0.05$.

Variation in the species richness and total abundance across periods were analysed using the Kruskal-Wallis (KW) test in SPSS 20, with pairwise differences between periods tested using the Mann-Whitney (MW) U-test. Data were transformed to meet the assumption of homogenous variance when required. Changes to total S and total N were used to interpret patterns in taxonomic and trait compositions, rather than constituting distinct hypotheses. Therefore, we did not apply statistical corrections for multiple testing. I present results for species richness and total abundance with all individuals accounted for. Excluding from these univariate analyses rare taxa that were removed for the multivariate analyses had a minor effect on *p* and no effect on statistical significance.

SIMPER in PRIMER v6 was used to identify modalities that contributed most to dissimilarity across periods that were significantly different in trait composition. The densities of the top six contributing modalities were then analysed statistically across periods using the KW and MW tests. No statistical correction was applied as these analyses were aimed at identifying changes implied by BTA. To skew the weighting toward less common modalities, which may be relatively variable and thus contribute to observed changes in trait composition across periods, SIMPER was performed after transforming modality densities by ln (x+1), followed again by analysis of top six contributors to dissimilarity using KW and MW tests. Differences in the densities of trait modalities across periods were analysed without transformations (unless required to meet test assumptions). When top contributors to dissimilarity differed depending on the period of comparison, modalities that were most frequently among the top six in the pairwise comparisons were selected for analysis.

RESULTS

Station M1

On average 100 taxa and 3700 individuals m^{-2} were recorded each year at M1. Total S and total N reached series lows of 64 and 1044 (both in 1986) and peaked at 128 (in 1993) and 7212 (in 1991), respectively. The ten dominant taxa over the duration of the time series accounted for over half of the total abundance, and consisted of six polychaetes, three bivalves, and an ophiuroid (see Supplementary Material, Table 3.7). The most common trait modalities included deposit feeding, shallow life zone, limited mobility and slow movement within the sediment (see Supplementary Material, Table 3.7). Short body length (10 - 29 mm) and short lifespan (1 - 2 years) were also prevalent. No sediment reworking mode was particularly common, but blind-ended burrow ventilation was often exhibited. Individuals that did not ventilate burrows were also common, and the majority of individuals present lacked a protective structure and did not add structural heterogeneity to the seabed.

Abrupt changes to taxonomic composition (< 60% similarity to the previous year; preceded or followed by ≥ five consecutive years of ≥ 60% similarity) were identified for the years 1986, 1992 and 2005 (Fig. 3.2a). Among these 'break points', change to taxonomic composition was most pronounced in 1986 (30% similarity to 1985); the only year of the three in which trait composition showed a similar degree of change (also 30% similarity to 1985; Fig 3.2a). Large declines in species richness (40% loss) and total abundance (80% loss) (Fig 3.2c), and reduced densities of dominant taxa (nine taxa declined and one remained stable; i.e. abundance changed by < 50 individuals m^{-2}; Fig 3.3a,b), indicate an uncompensated collapse of populations and associated functions in 1986. In 1992 and 2005 there was evidence for functional compensation; trait composition showed little change from the previous year (~80% similarity; Fig. 3.2a) and dominant taxa exhibited mixed responses (seven declined, two increased and one remained stable in 1992; two declined, four increased and four remained stable in 2005; Fig. 3.3a,b). Species richness increased by 25% from 1991 to 1992 as total abundance declined by 35% (Fig. 3.2c). In 2005 species richness increased by 10% and total abundance increased by 40% (Fig. 3.2c); however, as no data are available for 2004 these results represent net changes over two years (2003-05).

While acknowledging that, had it been available, the inclusion of 2004 data might affect the designation of 2005 as a break point, the time series was divided into four periods with respect to the three apparently abrupt changes in taxonomic composition: 1973-1985, 1986-1991, 1992-2003 and 2005-12. During 1986-91 there were short-term fluctuations in taxonomic composition (1986, 1988 and 1991 were all < 60% similar to preceding years; Fig. 3.2a), while trait composition fluctuated from 1986-88 (1986 and 1988 were < 60% similar to preceding years) but remained relatively stable between the years 1989-91 (all were ≥ 60% similar to preceding years; Fig. 3.2a). The periods 1973-85 and 1992-2003 were characterised by taxonomic and functional stability (all years were ≥ 60% and > 75% similar to the preceding year for taxonomic and trait compositions, respectively; Fig. 3.2a). Temporal variability increased again during 2005-12, with multiple years showing < 60% similarity to the preceding year in taxonomic composition, while year-to-year similarity in trait composition dropped to below 75% in 2007 (for the first time since 1992) and again in 2009 and 2012 (Fig. 3.2a).

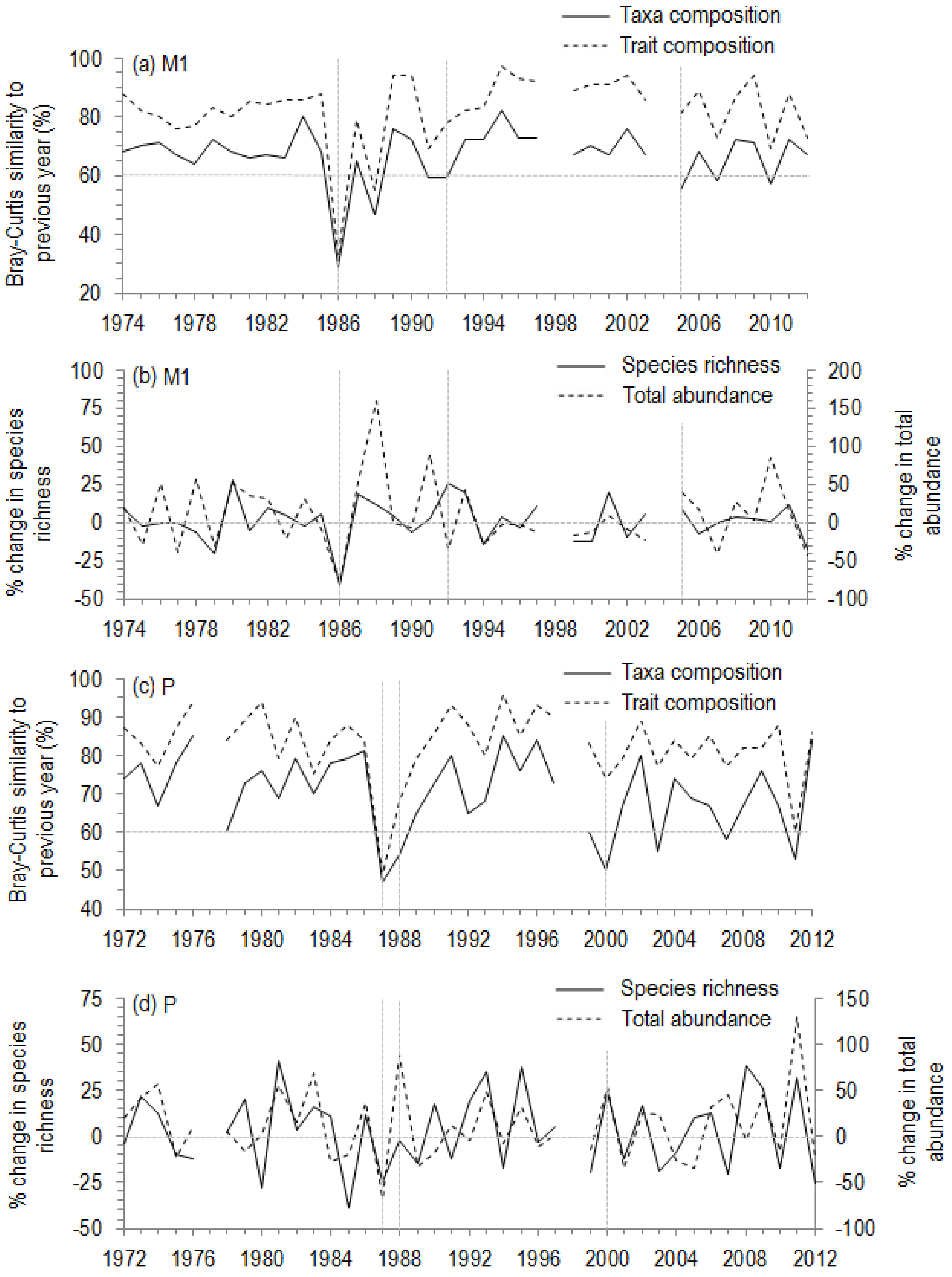

Fig. 3.2. Bray-Curtis similarity to the previous year in taxonomic and trait compositions (**a**, **c**) and species richness and total abundance (**b**, **d**) of macroinfauna at Dove stations M1 (**a**, **b**) and P (**c**, **d**). Abrupt changes in taxonomic composition (< 60% similarity to previous year, preceded or followed by ≥ five years of year-to-year stability) are marked by vertical grey dashed lines.

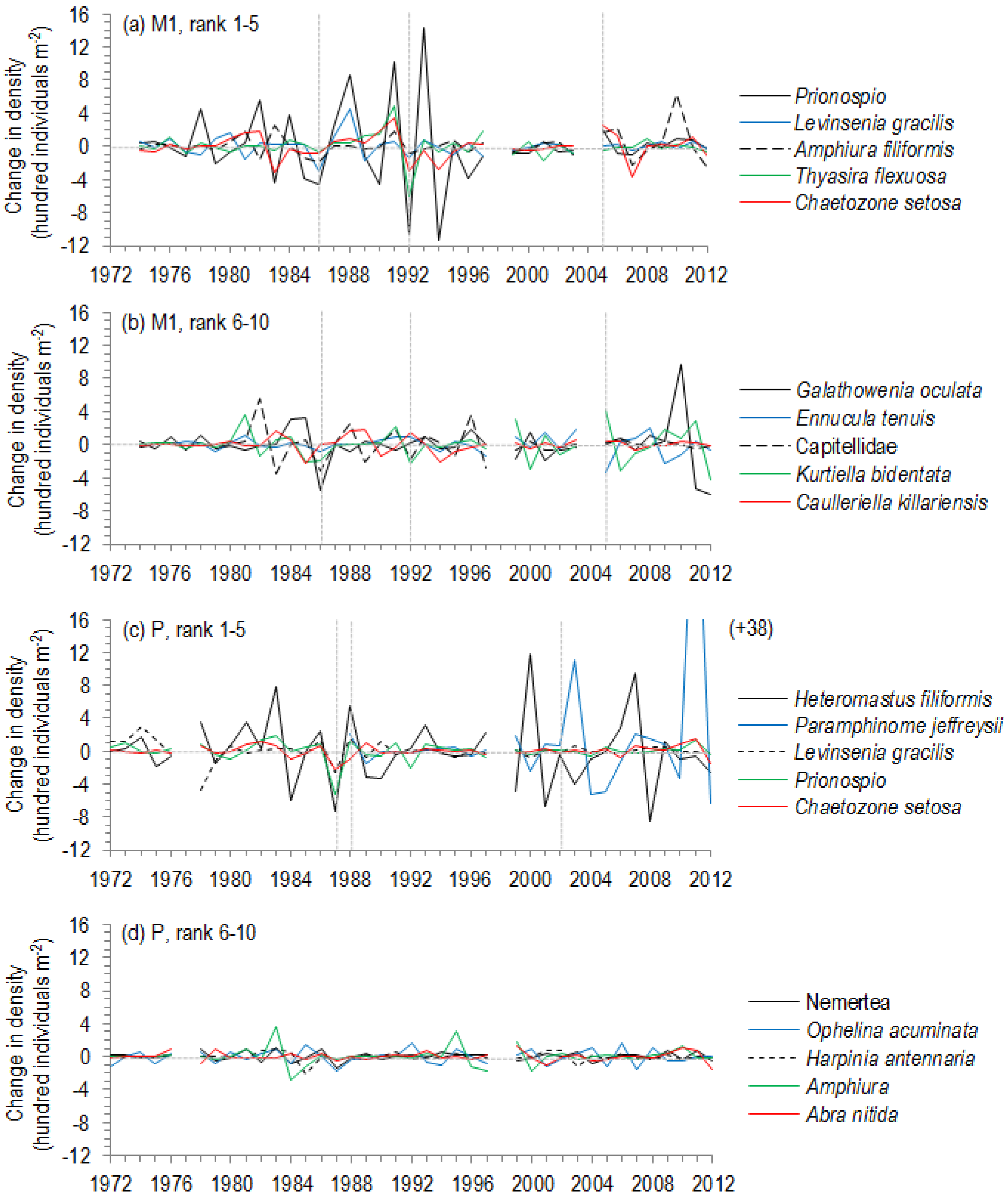

Fig. 3.3. Change in abundance from the previous year of the ten dominant macroinfaunal taxa at Dove stations M1 (rank 1-5 (**a**), rank 6-10 (**b**)) and P (rank 1-5 (**c**), rank 6-10 (**d**)). Abrupt changes in taxonomic composition (see Fig. 3.2) are marked by vertical grey lines.

Taxonomic composition was significantly different across all periods (Table 3.3; Fig. 3.4a), while only 1986-91 differed significantly from other periods in terms of trait composition (Table 3.3; Fig. 3.4c). Species richness was significantly lower during 1986-91 compared to other periods (Table 3.3; Fig. 3.5a); however, there were no significant differences in total abundance (Table 3.3; Fig. 3.5c). Compositional changes were therefore driven by shifts in relative taxa abundances, with substitutions of characteristically dissimilar taxa occurring during 1986-91 – when the community was relatively species-poor – and substitutions of similar taxa (functional compensation) occurring across other periods.

No individual modalities identified by SIMPER (using untransformed data) emerged as clear drivers of changes to trait composition during 1986-91 ($p > 0.05$; Table 3.4). This was due to high within-period variation in these modalities, which were each among the most commonly exhibited by the taxa (See Supplementary Material, Table 3.7). Using transformed modality data, two of the six modalities identified (sediment regenerator and < 1 years lifespan) occurred at significantly different densities in 1986-91 compared to other periods (Table 3.4). Declines in these modalities during 1986-91 predict reduced rates of nutrient regeneration and carbon turnover, respectively (Table 3.2).

Table 3.3. Differences in taxonomic composition (ANOSIM: Global R = 0.554), trait composition (ANOSIM: Global R = 0.112), species richness (Kruskal-Wallis: H = 24.000) and total abundance (Kruskal-Wallis: H = 0.846) of macroinfauna at Dove station M1 across periods divided by abrupt changes in taxonomic composition. A significant difference (in bold) was taken as $p < 0.05$. The R statistic for pairwise comparisons of taxonomic composition and trait composition are in brackets.

	P	1973-85 vs. 1986-91	1973-85 vs. 1992-2003	1973-85 vs. 2005-12	1986-91 vs. 1992-2003	1986-91 vs. 2005-12	1992-2003 vs. 2005-12
Taxa comp.	**< 0.001**	**0.004** **(0.366)**	**< 0.001** **(0.553)**	**< 0.001** **(0.709)**	**< 0.001** **(0.470)**	**0.002** **(0.701)**	**< 0.001** **(0.585)**
Trait comp.	**0.030**	**0.040** **(0.218)**	0.150 (0.053)	0.323 (0.015)	**0.042** **(0.244)**	**0.043** **(0.217)**	0.178 (0.064)
Species richness	**< 0.001**	**0.003**	**0.004**	**< 0.001**	**0.001**	**0.002**	0.709
Total abundance	0.838	-	-	-	-	-	-

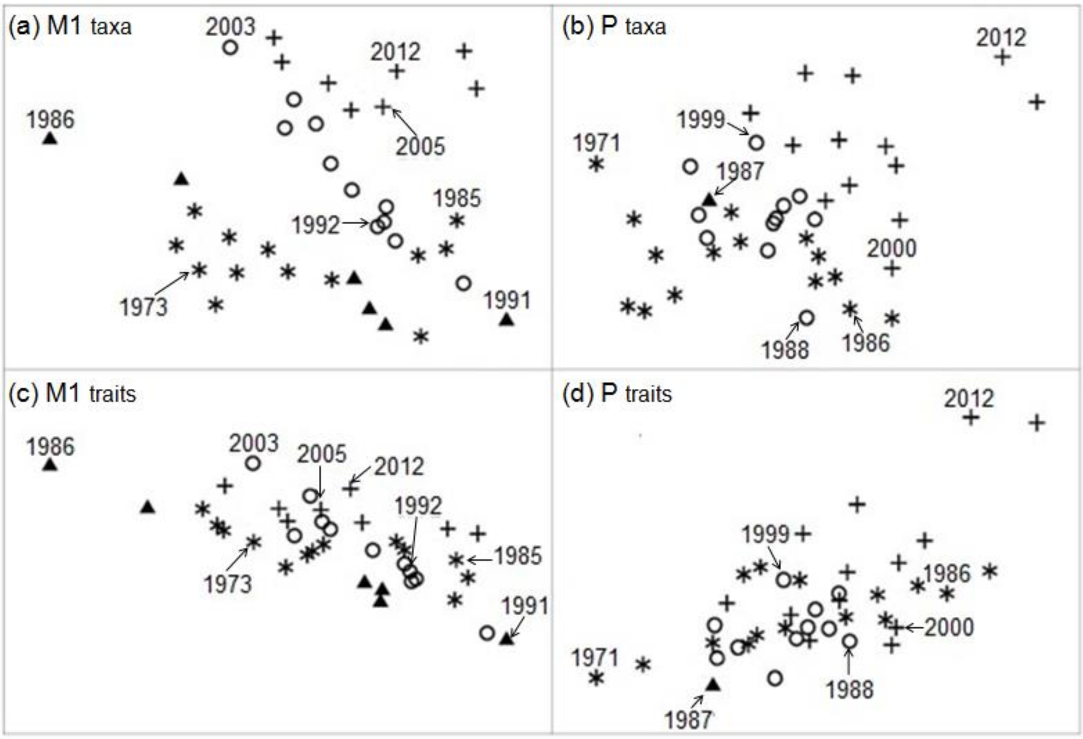

Fig. 3.4: nMDS ordinations of temporal variation in taxonomic composition (**a**, **b**) and trait composition (**c**, **d**) of macroinfauna at Dove stations M1 (**a**, **c**) and P (**b**, **d**). Periods are divided by abrupt changes in taxonomic composition (see Fig. 3.2): 1973-85 ✱, 1986-91 ▲, 1992-2003 ○ and 2005-12 + for M1; 1971-86 ✱, 1987 ▲, 1988-99 ○ and 2000-12 + for P. First and last years of periods are labelled. 2D stress = 0.16 (**a**), 0.13 (**b**), 0.04 (**c**) & 0.04 (**d**).

Station P

An average of 60 taxa and 2500 individuals m^{-2} were recorded each year at P. The lowest species richness recorded in any year was 35, in 1989, and the highest was 95, in 2011. Total abundance was at a series low of 825 in 1971 and peaked at 7960 in 2011. As at M1, polychaetes dominated the community at P; making up all of the five dominant taxa and six of the top ten (see Supplementary Material, Table 3.8). Other dominant taxa included an amphipod, a bivalve, an ophiuroid, and members of the phylum Nemertea. Together these taxa made up 70% of total abundance. Nine of the ten most common trait modalities exhibited by taxa at M1 were also among the top ten at P, the only difference being the replacement of blind-ended burrow ventilation by maximum body length of > 100 mm (see Supplementary Material, Table 3.8). The high density of the latter at P was due to the dominance of the threadlike capitellid *Heteromastus filiformis* (Claparède).

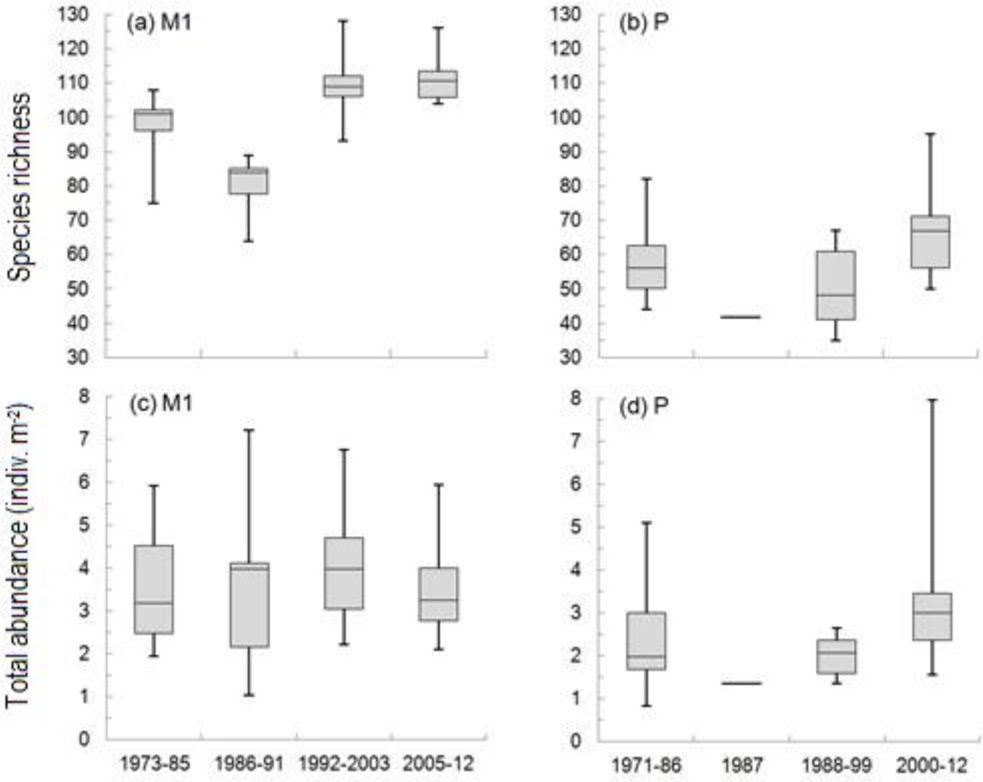

Fig. 3.5. Median, interquartile range and minimum and maximum values for species richness (**a**, **b**) and total abundance (**c**, **d**) of macroinfauna across periods divided by abrupt changes in taxonomic composition (see Fig. 3.2) at Dove stations M1 (**a**, **c**) and P (**b**, **d**).

Break points (< 60% similarity in taxonomic composition to the previous year; preceded or followed by ≥ five consecutive years of ≥ 60% similarity) were assigned to 1987, 1988 & 2000. Only the first was associated with a similarly large change in trait composition (~50% similarity to 1986; Fig. 3.2b). Species richness and total abundance both declined in 1987 (by 25% and 70%, respectively; Fig. 3.2d), as did the densities of dominant taxa (nine declined and one remained stable; Fig. 3.3c,d); indicating an uncompensated collapse of populations and associated functions. Total abundance recovered somewhat in 1988 (90% increase; Fig. 3.2d), as four of the five dominant taxa increased in numbers (including the first recording of *Paramphinome jeffreysii* (McIntosh); *Chaetozone setosa* (Malmgren) decreased in numbers) and the remainder of the top ten remained stable (Fig. 3.3c,d). Species richness, on the other hand, declined by just 2% (Fig. 3.2d) and trait composition in 1988 was 68% similar to 1987 (Fig. 3.2b). In 2000 there was evidence for functional compensation, as trait composition remained 75% similar to 1999 (Fig. 3.2b) and dominant taxa showed mixed responses (three decreased, two increased and five remained stable; Fig. 3.3c,d). From 1999 to 2000 species richness and total abundance increased by 25% and 55%, respectively (Fig. 3.2d).

Table 3.4. Differences in the number of individuals exhibiting twelve trait modalities in 1986-91 compared to other periods at Dove station M1. The analysed modalities were identified as top contributors to compositional dissimilarity using untransformed data (above double-border) and ln (x+1) transformed data (below double-border). Significant differences ($p < 0.05$) identified using Kruskal-Wallis tests are in bold. Changes to mean density are presented for modalities that differed significantly across periods. See Table 3.1 for list of traits matched to trait codes.

				1986-91 *vs*		
Trait code	Modality	H	*P*	1973-85	1992-2003	2005-12
(I)	No modification	1.133	0.769	-	-	-
(G)	Deposit	2.550	0.466	-	-	-
(H)	Shallow (< 5 cm)	0.375	0.945	-	-	-
(D)	Limited	2.309	0.511	-	-	-
(A)	1-2 yrs	1.419	0.701	-	-	-
(E)	Blind-ended burrow	0.651	0.885	-	-	-
(F)	Regenerator	13.039	**0.004**	**-4.8**	**-11.7**	**-6.1**
(I)	Cast or mound	5.272	0.153	-	-	-
(F)	Upward conveyor	4.369	0.224	-	-	-
(A)	< 1 yrs	8.720	**0.033**	**-166.6**	**-204.0**	**-245.3**
(F)	Downward conveyor	0.735	0.735	-	-	-
(B)	> 100 mm	7.441	0.059	-	-	-

The time series was divided into four periods for analysis: 1971-86, 1987, 1988-99 and 2000-12. Both taxonomic and trait compositions showed year-to-year stability during the periods 1971-86 and 1988-99 (≥ 60% and > 75% similarity, respectively), which were separated only by a brief fluctuation in both ecological properties in 1987 (Fig. 3.2b). Temporal variability in taxonomic composition increased during 2000-12 (often < 60% similarity between consecutive years), whereas trait composition generally remained stable (> 75% similarity; Fig. 3.2b). Stability in trait composition broke down, however, when there was a large increase in the abundance of *Paramphinome jeffreysii* in 2011 (Fig. 3.3c), which boosted total abundance (Fig. 3.2d) and ended a sustained period of compensatory population fluctuations (Fig. 3.2b).

Trait composition did not differ significantly between 1971-86 and 1988-99, but both were significantly different to 2000-12 (Table 3.5; Fig. 3.4d). Taxonomic composition, on the other hand, differed significantly across all periods (Table 3.5; Fig. 3.4b). The collapse of populations and associated functions in 1987 was therefore quickly reversed as a new species assemblage emerged during 1988-99. During 2000-12, there was a significant increase in species richness and total abundance compared to 1987-99 (Table 3.5; Fig. 3.5b,d); indicating that changes to trait composition across these periods resulted at least partly from increased aggregate density, as the assemblage became relatively diverse.

Multiple modalities explained changes to trait composition during 2000-12. Of the top six contributors to compositional dissimilarity, five increased significantly during 2000-12 compared to 1988-99 and three increased significantly compared to 1971-86 (Table 3.6). Only deposit feeding showed no significant variation across periods. Using transformed data, six different modalities emerged as the top contributors to compositional dissimilarity. Five of these increased significantly during 2000-12 compared to both other periods (Table 3.6). No significant differences were observed only for animals with > 10 years lifespan. Increases in the densities of these modalities predict enhanced rates of nutrient regeneration, carbon sequestration and turnover, and increased availability of food for fish, during 2000-12 (Table 3.2).

Table 3.5. Differences in taxonomic composition (ANOSIM: Global R = 0.339), trait composition (ANOSIM: Global R = 0.097), total S (Kruskal-Wallis: H = 10.334; 3 d.f.) and total N (Kruskal-Wallis: H = 9.525; 3 d.f.) of macroinfauna at Dove station P across periods divided by abrupt changes in taxonomic composition. A significant difference (in bold) was taken as $p < 0.05$. Pairwise analyses with 1987 were not possible as n = 1. The R statistic for pairwise comparisons of taxonomic composition and trait composition are in brackets.

	P	1971-86 vs. 1987	1971-86 vs. 1988-99	1971-86 vs. 2000-12	1987 vs. 1988-99	1987 vs. 2000-12	1988-99 vs. 2000-12
Taxa comp.	**< 0.001**	**-**	**0.012**	**< 0.001**	**-**	**-**	**< 0.001**
		-	**(0.187)**	**(0.523)**	**-**	**-**	**(0.361)**
Trait comp.	**0.023**	-	0.372	**0.038**	-	-	**0.012**
		-	(0.012)	**(0.096)**	-	-	**(0.016)**
Species richness	**0.016**	-	0.180	0.058	-	-	**0.005**
Total abundance	**0.023**	-	0.646	0.065	-	-	**0.004**

Table 3.6. Differences in the number of individuals exhibiting twelve trait modalities in 2000-12 compared to other periods at Dove station P. The analysed modalities were identified as top contributors to compositional dissimilarity using untransformed data (above double-border) and ln (x+1) transformed data (below double-border). Significant differences ($p < 0.05$) identified using Kruskal-Wallis tests are in bold. Changes to mean density are presented for modalities that differed significantly across periods. The modalities ’10-29 mm’ and ‘< 1 years’ were ln transformed prior to analysis to meet the assumption of homogenous variance. See Table 1 for list of traits matched to trait codes.

				2000-12 *vs.*		
Trait code	Modality	H	*P*	1971-86	1987	1988-99
(E)	No ventilation	13.625	**0.003**	**+1228.7**	+1856.0	**+1310.7**
(C)	Unprotected	10.953	**0.012**	**+952.9**	+1689.7	**+1194.5**
(I)	No modification	9.679	**0.022**	+833.6	+1786.6	**+1251.5**
(G)	Deposit	6.514	0.089	-	-	-
(D)	Slow movement	11.790	**0.008**	**+912.5**	+1503.2	**+1031.0**
(B)	10-29 mm	10.927	**0.012**	+851.0	+1373.8	**+1092.5**
(A)	< 1 yrs	21.467	**< 0.001**	**+980.7**	+1156.2	**+962.5**
(A)	> 10 yrs	5.003	0.172	**-**	-	-
(G)	Predator	21.993	**< 0.001**	**+528.3**	+594.3	**+516.5**
(C)	Shelled	12.686	**0.005**	**+138.7**	+189.8	**+129.8**
(B)	< 10 mm	14.100	**0.003**	**+150.1**	+287.0	**+154.2**
(F)	Diffusive	13.349	**0.004**	**+912.0**	+1139.8	**+967.8**

DISCUSSION

Previous analyses of the Dove benthic time series show long-term variation in taxonomic composition (Frid et al. 2009a, b; **Chapter 2**); with natural and anthropogenic factors apparently influencing community dynamics (Buchanan & Moore 1986; Buchanan 1993; Frid et al. 1999; Bremner et al. 2003a; Bremner et al. 2005; Frid et al. 2009a, b; **Chapter 2**). Using established associations between species traits and key ecological functions, I applied biological traits analysis (BTA; Bremner et al. 2003b) and found effect trait composition (*sensu* Lavorel & Garnier 2002) to be statistically indistinguishable across periods that experienced significant changes to taxonomic composition at stations M1 and P (Fig. 3.4; Tables 3.3 & 3.5). Periods of significantly altered trait composition did, however, occur at both stations (Fig. 3.4; Tables 3.3 & 3.5). It is therefore inferred that density compensation by characteristically similar (redundant) taxa acted to buffer changes to ecological functioning over time (*sensu* Naeem 1998), but that substitutions of dissimilar taxa and uncompensated population fluctuations caused temporary disruptions to functioning.

A previous trait analysis by Frid (2011) suggested that key ecological functions have varied temporally at stations M1 and P due to changing aggregate density of infauna. In contrast to the present study, which found no differences in aggregate density across periods at M1, a crash in function delivery was implied during the late 1990s and 2000s at this station (however, both studies reported increased availability of food for fish at P in the 2000s). Whereas Frid (2011) focused on taxa with the highest inter-period variability, over 98% of total N was used to derive trait composition here. Taken together, these results suggest that the functional impact of the most temporally variable taxa can be buffered by changes in the densities of taxa with relatively low temporal variability. These findings echo previous suggestions that deriving traits for a subset of a community dataset may provide an incomplete picture of ecological functioning (Bremner 2008). It should, however, be noted that the approach to assessing functioning differed between the two studies. For example, the former used traits to reconstruct temporal patterns in specific functions; whereas the present study assessed temporal changes to trait composition and then inferred the consequences for specific functions. The results of the two studies are therefore not strictly comparable.

The results of this study are largely consistent with others that have applied BTA to assess temporal variability in the functioning of benthic communities. Veríssimo et al. (2012) analysed changes in the subtidal macroinfauna before and after the environmental restoration of a Portuguese estuary. They found that, despite shifts in taxonomic composition, trait composition either persisted or changed and recovered during the five-year study period at each of 15 sites. Similar patterns of functional change and recovery have been reported for epifauna responding to a cold winter in the German Bight (Neumann & Kröncke 2011) and macroinfauna responding to hypoxia events over a 19-year period at a site in the south-western Baltic Sea (Gogina et al. 2014). Benthic invertebrate communities have also been shown to exhibit a level of seasonal stability in trait expression, despite taxonomic composition being highly variable on this timescale (Bêche et al. 2006; Munari 2013); while recent analyses suggest that similar patterns emerge across millennia (Caswell & Frid 2013; Frid & Caswell 2016). Substitutions of characteristically similar benthic species may therefore occur widely and across multiple temporal scales, thus acting to conserve ecological functioning.

The capacity for functional compensation has previously been demonstrated using direct measurements of biomass/abundance stocks or rates of production in simple, low diversity assemblages; with examples found in microbes (Jiang 2007), terrestrial plants (Hector et al. 2010), nematodes (Ruess et al. 2001) and marine fishes (Dulvy et al. 2002). Results of the present study, and those mentioned above, therefore suggest that such patterns of functional stability extend to natural, biodiverse systems experiencing long-term compositional change. Moreover, my finding that functional stability can occasionally break down is consistent with counter-examples in the literature, such as an experiment which found no evidence of density compensation among protist species subjected to environmental warming (Fox & Morin 2001) and another that found compensation among stream insects to depend on which species was experimentally removed (Ruesink & Srivastava 2001). Both direct and indirect analyses therefore suggest that, while ecological functioning can be sustained over time, aperiodic disruption can occur under some conditions.

Alterations to effect trait composition occurred when taxonomic composition shifted at approximately the same time at both stations (1986 at M1 and 1987 at P; Fig. 3.2a,c). These ecological changes coincided with the North Sea climatic regime shift (Beaugrand 2004), and therefore the implied alteration to benthic functioning may have been driven by broad-scale hydro-climatic forcing or the associated changes to the North Sea ecosystem. For example, community composition of the plankton changed around this time (Beaugrand 2004) and detrital flux to the seabed surrounding the stations was estimated to be particularly low in 1986 (see **Chapter 2**, Fig. 2.3d). Given that deposit feeders dominate at both sites, it is plausible that such changes to the quantity and, possibly, quality of detrital food supply caused the large, uncompensated declines in species populations and the ecological functions they deliver. This result suggests that climatic variability can cause temporary changes to benthic functioning, even within systems exhibiting long-term functional stability; a finding that echoes the results of Neumann & Kröncke (2011).

Following the abrupt functional change in 1986/87, trait composition at station P recovered after one year whereas M1 experienced a period of significantly altered, and temporally unstable, trait composition (1986-91). The rapid functional recovery at P possibly reflects the conditions at the site, which lies within the grounds of a *Nephrops* fishery. Given that the seabed at P is regularly subjected to trawling (Frid et al. 1999), it follows that the community should be comprised of species that are resilient to disturbances (see Jennings & Kaiser 1998); thus facilitating recovery albeit with an altered taxonomic composition. This conjecture appears to be supported by a scarcity of disturbance-sensitive species and dominance by the opportunistic capitellid *Heteromastus fiiformis* at P (see Supplementary Material, Table 3.8); whereas three disturbance-sensitive bivalves were among the top 10 most common taxa at M1 (see Supplementary Material, Table 3.7). While previous studies reveal an impact of fishing disturbance on the trait composition of benthos (e.g. Bremner et al. 2005; Tillin et al. 2006; de Juan & Demestre 2012), to my knowledge no study has yet assessed the effect of fishing disturbance history on the rate of functional recovery from other perturbations, such as climatic fluctuations.

The significant change to trait composition at M1 during 1986-91 (Table 3.3; Fig. 3.4c) suggests that characteristically similar taxa lacked the necessary range of population responses to sustain ecological functioning through this period. Given the decline in species richness and increased community variability, it is possible that the 1986 event eliminated redundant taxa that were necessary for functional compensation to occur; thus impairing the delivery of ecological functions, as argued by Naeem (1998). Substitutions of characteristically dissimilar taxa did, however, maintain the same aggregate density during 1986-91 as the preceding period. The association between species sensitivity and functional characteristics (a major determinant of the ecological consequences of species extinction; Solan et al. 2004) therefore appears to vary over time and, possibly, with respect to the drivers of ecological change.

Changes to trait composition at P during 2000-12 (Table 3.4; Fig. 3.4d) involved an increase in total N (Fig. 3.5d) as the polychaete *Paramphinome jeffreysii* experienced rapid population rise (Fig. 3.3c); a trend that has occurred throughout much of the central and northern North Sea since its colonisation during the last 30 years (Kröncke et al. 2011). An increase in species richness and in the density of trait modalities not exhibited by *Paramphinome,* such as ‘shelled’ and ‘< 10 mm maximum body length’, indicate that taxa other than *Paramphinome* also contributed to the enhanced rates of ecological functions predicted for this period (Table 3.6). These results can therefore be considered as complementary to those at M1, with species gains (in a relatively species-poor community; P) and losses (in a relatively species-rich community; M1) both associated with changes to the functional structure of communities (a topic addressed for marine systems in Byrnes et al. (2007)). It is currently unclear whether the *Paramphinome* will decline in numbers in the coming years, or if/how the community and functioning will respond to the proliferation of this species in the long term. Continued tracking of this species will answer these questions and provide insights into the ecological consequences of species invasions.

In applying BTA, I assumed that the characteristics and density of a species determine its functional potential. While these assumptions are empirically supported (Chapin et al. 1997), it should be noted that species can show plasticity in trait expression with respect to physical habitat (Ólafsson 1986), levels of disturbance (Cesar & Frid 2012) and potentially many other environmental conditions. I used fuzzy coding of traits to address this issue (Chevenet et al. 1994), but this reduces specificity, making it possible that temporal changes to trait composition were underestimated as a result. The results therefore represent a conservative estimate of functional change over time. Furthermore, the degree to which species drive functioning may also vary with respect to environmental context (Hiddink et al. 2009) or the nature of interspecific interactions, i.e. facilitative (Cardinale et al. 2002) or antagonistic (Polley et al. 2003) (see **Chapter 5**). This issue will need to be resolved if we are to progress from inferring changes to functional potential and use species traits to accurately predict levels of functional delivery across a range of biotic and abiotic conditions.

ACKNOWLEDGEMENTS

Thanks must first go to the late Jack Buchanan for starting the time series used in this study. I thank the masters and crew of the *RV Bernicia* and *RV Princess Royal*, Peter Garwood and staff at the Dove Marine Laboratory for their efforts in data collection. Thanks also go to Eivind Oug and staff at NIVA for kindly providing species traits information collected by their team.

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SUPPLEMENTARY MATERIAL

Appendix 3.1. Sampling effort over time.

During the 1970s sampling effort varied between 10 and 30 grabs at P and up to 20 grabs at M1. Since 1980, taking five replicate grab samples has been standard at both stations. This change in effort means that, if the community remained unchanged, early years will contain more rare taxa and therefore appear to be more species-rich, which has implications when using ordinations of community composition or biodiversity indices. As the original raw data are no longer available, I proceeded to use the full dataset comprising of all samples. However, removal of the least abundant taxa from the community dataset prior to analysis will reduce this effect. Examination of the published rarefraction curve for the early years (1971-72) (Buchanan & Warwick 1974) also reassures us that any influence will be minor.

Table 3.7. Mean densities and % contributions of the ten dominant taxa (above double-border) and ten most common trait modalities (below double-border) over the 40-year time series at Dove station M1, in the central-western North Sea.

Taxonomic group/ Trait	Taxon/ modality	Mean density (indiv. m^{-2})	% of total N/ % of given trait
Polychaeta	*Prionospio* spp.	445.9	11.9
Polychaeta	*Levinsenia gracilis*	218.9	5.9
Ophiuroidea	*Amphiura filiformis*	212.1	5.7
Bivalvia	*Thyasira flexuosa*	179.3	4.8
Polychaeta	*Chaetozone setosa*	172.8	4.6
Polychaeta	*Galathowenia oculata*	161.9	4.3
Bivalvia	*Ennucula tenuis*	139.4	3.7
Polychaeta	Capitellidae	138.8	3.7
Bivalvia	*Kurtiella bidentata*	129.5	3.5
Polychaeta	*Caulleriella killariensis*	110.9	3.0
-	Top ten combined	1909.5	51.1
Epi. hab. mod.	No modification	2950	79.9
Life zone	Shallow	2586	70.1
Feeding mode	Deposit	2448.3	66.3
Protective struct.	Unprotected	1898.1	51.4
Lifespan	1 - 2 yrs	1739.2	50.3
Burr. vent. mode	No ventilation	1758.6	47.8
Mob. within sed.	Limited	1723.9	46.7
Burr. vent. mode	Blind-ended burrow	1685.8	45.9
Max. body length	10 - 29 mm	1605.3	44.7
Mob. within sed.	Slow movement	1341.2	36.3

Table 3.8. Mean densities and % contributions of the ten dominant taxa (above double-border) and ten most common trait modalities (below double-border) over the 42-year time series at Dove station P, in the central-western North Sea.

Taxonomic group/ Trait	Taxon/ modality	Mean density (indiv. m^{-2})	% of total N/ % of given trait
Polychaeta	*Heteromastus filiformis*	683.8	26.4
Polychaeta	*Paramphinome jeffreysii*	307.8	11.9
Polychaeta	*Prionospio* spp.	180.2	6.9
Polychaeta	*Levinsenia gracilis*	179.8	6.9
Polychaeta	*Chaetozone setosa*	111.7	4.3
Nemertea	Nemertea	79.5	3.1
Polychaeta	*Ophelina acuminata*	74.2	2.9
Amphipoda	*Harpinia antennaria*	69.2	2.7
Ophiuroidea	*Amphiura* spp.	69.2	2.7
Bivalvia	*Abra nitida*	64.9	2.5
-	Top ten combined	1820.3	70.2
Feeding mode	Deposit	2041.3	79.7
Burr. vent. mode	No ventilation	1764.4	71.3
Protective struct.	Unprotected	1718.7	67.1
Epi. hab. mod.	No modification	1717.2	67.0
Lifespan	1 - 2 yrs	1517.3	61.6
Life zone	Shallow	1435.6	56.0
Mob. within sed.	Limited	1229.7	48.0
Mob. within sed.	Slow movement	1121.5	43.7
Max. body length	10 - 29 mm	1064.9	42.9
Max. body length	> 100 mm	847.8	34.1

Chapter 4

Species densities, biological interactions and benthic ecosystem functioning: an *in situ* experiment

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Accepted in *Marine Ecology Progress Series*

ABSTRACT

Understanding how biota affect the functioning of ecosystems is imperative if we are to predict the impacts of ongoing biodiversity change on ecosystem service provision. Evidence from marine sediments – the most widespread habitat on earth – suggests that ecological function delivery is driven by the presence and densities of certain species. However, most experiments have been conducted using fixed density treatments and run for short durations (< 4 weeks) within homogenous laboratory microcosms. In nature, the impact of changing density in one species may depend on consequent changes in the densities of others. Moreover, evidence from vegetation assemblages suggests that the influence of complementarity among species increases in heterogeneous environments and over time. Here, a realistic pattern of biodiversity change was simulated by transplanting the macroinfaunal bivalve *Scrobicularia plana* into an intertidal mudflat at various densities. The impact on redox potential discontinuity (RPD) depth (a proxy for benthic functioning) was measured at 1, 5 and 9 weeks. Increasing *S. plana* density negatively affected RPD depth (i.e. RPD depth became shallower) by causing the density of a functionally dominant species, *Corophium volutator*, to decline. Furthermore, the influence of density-dependent interspecific interactions (among macroinfauna) on RPD depth became increasingly positive as the experiment progressed. The results reaffirm the direct functional importance of certain species in a natural ecosystem and highlight the indirect importance of other species to which their density is tightly coupled. An implication is that species loss could enhance functioning if it causes the density of a functionally dominant species to increase. Nevertheless, the apparent temporal emergence of interspecific facilitation suggests that diverse species assemblages promote high function delivery.

INTRODUCTION

In an era of rapid environmental change there is a need to determine how alterations to biodiversity affect the functioning of ecosystems (Naeem et al. 2012). It is now well established that changes to species densities can impact key ecological functions, such as nutrient cycling and productivity, with the magnitude of impact depending on the organism's biological traits (Chapin et al. 1997; Diaz & Cabido 2001). Evidence from field experiments suggests that complementarity enhances functioning when more species are present (i.e. the community performs better than expected from the performances of the individual constituent species; Loreau & Hector 2001). More recent laboratory microcosm experiments have shown that complementarity can emerge through interspecific facilitation (positive species interactions; Cardinale et al. 2002; Tiunov & Scheu 2005) and niche partitioning (the ability of different species to utilise different sections of the niche space; Caliman et al. 2011; Cardinale 2011). However, with most experimental assemblages having been constructed randomly from a species pool (Tilman et al. 2014), questions have been raised about the applicability of findings to natural communities experiencing non-random compositional change (e.g. Srivastava & Vellend 2005). Indeed, studies have shown that the impact of biodiversity loss on function delivery depends on the order of extinction and differs between random and realistic scenarios (Solan et al. 2004; Larsen et al. 2005; Bracken et al. 2008; Bracken & Low 2012). In marine systems, the issue of real-world applicability is particularly pertinent as most experiments have been conducted within controlled and homogenous environments (Gamfeldt et al. 2015). Efforts to increase realism in biodiversity-ecosystem function (BEF) research are now being encouraged (e.g. Hillebrand & Matthiessen 2009; Gamfeldt et al. 2015).

Marine sediments are the most widespread habitat on Earth and play a major role in climate regulation, waste assimilation and the production of food for human consumption (Snelgrove et al. 2014). Therefore, to predict the impact of global change on the provision of these ecosystem services, we must determine how ongoing changes to biodiversity affect the underlying functioning of marine sediments. Experimental evidence supports the proposition that marine sediment biodiversity regulates ecosystem functioning (Gamfeldt et al. 2015; Strong et al. 2015). Consistent with terrestrial counterparts, studies point to the importance of certain species (or species-specific traits) in driving function delivery (Emmerson et al. 2001; Ieno et al. 2006; Norling et al. 2007; Godbold et al. 2009a,b; Braeckman et al. 2010; Godbold et al. 2011). For example, a study of Skagerrak macroinfauna found that oxygen consumption and benthic-pelagic nutrient fluxes were dominated by the deep-burrowing thalassinid shrimp *Calocaris macandreae* (Norling et al. 2007), while organic matter consumption by enchinoderm species from Gullmarfjord, Sweden, was found to be dominated by the active deposit-feeding sea urchin *Brissopsis lyrifera* (Godbold et al. 2009a). Aggregate density, or the density of functionally dominant species, also appears to be an important factor (Emmerson et al. 2001; Ieno et al. 2006; Braeckman et al. 2010), whereas complementarity among species has not emerged as an important driver of marine sediment functioning (but for evidence of complementarity in the functioning of freshwater/brackish sediments, see Mermillod-Blondin et al. 2003; Karlson et al. 2010; Caliman et al. 2011).

The abovementioned marine sediment BEF studies have generally used short-term experiments (< 4 weeks), conducted within homogenous laboratory microcosms (but see Godbold et al. 2009b, 2011), to isolate biotic influence over functioning from the confounding effects of environmental heterogeneity. The typically small number of species considered has permitted the examination of all (or many) possible assemblages, thus allowing biodiversity effects caused by complementarity to be distinguished from those caused by the presence and/or density of individual species (Ieno et al. 2006; Benedetti-Cecchi & Maggi 2012). However, complementarity among species has been shown in vegetation assemblages to increase over time and in heterogenous environments (e.g. Stachowicz et al. 2008; Wacker et al. 2008), raising the possibility that complementarity would emerge in marine sediments if experiments were run in the field and for longer durations. The impact of changing density in one species may also depend on consequent changes in the densities of other species (e.g. Ruesink & Srivastava, 2001; O’Connor & Crowe 2005); a possibility that is excluded when using closed microcosms with fixed density treatments. Therefore, while the design of such experiments has allowed BEF mechanisms to be unambiguously identified, the degree to which findings characterise BEF relationships in natural marine sediments is unclear. To assess how real-world biodiversity change affects ecosystem functioning requires that biodiversity is manipulated within natural, open ecosystems.

Here, a field experiment was conducted over an extended period (9 weeks) to determine how realistic changes in species densities impact benthic ecosystem functioning. I transplanted the macroinfaunal bivalve *Scrobicularia plana* into plots on an intertidal mudflat and measured the redox potential discontinuity (RPD) depth – an index of sediment oxygen content (Gerwing et al. 2015), which in turn drives organic matter decomposition (Hulthe et al. 1998) and nutrient regeneration (Ruardij & van Raaphorst 1995). Sediment reworking and burrow ventilation by macroinfauna act to increase RPD depth (Solan et al. 2004; Birchenough et al. 2012), which may create a positive feedback by improving conditions for other macroinfauna that also perform these activities (Bouma et al. 2009). I propose that such facilitative interactions will manifest among individuals of different species, which are likely to occupy different niches (Silvertown 2004), whereas intraspecific interactions are more likely to cause interference and, thus, reduced activity (e.g. Duport et al. 2006). Experimental plots were sampled on three occasions; it was predicted that RPD depth would initially respond to *S. plana* density or consequent changes to physicochemical conditions or the density of another species (see below; 'Study species and potential paths of impact on functioning’), but over time would be increasingly driven by positive density-dependent interspecific interactions (reflecting interspecific facilitation) and/or negative density-dependent intraspecific interactions (reflecting intraspecific antagonism) among the macroinfaunal assemblage.

Study species and potential paths of impact on functioning

Scrobicularia plana is a large (up to 65 mm) and thus potentially functionally dominant bivalve (Thrush et al. 2006; Norkko et al. 2013) that lives buried to depths of 20 cm in muddy intertidal sediments throughout the coasts of the NE Atlantic (Santos et al. 2011). Local densities of *S. plana* can vary from absent to hundreds of individuals per square metre within a few years (Essink et al. 1991; Ysebaert & Herman 2002). Its patchy distribution is apparently caused by sensitivity to local environmental conditions at the time of settlement (Santos et al. 2011), whereas adults are tolerant of a wide range of physical and chemical conditions (Freeman & Rigler 1957; Beaukema 1979; Boldina-Cosqueric et al. 2010). Realistic biodiversity change can therefore be simulated by transplanting *S. plana* adults into suitable habitats where its density is low.

From its burrow, *S. plana* extends its siphons to the sediment surface where it draws down water for respiration (Green 1967), feeds on settled or suspended detritus and expels pseudofaeces (Hughes 1969). The species therefore has the potential to directly increase sediment oxygen content through burrow irrigation, while consumption and deposition of organic matter could indirectly increase or decrease oxygen content, respectively, by altering sediment oxygen demand (Gray et al. 2002). Such activities may also facilitate or inhibit other species within the assemblage (Bouma et al. 2009), which could in turn impact the functioning of the ecosystem.

Four paths through which *S. plana* density may affect RPD depth were hypothesised (Fig. 1). The first, P1, is a direct positive effect (an increase in RPD depth) due to burrow irrigation. P2 is an indirect positive effect mediated by net consumption of sediment organic matter and a subsequent decrease in sediment oxygen demand; whereas P3 is an indirect negative effect mediated by net deposition of organic matter (pseudofaeces) and a subsequent increase in sediment oxygen demand. P4 is an indirect negative effect mediated by a decrease in the density of another widely distributed burrowing macroinvertebrate *Corophium volutator*. Previous studies have shown that *C. volutator* has a positive influence on RPD depth (e.g. Limia & Raffaelli 1997) and is negatively affected by large bivalves (e.g. Jensen 1985; Beadman et al. 2004).

Changes to density-dependent intra- and interspecific interactions within the macroinfaunal assemblage represent additional mechanisms by which the transplants were predicted to affect RPD depth; through antagonism and facilitation, respectively. As these mechanisms do not relate specifically to *S. plana* they were considered separately to the aforementioned paths.

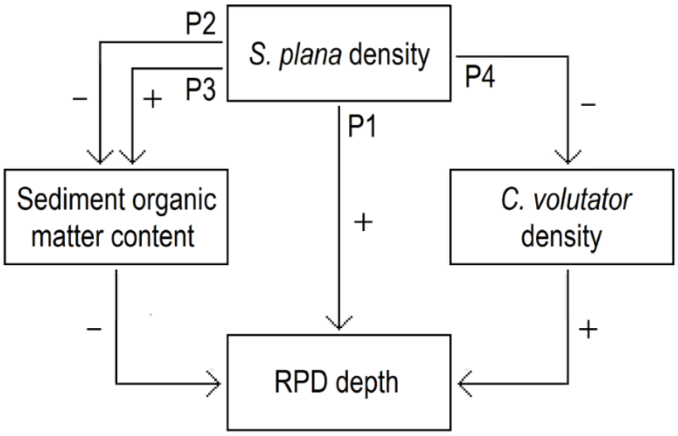

Fig. 4.1. Hypothesised paths for an impact of *Scrobicularia plana* density on RPD depth: path 1 (P1) is a direct positive effect; path 2 (P2) is an indirect positive effect mediated by a decrease in sediment organic matter content, which is expected to have negative influence over RPD depth; path 3 (P3) is an indirect negative effect mediated by an increase in sediment organic matter content; and path 4 (P4) is an indirect negative effect mediated by a decrease in the density of *Corophium volutator*, which is expected to have a positive influence over RPD depth.

MATERIALS AND METHODS

Experimental site

The experiment was conducted on an intertidal mudflat in the Mersey Estuary, Liverpool, UK (53° 21′ 22″ N, 02° 55′ 28″ W). At the time of the experiment, the macroinfaunal assemblage was dominated by the mud shrimp *C. volutator*, the ragworm *Hediste diversicolor* and oligochaetes *Tubificoides* spp. *S. plana* occurred sporadically and at low density, as did the bivalve *Macoma balthica* and the polychaete *Eteone longa*. Few epifaunal invertebrates inhabited the site, but the shore crab *Carcinus maenas* and the brown shrimp *Crangon crangon* were present. The gastropod *Hydrobia ulvae* was abundant on the upper shore but was apparently absent mid-shore, where the experiment was conducted (D.S. Clare; personal observation). Sediment organic matter content at the site was ~7%.

Running the experiment

S. plana adults (> 20 mm) were transplanted into circular plots on the seabed (20 cm diameter; 0.03 m^2) at three densities – 510 g m^{-2} (1.0 × D), 1020 g m^{-2} (2.0 × D), and 255 g m^{-2} (0.5 × D) – and contained using cages (described in detail below). D refers to the density of the species at the donor site on the Dee Estuary, Wirral Peninsula, UK (53° 21′ 14″ N, 3° 10′ 18″ W), where it was relatively abundant at the time of the experiment (40 individuals m^{-2} on the Mersey *vs.* 400 individuals m^{-2} on the Dee). Control plots (no cage; no transplanted individuals) and procedural control plots (cage; no transplanted individuals) were also used.

A randomised block design was used (Hurlbert 1984), in which four blocks were spaced at 10 m intervals across the shore at an elevation of 1 m above mean sea level. Each block consisted of 15 plots – one replicate of each of the five treatments, for three experiment durations (1, 5 and 9 weeks) randomly allocated within a 5 x 3 grid (Block 1 is shown in Fig. 4.2). A total of 60 plots were used.

S. plana were collected from the donor site on the 29th July 2013, transported to the laboratory and incubated in aerated aquaria at the approximate temperature and salinity of the study site (15°C; 30 psu). Water in the aquaria was partially replaced each day to prevent the build-up of excreted toxins. Immediately prior to transplantation, *S. plana* were weighed in the laboratory and transported to the study site in containers filled with water from the aquaria.

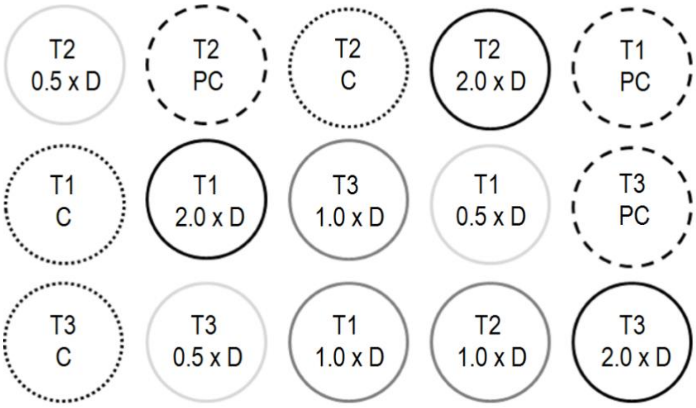

Fig. 4.2. Schematic of plots (20 cm diameter) within experiment block 1 (not to scale; plots spaced 2 m apart). The density of *Scrobicularia plana* transplanted into each plot is expressed in terms of the mean density of the species at the donor site (D): 1.0 × D (dark grey ring), 0.5 × D (light grey) and 2.0 × D (black). Control plots (no cage; no transplanted individuals; dotted ring) and procedural control plots (cage; no transplanted individuals; dashed ring) are shown. Each treatment was replicated for three sampling occasions: 1 week (T1), 5 weeks (T2) and 9 weeks (T3).

The four blocks were set up on consecutive days, one block each day, from 30th July to 2nd August 2013. Transplanted individuals were placed onto the sediment surface in an even distribution over the plot area. Stainless steel cages (1 cm^2 mesh size), with wire net roofs (1 cm^2 mesh), were fitted to plastic corers (20 cm diameter × 30 cm depth) and pushed into the mud to contain the plots, such that the top of the corer was level with the sediment surface and the cage extended 20 cm above the seabed (Fig. 4.3). This prevented transplanted *S. plana* from being swept away by currents or being depredated by birds while allowing other, comparatively small, invertebrates to relocate in response to the experimental treatments.

Data collection

One replicate of each of the five treatments was sampled from each block at 1 week (T1), 5 weeks (T2), and 9 weeks (T3) after the block was laid. Each sampling occasion coincided with the ‘spring’ period of the tidal cycle. Pools developed within the plots during the experiment as corers experienced a net loss of sediment. This was not yet apparent at T1. At T2 weeks all pools were < 1 cm deep. By T3 pools had reached an average depth of 6 cm (± 0.2 cm SE).

Fig. 4.3. Cages before and after being inserted into the sediment to contain *Scrobicularia plana* within plots at the experiment site on the Mersey Estuary, Liverpool.

At sampling, intact cores were lifted from the seabed, capped at the bottom and placed upright onto plastic trays. This maintained the sediment profile and prevented contained animals from escaping during transportation back to the laboratory. For control plots, corers with the same dimensions as those used to contain the experimental plots were pushed down into the sediment until the upper edge was level with the sediment surface. Sampling then proceeded in the same way as described for experimental plots.

Upon returning to the laboratory (< 1 hour after sampling) a transparent corer (5 cm diameter) was used to extract sediment from the centre of each plot, such that the entire vertical section was removed. A ruler was used to measure RPD depth through the corer to the nearest 0.5 cm (*sensu* Gerwing et al. 2013), with four measurements taken at 90° to each other and averaged to give the mean value for each plot. Additional measurements of RPD depth taken from the remaining sediment in T1 plots confirmed that this sub-sampling procedure gave an accurate representation of the mean values for the plots.

Sediment extracted using the transparent corer was sliced into two equal vertical sections and any *S. plana* individuals were removed using forceps. Surface sediment (0 - 1 cm) was retained from one section and the bulk core (0 - 20 cm) was retained from the other. These samples were frozen at -15°C and later dried at 90°C, homogenised and percent organic matter content calculated by weighing before and after incineration at 550°C (Buchanan & Kain 1984). Because *S. plana* both feeds and deposits pseudofaeces on the sediment surface, I focussed on surface sediment organic matter content in the analyses; however, the relationship between surface and bulk organic matter content is shown in the Supplementary Material (Table 4.5, Fig. 4.7).

The sediment remaining in each plot was sieved through 0.5 mm mesh and the residue preserved in 70% ethanol. After 1-2 months, to allow biomass to stabilise following preservation (Wetzel et al. 2005), the retained fauna (including *S. plana* removed from sediment used to calculate organic matter content) were identified to the lowest taxonomic level possible, enumerated and weighed after soaking in freshwater and draining through filter paper for 30 minutes (fresh biomass). I based densities on biomass rather than abundance as the former is a particularly good predictor of a species' relative contribution to their associated functions (Garnier et al. 2004). For bivalves, biomass was taken as the flesh weight only. With the exception of *S. plana*, for which all individuals were retained, densities were corrected to account for the loss of biomass contained within the sediment used for organic matter content analysis. Densities were standardised to g m^{-2}.

Data analysis

Analyses were performed using R statistical software (version 3.1.2, R Development Core Team 2014). Type II sums of squares were used in all general linear models and null hypotheses were rejected at $p < 0.05$. Assumptions of homoscedasticity and normality of residuals were checked by inspection of plots of residuals against fits and normal quantile plots, respectively.

Cage effect

General linear models were used to test whether the density of each species and sediment organic matter content differed between control and procedural control plots (i.e. whether there was an experimental artifact associated with the cage). Block and Time were included in the models; each explanatory variable was treated as a factor. Since there was a significant cage effect, control plots were removed from further analyses and the procedural control plots were used as the 'no *S. plana* addition' baseline.

***S. plana* density *vs.* RPD depth**

A general linear model was used to test the relationship between RPD depth and *S. plana* density, with Time and Block included as explanatory variables. Since it was predicted that species-specific density effects would weaken over time as biological interactions become more important, the interaction between *S. plana* density and Time was also tested. *S. plana* density reflected a gradient from low to high biomass among plots at each sampling occasion (i.e. did not divide into the initial density categories) and was therefore treated as a quantitative explanatory variable, whereas Time and Block were treated as factors. (An analogous general linear model in which *S. plana* density was treated as a factor based on the initial densities categories revealed a significant treatment effect, with the differences among treatments being greatest for high density addition plots in comparison to no addition and low density addition plots; see Supplementary Material, Table 4.6, Fig. 4.8.). Total biomass was initially included as an explanatory variable in the model to assess whether the effect of *S. plana* density on RPD depth was confounded by variation in total biomass. This term was removed as it did not affect the statistical significance of the relationship between RPD depth and *S. plana* density and was itself not significantly related to RPD depth (see Supplementary Material, Table 4.7).

Conditional on a significant relationship between RPD depth and *S. plana* density (or a significant *S. plana* density*Time interaction), analogous general linear models were used to test the relationship between *S. plana* density and the hypothesised mediators of the effect of *S. plana* density on RPD depth: sediment organic matter content and *C. volutator* density. If relationships were significant then the relevant mediators were retained. If relationships were not significant then the relevant mediators were dropped from further analyses as they did not constitute potential mechanisms through which *S. plana* density could affect RPD depth. Any hypothesised mediators that were dropped from the analysis were also tested for their relationships with RPD depth (with Time, the interaction between the hypothesised mediator and Time, and Block included in the model) in order to determine whether they could be ruled out as having an influence over functioning.

Causal Mediation Analysis, a generalization of linear structural equation modelling (Imai et al. 2010), was used to partition any effect of *S. plana* density on RPD depth into direct and indirect paths (via the retained mediator). Two regression models were created as the basis of the mediation analysis: the first expressing variation in the mediator in relation to *S. plana* density (the 'mediator model') and the second expressing variation in RPD depth in relation to the mediator and *S. plana* density (the 'outcome model'). Block and Time were included in the models as pre-treatment explanatory variables. Temporal interactions were not incorporated as they were statistically insignificant in the preceding general linear models (see Table 4.2). The objects of the mediator and outcome models were then fed into the mediate function in the R package **mediation** (Tingley et al. 2014), which computes the *average direct effect* (ADE; i.e. the direct effect of *S. plana* density), the *average causal* *mediation effect* (ACME; i.e. the indirect effect of *S. plana* density via the mediator) and the *total effect* (i.e. the sum of ADE and ACME) using the general algorithms described in Imai et al. (2010). A non-parametric bootstrap approach was used to estimate bias-corrected 95% confidence intervals for the ADE, ACME and total effect from 10,000 iterations (Tingley et al. 2014).

Sensitivity analysis was used to assess the robustness of the ACME to the violation of 'sequential ignorability' (Imai et al. 2010). Sequential ignorability is the assumption that relationships between the treatment (*S. plana* density), the mediator and the outcome (RPD depth) are not confounded by other potential explanatory variables. Robustness was determined with respect to the range of ρ (the correlation between the residuals for the 'mediator' and 'outcome' models) under which the confidence intervals for ACME overlapped with zero. Relationships between the mediator and the densities of sampled taxa were inspected to identify any potential confounders of the relationship between the mediator and the outcome. Treatment assignment was assumed to be independent of potential outcomes and mediators, given the randomised experimental design.

Density-dependent intra- and interspecific interactions *vs.* RPD depth

To assess whether antagonism and/or facilitation among macroinfauna influence RPD depth, indices representing the potential for density-dependent intraspecific interactions (the sum of squared biomasses; Intra) and density-dependent interspecific interactions (the sum of products of biomasses for pairs of different species; Inter) were calculated for each plot. To obtain these indices, it was assumed that the expected RPD depth at a given time and in a given block is an unknown function of the biomasses of each of the s species within the assemblage. If this function is continuous and sufficiently smooth, it can be approximated using a second-order Taylor polynomial (e.g. Riley et al. 2002, section 5.7). With the simplifying assumptions that intra- and interspecific density-dependent interactions act in the same way for all species or pairs of species, respectively, the following regression model is obtained:

$$\text{RPD depth} = \alpha + \sum_{i=1}^{s} \beta_i b_i + \gamma \sum_{i=1}^{s} b_i^2 + \delta \sum_{i=1}^{s} \sum_{j=i+1}^{s} b_i b_j + \epsilon,$$

where α is an intercept, β_i is the effect of the biomass b_i of the ith species on RPD depth, γ is the effect of the intraspecific index $\text{Intra} = \sum_{i=1}^{s} b_i^2$ (the sum of squared biomasses; g^2 m^{-4})

on RPD depth, δ is the effect of the interspecific index Inter $= \sum_{i=1}^{s} \sum_{j=i+1}^{s} b_i b_j$ (the sum of products of biomasses for pairs of different species; g^2 m^{-4}) on RPD depth, and ϵ is a normally-distributed error term.

The densities of each taxon were included in the model in order to account for the individual effects of species densities before testing for the effects of their interactions. The factors Block and Time were also included in the model, and Intra*Time and Inter*Time were tested as per the predictions that the effects of intra- and interspecific interactions on RPD depth would become increasingly negative (antagonism) and positive (facilitation) over time, respectively. The effects of taxa densities on RPD depth were assumed not to vary over time on the premise that any changes in activity will result from interactions among organisms and thus will be picked up by Intra and Inter.

RESULTS

Cage effect

Sediment organic matter content and the densities of all but two taxa did not differ significantly between control and procedural control plots (Table 4.1). The cage effect consisted of a significant increase in *Corophium volutator* density and a significant decrease in *Tubificoides* spp. density (Table 4.1; Fig. 4.4).

Scrobicularia plana density *vs.* RPD depth

There was a significant negative linear relationship between RPD depth and *S. plana* density (Table 4.2; Fig. 4.5a). RPD depth varied significantly over time and was deepest at T1 and shallowest at T2, but *S. plana* density*Time was not significant (Table 4.2; Fig. 4.5a).

C. volutator density decreased linearly with increasing density of *S. plana* and was higher at T1 than at T2 and T3 (Table 4.2; Fig. 4.5b). *S. plana* density*Time was not significant (Table 4.2; Fig. 4.5b). Sediment organic matter content did not vary significantly with respect to *S. plana* density (Table 4.2). Therefore, only *C. volutator* density was retained as a possible mediator of the effect of *S. plana* density on RPD depth. Sediment organic matter content was ruled out as having an influence on RPD depth (see Supplementary Material, Table 4.8, Fig. 4.9).

Table 4.1. General linear model summary of variation in taxa densities across experimental blocks, over time (1 week, 5 weeks and 9 weeks) and in response to the experimental cage. Significant *p*-values (< 0.05) are in bold.

Source	d.f.	*F*	*p*
Corophium volutator			
Block	3	2.316	0.1122
Time	2	16.520	**0.0001**
Cage	1	32.797	**< 0.0001**
Residuals	17		
Hediste diversicolor			
Block	3	1.798	0.1858
Time	2	8.987	**0.0022**
Cage	1	0.036	0.8512
Residuals	17		
Tubificoides spp.			
Block	3	1.351	0.2911
Time	2	2.460	0.1153
Cage	1	15.447	**0.0011**
Residuals	17		
Macoma balthica			
Block	3	0.525	0.6710
Time	2	1.067	0.3659
Cage	1	0.576	0.4585
Residuals	17		
Eteone longa			
Block	3	1.320	0.3007
Time	2	2.099	0.1532
Cage	1	3.381	0.0835
Residuals	17		
Scrobicularia plana			
Block	3	1.673	0.2104
Time	2	0.638	0.5406
Cage	1	1.218	0.2852
Residuals	17		
Organic matter content			
Block	3	2.150	0.1316
Time	2	7.038	**0.0059**
Cage	1	0.031	0.8619
Residuals	17		

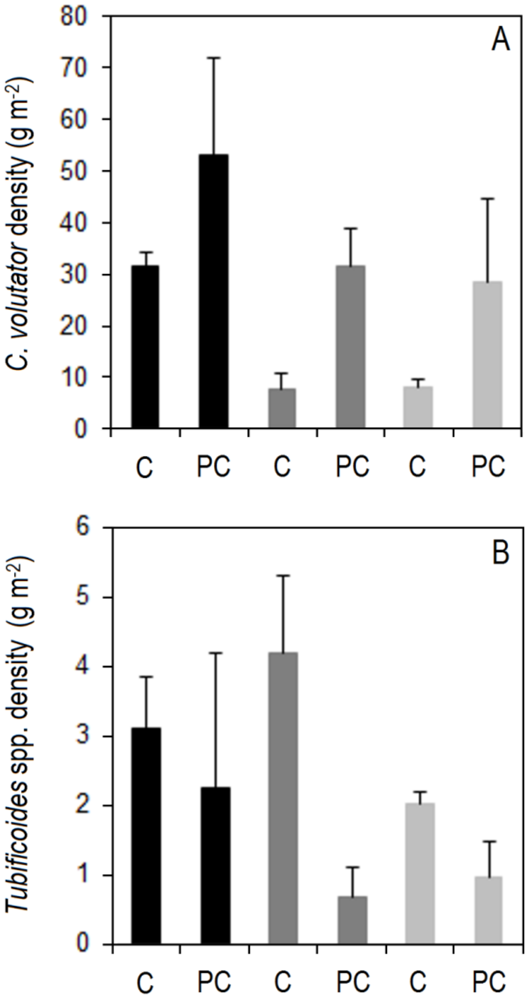

Fig. 4.4. Variation in the densities of (A) *Corophium volutator* and (B) *Tubificoides* spp. (with 95% confidence intervals) in response to the experimental cage (C = control; no cage & PC = procedural control; cage) at T1 (1 week; black), T2 (5 weeks; dark grey) and T3 (9 weeks; light grey).

Table 4.2. General linear model summary of variation in redox potential discontinuity (RPD) depth, sediment organic matter content and *Corophium volutator* density across experimental blocks, over time (1 week, 5 weeks & 9 weeks) and in relation to *Scrobicularia plana* density. Significant *p*-values (< 0.05) are in bold.

Term	d.f.	*F*	*p*
RPD depth			
Block	3	0.357	0.7842
Time	2	11.128	**0.0002**
Scrobicularia plana	1	6.421	**0.0154**
*Scrobicularia plana**Time	2	1.139	0.3306
Residuals	39		
Organic matter content			
Block	3	1.664	0.1905
Time	2	6.031	**0.0052**
Scrobicularia plana	1	1.030	0.3163
*Scrobicularia plana**Time	2	1.756	0.1861
Residuals	39		
Corophium volutator			
Block	3	3.842	**0.0168**
Time	2	27.343	**< 0.0001**
Scrobicularia plana	1	17.271	**0.0002**
*Scrobicularia plana**Time	2	0.415	0.6635
Residuals	39		

Causal Mediation Analysis revealed no significant ADE; however the ACME and the total effect were statistically significant (Table 4.3). The linear decline in RPD depth with increasing *S. plana* density (Fig. 4.5a) was therefore fully mediated by a negative impact on the density of *C. volutator* (Fig. 4.5b), which had a positive influence over RPD depth (Fig. 4.5c) (i.e. path 4; Fig. 4.1).

Sensitivity analysis revealed that the confidence intervals for ACME overlap zero when $0.13 < \rho < 0.60$, which makes the ACME robust to small violations of sequential ignorability. Inspection of the relationships between the densities of *C. volutator* and other taxa revealed only one potential confounder in *Hediste diversicolor*; to which *C. volutator* was negatively related (see Supplementary Material, Table 4.9, Fig. 4.10). This correlation was deemed unlikely to undermine the ACME (see Discussion).

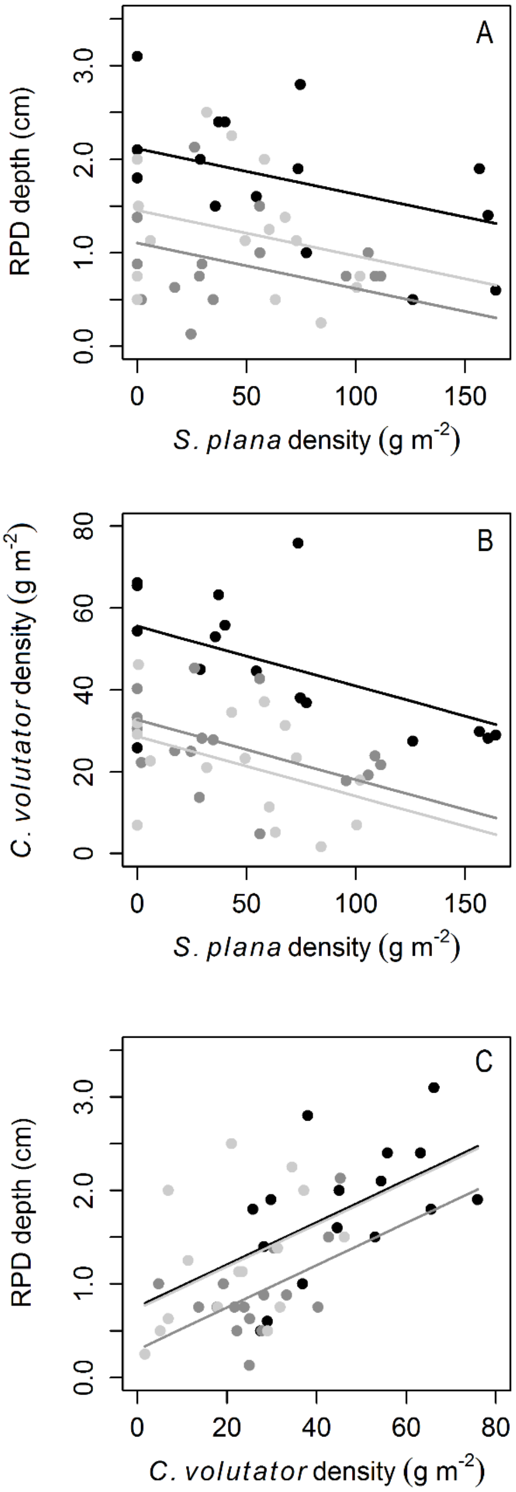

Fig. 4.5. Relationships between (A) redox potential discontinuity (RPD) depth and *Scrobicularia plana* density, (B) *Corophium volutator* density and *S. plana* density, and (C) RPD depth and *C. volutator* density at T1 (1 week; black), T2 (5 weeks; dark grey) and T3 (9 weeks; light grey). Trend lines were predicted from models with no interactions between the explanatory variables and Time, as these terms were statistically insignificant, and with Block fixed to ‘A’.

Table 4.3. The average direct effect (ADE), average causal mediation effect (ACME; mediated by *Corophium volutator* density) and total effect of *Scrobicularia plana* density on redox potential discontinuity (RPD) depth. Estimated effects (with 95% confidence intervals) are presented. Significant *p*-values (< 0.05) are in bold.

	Estimate	95% confidence intervals	*p*
ADE	-0.0016	-0.0056, 0.0025	0.4416
ACME	-0.0033	-0.0067, -0.0010	**0.0044**
Total Effect	-0.0049	-0.0089, -0.0010	**0.0168**

Density-dependent intra- and interspecific interactions *vs.* RPD depth

The relationship between RPD depth and Intra was initially slightly positive and became increasingly negative over time (Fig. 4.6a). While this result is consistent with a temporal increase in the effect of intraspecific antagonism on function delivery**,** the null hypothesis of no Intra*Time interaction could not be rejected (*p* = 0.079; Table 4.4).

The effect of Inter on RPD depth varied significantly over time (Table 4.4, Inter*Time). The relationship between RPD depth and Inter was initially slightly negative and, as predicted, became increasingly positive as the experiment progressed, indicating a temporal increase in the effect of interspecific facilitation on function delivery (Fig. 4.6b).

Table 4.4. General linear model summary of variation in RPD depth across experimental blocks, over time (1 week, 5 weeks & 9 weeks), in relation to taxa densities and in relation to indices for density-dependent intraspecific interactions (Intra) and interspecific interactions (Inter). Significant *p*-values (< 0.05) are in bold.

Source	d.f.	*F*	*p*
Block	3	0.197	0.8974
Time	2	3.796	**0.0339**
Scrobicularia plana	1	0.130	0.7208
Corophium volutator	1	0.119	0.7322
Hediste diversicolor	1	1.549	0.2229
Tubificoides spp.	1	2.151	0.1529
Macoma balthica	1	1.344	0.2555
Eteone longa	1	0.446	0.5094
Intra	1	1.194	0.2833
Inter	1	0.199	0.6585
Intra*Time	2	2.766	0.0790
Inter*Time	2	4.562	**0.0186**
Residuals	30		

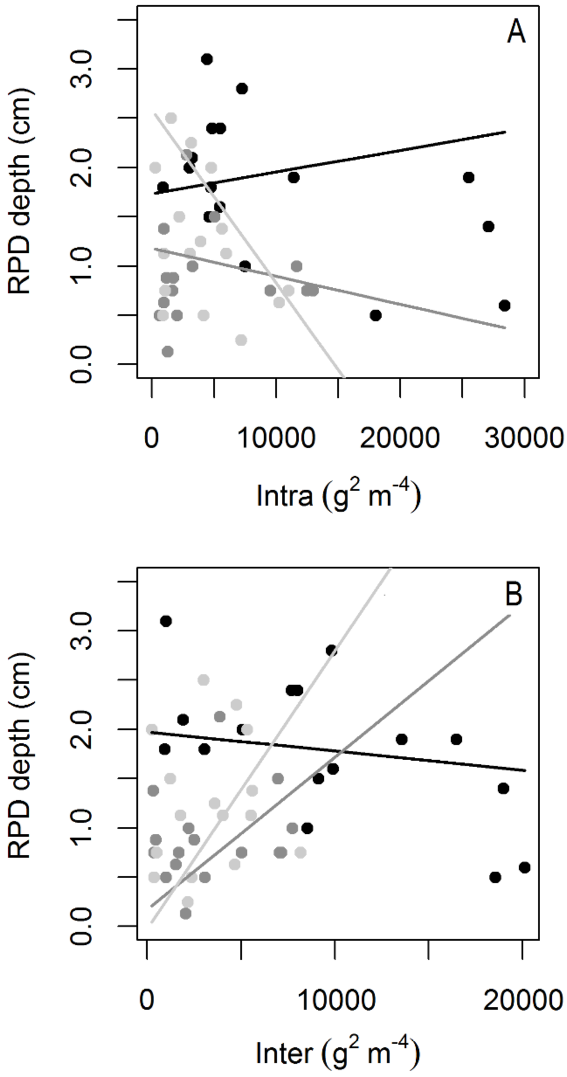

Fig. 4.6. Relationships between (A) redox potential discontinuity (RPD) depth and density-dependent intraspecific interactions (Intra), and (B) RPD depth and density-dependent interspecific interactions (Inter). Data are presented for sampling occasions T1 (1 week; black), T2 (5 weeks; dark grey) and T3 (9 weeks; light grey). Trend lines were predicted after fixing Block to 'A' and all covariates (except the term of interest) to the mean values across sampling occasions.

DISCUSSION

Previous BEF experiments conducted within marine sediments have suggested that biotic influence over function delivery is driven by individual, functionally dominant, species (Gamfeldt et al. 2015). Complementarity among species, although prevalent in terrestrial plant assemblages (Loreau & Hector 2001; Tilman et al. 2014) and possibly freshwater sediments (Mermillod-Blondin et al. 2003; Caliman et al. 2011), has not previously been identified as an important driver of marine sediment functioning (Gamfeldt et al. 2015; Strong et al. 2015). Results presented here reaffirm a direct functional importance of certain marine benthic species, but also point to the indirect functional importance of other species to which their density is tightly coupled. Additionally, the results suggest that interspecific facilitation and possibly intraspecific antagonism play roles in benthic ecosystem functioning, and that these effects increase over time (on the scale of weeks). This study therefore provides some evidence in marine sediments for BEF mechanisms that have previously had little support.

In accordance with other studies that manipulated the density of large bivalves (e.g. Jensen 1985; Beadman et al. 2004), the density of the mud shrimp *Corophium volutator* decreased with increasing density of *Scrobicularia plana* (Fig. 4.5b). Such declines in *Corophium* density have previously been attributed to disturbance of its burrows due to sediment reworking by the common cockle *Cerastoderma edule* (Jensen 1985) and surface organic matter deposition (faeces and pseudofaeces) by the blue mussel *Mytilus edulis* (Beadman et al. 2004). Since *S. plana* disturbs the sediment both through feeding and organic matter deposition, it is possible that either or both of these activities explain the negative impact on *C. volutator* density. Indeed, I found no evidence for net organic matter deposition or consumption by *S. plana*, suggesting that both processes may have contributed to a similar degree. However, neither of these mechanisms are explicitly demonstrated by the analyses of this study. While *S. plana* density had a negative impact on the *C. voluator* population, *C. volutator* density increased as a result of a cage effect in this study, but not beyond the range of abundance observed in natural populations in the UK (a maximum of 75,000 individuals m^{-2} were recorded here, compared to over 100,000 individuals m^{-2} recorded in the Stour Estuary, Suffolk; Hughes 1988). This experimental artifact was therefore deemed not to have created unrealistic conditions.

The reduction in RPD depth with decreasing *C. volutator* density (Fig. 4.5c) is consistent with previous observations (Limia & Raffaelli 1997) and could possibly be due to a reduced capacity of *Corophium* populations to rework the sediment as density declines (De Backer et al. 2011). Reduced densities of ‘bioturbator’ species have been found to negatively impact marine sediment functioning in various studies, including those conducted in the field (e.g. Lohrer et al. 2004; Norkko et al. 2013). While the ACME (the impact of *S. plana* density on RPD depth via *C. volutator* density) in my analysis was robust only to small violations of sequential ignorability (i.e. the non-existence of confounders; see Imai et al. 2010), the only potential confounder identified within the macroinfaunal assemblage was the density of the ragworm *Hediste diversicolor*; to which *C. volutator* density was negatively related. Since *H. diversicolor* reworks the sediment and ventilates burrows (Christensen et al. 2000; Hale et al. 2014), and thus any influence of this species on RPD depth would be expected to be positive, it was deemed unlikely that the negative correlation with *C. volutator* density undermined the ACME. The absence of a direct influence of *S. plana* density on RPD depth could be due to its low mobility and high per capita biomass, as ventilation of vertical burrows by relatively few individuals may be insufficient to increase oxygen penetration at the patch scale.

Although the influence of *S. plana* density (via *C. volutator* density) on RPD depth did not weaken temporally, the influence of density-dependent interspecific interactions on RPD depth did become increasingly positive over time, as predicted (Fig. 6b). This result suggests that interspecific facilitation may become an increasingly important driver of benthic ecosystem functioning as time progresses, which is consistent with the temporal emergence of complementarity among marine macroalgae in natural, environmentally heterogeneous systems (e.g. Stachowicz et al. 2008). To date, most marine sediment BEF experiments have been conducted within homogenous laboratory microcosms. Others have been conducted for short durations (≤ 2 weeks) in field mesocosms (e.g. Godbold et al. 2009b) or environmentally heterogeneous laboratory microcosms (e.g. Godbold et al. 2011). The results of our field experiment suggest that the same meticulously-designed experiments, if conducted for longer durations and in natural heterogeneous environments, may show complementarity to be a more important driver of ecosystem functioning than previously suggested. That said, short-term microcosm experiments using freshwater sediments have shown consistent complementarity effects among macroinfauna (e.g. Mermillod-Blondin et al. 2003; Caliman et al. 2011), which appear to increase in strength for more integrative measures of ecosystem functioning (Caliman et al. 2012, 2013). It is therefore possible that the apparent dominance of individual species over marine sediment functioning is biased by a tendency for previous studies to focus on a few simple ecosystem functions (e.g. benthic-pelagic nutrient flux). Here, our focus on RPD depth, a sedimentary property that influences multiple benthic ecosystem functions (Solan et al. 2004; Teal et al. 2010), may have left us well-placed to detect biotic effects relating to complementarity. Therefore, as well as conducting longer experiments in the field, future BEF studies may be more likely to detect complementarity by considering more integrative measures of ecosystem functioning.

Unlike most BEF studies, I considered the influence of intraspecific interactions on ecosystem functioning in my analyses. Whereas any trait dissimilarities among species will aid their ability to partition niches and may promote facilitation (Hooper et al. 2005), high densities of a single species may lead to reduced individual performance, if, for example, space limitation causes territorial behaviour and reduced activity (Bridges et al. 1996). Consistent with an increasing effect of intraspecific antagonism over time, I found that the relationship between RPD depth and density-dependent intraspecific interactions became increasingly negative as the experiment progressed (Fig. 4.6a); however, the null hypothesis could not be categorically rejected (p=0.079). The results therefore provide weaker evidence for intraspecific antagonism than interspecific facilitation as a driver of ecosystem functioning. I also note here that while the development of pools during the experiment represents a potential confounder of the relationships between intra- and interspecific interactions and RPD depth, the consistent relationship between *S. plana* density and RPD depth (via *C. volutator* density) over time suggests that the pools did not have a major influence on relationships between the macroinfaunal assemblage and benthic functioning.

In line with calls to increase realism in BEF research (e.g. Hillebrand & Matthiessen 2009) I used an *in situ* experiment to assess how the functioning of an intertidal mudflat was impacted after simulating a realistic pattern of biodiversity change. While some consistency was found with laboratory experiments that have assessed marine sediment BEF relationships (i.e. the importance of the density of functionally dominant species), the suggestion that additional mechanisms are in operation reiterates the need to manipulate natural assemblages to understand how ongoing biodiversity change is likely to impact ecosystem functioning (see Gamfeldt et al. 2015). Contrary to the modern paradigm of biodiversity conservation, the results of this study imply that a decline or loss of a population can enhance function delivery if it causes the population of a functionally dominant species to increase. Likewise, a non-native species introduction could reduce function delivery if it causes the population of a functionally dominant native species to decline or go extinct (see Gurevitch & Padilla 2004). Perhaps most noteworthy from a conservation perspective, however, is the finding that the effects of interspecific facilitation and, possibly, intraspecific antagonism increased as the experiment progressed, which suggests that diverse species assemblages may generally promote high function delivery.

This study provides an incremental step forward in developing our understanding of the impact of real-world biodiversity change on the processes that underpin ecosystem service provision. While I have built on previous studies by conducting the experiment in the field and for a longer duration, as with all small-scale experiments there remain issues regarding the wider implications of the results. I selected a low diversity system for the study site, which is typical of intertidal mudflats, and it is under these conditions that I am most confident that the findings will generally apply. The evidence presented here, and elsewhere for low diversity marine systems (see Gamfeldt et al. 2015; Strong et al. 2015), highlights the importance of protecting species whose associated functions underpin ecosystem service provision (e.g. waste assimilation is underpinned by decomposition, which mainly occurs above the RPD depth (Teal et al. 2010)). My results also suggest that those charged with environmental and biodiversity protection need to consider the potential importance of species that have no apparent direct influence over functioning, but may influence the densities of species that do. The degree to which the results apply to more diverse marine sediments (and other ecosystems), with high functional redundancy, remains unclear. Individual species may be of lesser importance under these conditions, but species losses could potentially induce changes to many populations and thus have large indirect impacts on functioning. Studies have yet to experimentally assess how changes to biodiversity affect ecosystem functioning in species-rich benthos, but methods are being proposed to integrate the design of such experiments with broad-scale patterns in seafloor biodiversity (e.g. Snelgrove et al. 2014). For now, the evidence presented here for complementarity among species supports the general principle of maintaining diverse species assemblages so as to avoid potential declines in function delivery associated with biotic impoverishment.

ACKNOWLEDGEMENTS

I thank David Annett and Lélis Antonio Carlos Júnior for their assistance with fieldwork and figure preparation, respectively.

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SUPPLEMENTARY MATERIAL

Table 4.5. General linear model summary of variation in surface sediment organic matter content across experimental blocks, over time (1 week, 5 weeks & 9 weeks) and in relation to bulk sediment organic matter content. Significant *p*-values (< 0.05) are in bold.

Term	d.f.	F	*p*
Block	3	0.748	0.5301
Time	2	6.937	**0.0026**
Bulk organic matter content	1	1.215	0.2771
Bulk organic matter content*Time	2	5.702	**0.0067**
Residuals	39		

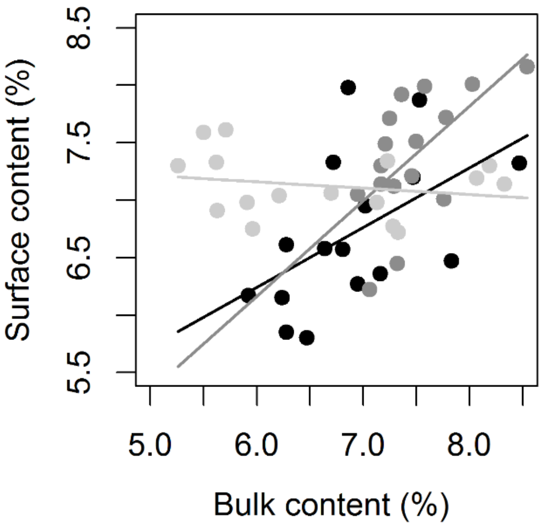

Fig. 4.7. The relationship between surface (0 - 1 cm) and bulk (0 - 20 cm) sediment organic matter content at T1 (1 week; black), T2 (5 weeks; dark grey) and T3 (9 weeks; light grey).

Table 4.6. General linear model summary of variation in redox potential discontinuity (RPD) depth across experimental blocks, over time (1 week, 5 weeks & 9 weeks) and in relation to *Scrobicularia plana* density based on the initial density addition categories (0 g m^{-2}, 255 g m^{-2}, 510 g m^{-2} and 1020 g m^{-2}). Significant *p*-values (< 0.05) are in bold.

Term	d.f.	F	*p*
Block	3	0.302	0.8239
Time	2	10.044	0.0004
Scrobicularia plana	3	2.934	**0.0477**
*Scrobicularia plana**Time	6	1.654	0.1636
Residuals	33		

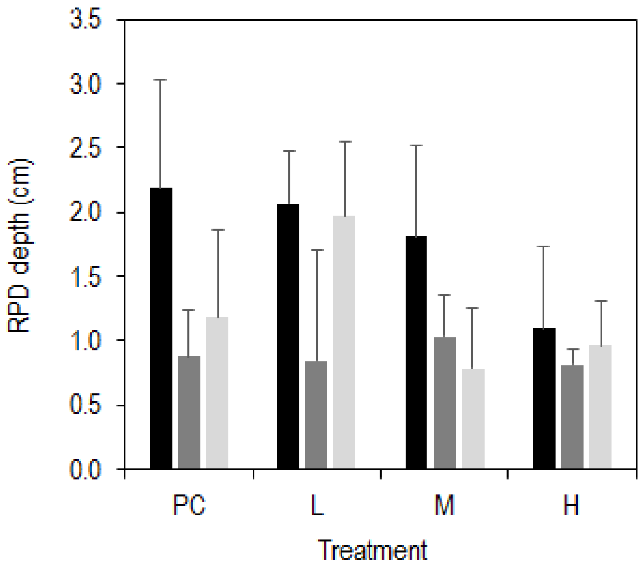

Fig. 4.8. Variation in redox potential discontinuity (RPD) depth (with 95% confidence intervals) across experimental plots with no *Scrobicularia plana* addition (procedural control plots; PC), low density *S. plana* addition (255 g m^{-2}; L), medium density *S. plana* addition (510 g m^{-2}; M) and high density *S. plana* addition (1020 g m^{-2}; H) at T1 (1 week; black), T2 (5 weeks; dark grey) and T3 (9 weeks; light grey).

Table 4.7. General linear model summary of variation in redox potential discontinuity (RPD) depth across experimental blocks, over time (1 week, 5 weeks & 9 weeks) and in relation to total biomass and *Scrobicularia plana* density. Significant *p*-values (< 0.05) are in bold.

Term	d.f.	F	*p*
Block	3	0.606	0.6155
Time	2	1.816	0.1765
Total biomass	1	3.246	0.0796
Scrobicularia plana	1	6.127	**0.0179**
*Scrobicularia plana**Time	2	0.959	0.3923
Residuals	38		

Table 4.8. General linear model summary of variation in redox potential discontinuity (RPD) depth across experimental blocks, over time (1 week, 5 weeks & 9 weeks) and in relation to sediment organic matter content. Significant *p*-values (< 0.05) are in bold.

Term	d.f.	F	*p*
Block	3	0.277	0.8416
Time	2	4.151	**0.0232**
Organic matter content	1	1.512	0.2263
Organic matter content*Time	2	0.444	0.6448
Residuals	39		

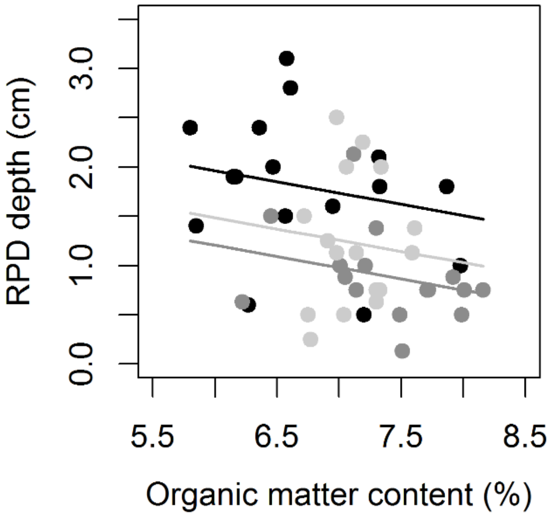

Fig. 4.9. The relationship between RPD depth and sediment organic matter content at T1 (1 week; black), T2 (5 weeks; dark grey) and T3 (9 weeks; light grey).

Table 4.9. General linear model summary of variation in the density of *Corophium volutator* across experimental blocks, over time (1 week, 5 weeks & 9 weeks) and in relation to the density of *Hediste diversicolor*. Significant *p*-values (< 0.05) are in bold.

Term	d.f.	F	*p*
Block	3	3.750	**0.0185**
Time	2	24.673	**< 0.0001**
Hediste diversicolor	1	10.702	**0.0022**
*Hediste diversicolor**Time	2	0.063	0.9392
Residuals	39		

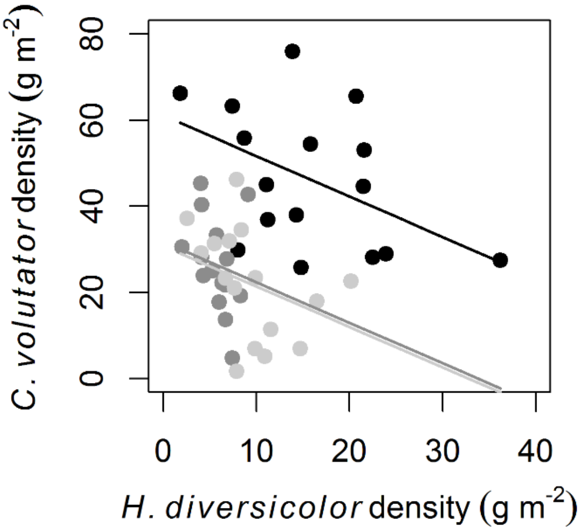

Fig. 4.10. The relationship between *Corophium volutator* density and *Hediste diversicolor* density at T1 (1 week; black), T2 (5 weeks; dark grey) and T3 (9 weeks; light grey).

Chapter 5

Interspecific interactions may alter relationships between species densities and the delivery of ecological functions

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ABSTRACT

There is now a large body of research focussed on the impacts of biodiversity loss on ecosystem functioning. The impacts of shifts in species densities are not well-studied, despite this pattern of biodiversity change being pervasive. Theory and experimentation suggest that the impacts of changing densities should be predictable based on the biological traits of the species involved. However, interactions among species may affect density-function relationships, with the strength and sign of interactions potentially depending on environmental context (e.g. homogenous *vs.* heterogeneous conditions) and the function considered. Here, I assessed how concurrent changes to the densities of two common marine macroinfauna, *Corophium volutator* and *Hediste diversicolor*, affected the ecological functions of organic matter consumption and benthic-pelagic nutrient flux. Complementary experiments were conducted within homogenous laboratory microcosms and field plots. When the densities of the two species were increased within microcosms, interspecific interactions enhanced the effects that individual species had on organic matter consumption (i.e. interspecific facilitation) and reduced individual effects on nutrient flux (i.e. interspecific antagonism). Trait-based predictions of density-function relationships were only consistently supported when the density of the other species was low. In field plots, increasing the density of either species had a positive effect on organic matter consumption (with no significant interspecific interactions) but no effect on nutrient flux. The results suggest that species density-function relationships can be altered by interspecific interactions, which can be either facilitative or antagonistic depending on the function considered. The impacts of shifts in species densities may therefore not be predictable from biological traits alone. Possible explanations for why interactions were detected in microcosms but not field plots are discussed.

INTRODUCTION

The impact of biodiversity change on the functioning of ecosystems is a pressing environmental concern (see Cardinale et al. 2012; Pereira et al. 2012). An extensive body of research shows that the delivery of key ecological functions, such as resource acquisition and nutrient retention, tends to decline with decreasing species richness (Hooper et al. 2005; Tilman et al. 2014). Less attention, however, has been given to the consequences of turnover in species composition or shifts in species densities. The impacts of these phenomena are pertinent given the degree and ubiquity with which they are currently occurring (Dirzo et al. 2014; Dornelas et al. 2014; McGill et al. 2015), with examples ranging from plankton (Beaugrand et al. 2002) through to birds (Inger et al. 2015) and primates (Peres & Dolman 2000).

Experimental evidence suggests that the delivery of ecological functions varies with respect to the presence and density of species with particular biological traits (Chapin et al. 1997; Hillebrand & Matthiessen 2009). In terrestrial plant assemblages, for example, carbon sequestration is driven by populations of slow-growing and long-lived species (De Deyn et al. 2008), whereas nutrient cycling is highly affected by nitrogen-fixers (Graham & Vance 2003). The impacts of shifts in species densities on ecosystem functioning should therefore be predictable based on the traits of the species involved. However, interspecific interactions may also affect how biota influence the delivery of ecological functions, either through facilitation (i.e. positive interactions; Cardinale et al. 2002; Tiunov & Scheu 2005) or antagonism (i.e. negative interactions; Polley et al. 2003; Jousset et al. 2011). If so, then the effects of changing species densities could be amplified or weakened depending on community composition, thus undermining our ability to predict changes to functioning using biological traits. To date, the role of interspecific interactions in regulating function delivery has generally been demonstrated under controlled environmental conditions (but see Polley et al. 2003). The degree to which interspecific interactions influence density-function relationships within natural systems is unclear. It is possible that such effects will be overshadowed (Srivastava & Vellend 2005; Strong et al. 2015), weakened (Tiunov & Scheu 2005; Jousset et al. 2011) or reversed in sign (Maestre et al. 2010) by environmental heterogeneity.

The amphipod *Corophium volutator* and the polychaete *Hediste diversicolor* are ideal model organisms for assessing the impacts of shifts in species densities on ecosystem functioning. Commonly found within intertidal soft sediments of the temperature North Atlantic, these species often dominate infaunal biomass (Jackson et al. 1985; Murdoch et al. 1986; Scaps 2002; Ysebaert et al. 2005; Barbeau et al. 2009) and are therefore likely to be major contributors to their associated ecological functions (Grime 1998; Gaston 2010). While co-occurrence is commonplace, negative correlations between the densities of *C. volutator* and *H. diversicolor* have been reported at multiple sites (e.g. Ólafsson & Persson 1986; Hughes & Gerdol 1997; Clare et al. 2015). Experiments suggest that various factors may explain this relationship, including interspecific competition for food and space (Ólafsson & Persson 1986; Rönn et al. 1988; Smith et al. 1996); however, in other studies a clear relationship between the densities of *C. volutator* and *H. diversicolor* has not been apparent (e.g. Flach 1992; Jensen & André 1993). Temporal shifts in the dominance of the two species can occur (Ysebaert & Herman 2002), and may reflect context-dependent outcomes of interspecific interactions under changing environmental conditions (see Maestre et al. 2010; Drolet et al. 2013) or an increase in the density of one species after the population of the other collapses (Ólafsson & Persson 1986).

In the present study, I investigated the impact of concurrent changes in the densities of *C. volutator* and *H. diversicolor* on organic matter consumption and benthic-pelagic nutrient flux (hereafter nutrient flux); key ecological functions that underpin waste assimilation and pelagic primary production, respectively. *C. volutator* constructs shallow burrows (< 5 cm) from which it feeds on organic matter on the sediment surface (Meadows & Reid 1966; Gerdol & Hughes 1994), whereas *H. diversicolor* flushes relatively deep burrows (< 15 cm) as a means of suspension-feeding and obtaining oxygen (Riisgård 1991; Scaps 2002). It was therefore predicted that an increase in the density of *C. volutator* would lead to enhanced organic matter consumption and that an increase in *H. diversicolor* density would lead to enhanced nutrient flux (Fig. 5.1, solid black lines). It is noted, however, that burrow construction by *C. volutator* is likely to cause a flux of nutrients from the upper sediment layers (Pelegri et al. 1994), and that disturbance of these burrows by *H. diversicolor* may enhance this process (Hale et al. 2014; Fig. 5.1, dotted line). Additionally, the trophically-plastic *H. diversicolor* can feed on deposits (Scaps 2002), and the density of *C. volutator* may affect the degree to which this occurs; either positively, as sediment resuspension by *C. voluator* (see de Deckere et al. 2000) might inhibit the efficiency with which *H. diversicolor* can suspension-feed (Fig. 5.1, dashed lines), or negatively, due to interspecific competition or behavioural avoidance (Fig. 5.1, grey lines). It was therefore postulated that the influence of the densities of the two species on ecosystem functioning may interact. These hypotheses were tested using complementary experiments in laboratory microcosms and field plots to assess whether any effects observed for each ecological function under homogenous conditions are also observed under natural, heterogeneous conditions.

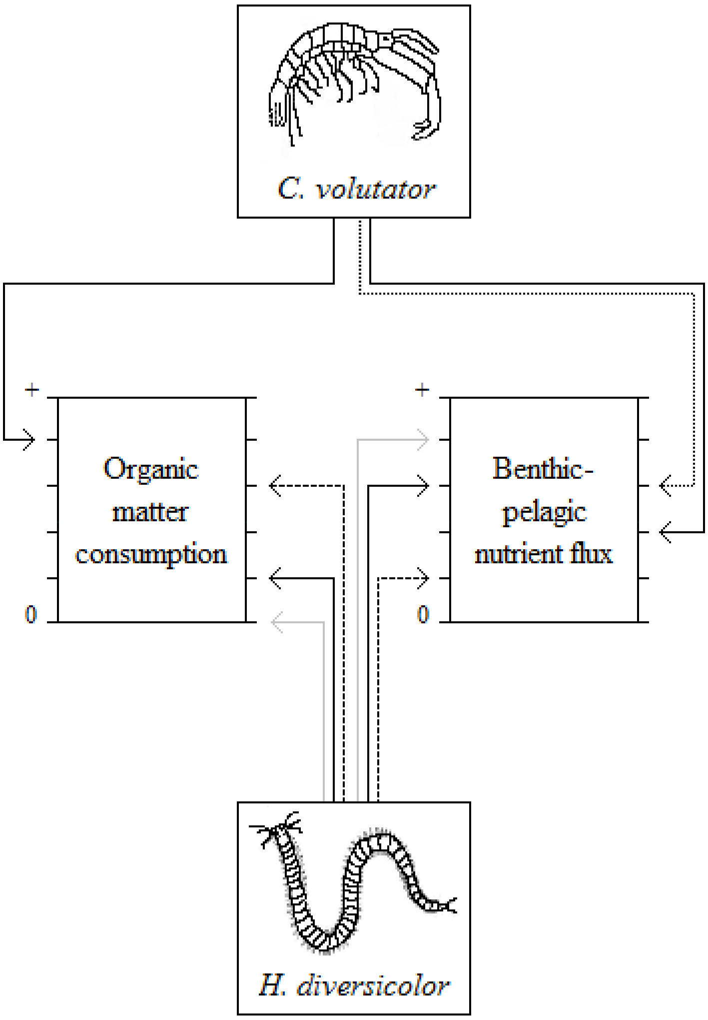

Fig 5.1. The predicted effects that increasing the densities of *Corophium voluator* and *Hediste diversicolor* will have on organic matter consumption and benthic-pelagic nutrient flux, from 0 (no effect) toward an increasingly positive effect. The solid black lines represent predictions based on the biological traits of *C. volutator* and *H. diversicolor*. For *C. volutator*, the dotted line represents how an interaction with *H. diversicolor* may enhance its effect on nutrient flux. For *H. diversicolor*, the dashed lines represent how an interaction with *C. volutator* may enhance its effect on organic matter consumption and reduce its effect on nutrient flux; whereas the grey lines represent how a different interaction with *C. volutator* may reduce its effect on organic matter consumption and enhance its effect on nutrient flux.

MATERIALS AND METHODS

The study consisted of two experiments: one conducted within laboratory microcosms and the other conducted *in situ* within an intertidal mudflat on the Mersey Estuary, Liverpool, UK (53° 21′ 22″ N, 02° 55′ 33″ W). Assemblages of varying densities of *Corophium volutator* and *Hediste diversicolor* were created for both experiments. The mass of consumed organic matter and nutrient concentrations were measured directly in the microcosms but by proxy in field due to methodological constraints.

The experiments were run for 12 days, which roughly corresponds to the duration of most other studies that have assessed biotic influence over ecosystem functioning using benthic macroinfauna. The effects of macroinfaunal species on functioning are known to manifest within such short periods (e.g. Godbold et al. 2009a; Braeckman et al. 2010); however, the effects of interactions among species may become more prominent beyond this period (see **Chapter 4**). Practical issues regarding the rapid depletion of organic detritus added to microcosms and difficulties in maintaining the desired species density treatments in field plots over time made a longer experiment duration unfeasible.

Experimental procedure

Microcosm experiment

The macroalga *Ulva intestinalis* and sediment containing *C. volutator* and *H. diversicolor* were collected from the field experiment site. The sediment was sieved through 0.5 mm mesh and retained individuals of the two study species were incubated in aerated aquaria at the approximate temperature and salinity of the field site (15°C; 30 psu). Sieved sediment was captured, allowed to settle for 24 hours and homogenised after draining the overlying water. *U. intestinalis* was rinsed with seawater and dried at 70°C.

Ten treatments consisting of mixtures of *C. volutator*, *H. diversicolor* and organic detritus (*U. intestinalis*) were created within laboratory microcosms (approximately 0.01 m^2). The first five treatments represented a progressive shift from *C. volutator* (*Cor*) to *H. diversicolor* (*Hed*) dominance: 1) 1.00 g *Cor*, 0.00 g *Hed*; 2) 0.75 g *Cor*, 0.25 g *Hed*; 3) 0.50 g *Cor*, 0.50 g *Hed*; 4) 0.25 g *Cor*, 0.75 g *Hed*; 5) 0.00 g *Cor*, 1.00 g *Hed*. Initial total biomass was set to 1 g to match macroinfaunal density at the field site at the time of the experiment. Three additional treatments, reflecting an increase in *H. diversicolor* density while *C. volutator* density remained consistently high, were also included: 6) 1.00 g *Cor*, 0.25 g *Hed*; 7) 1.00 g *Cor*, 0.50 g *Hed*; 8) 1.00 g *Cor*; 1.00 g *Hed*. These treatments were used to aid comparisons between microcosm and field experiments, as incrementally increasing the density of *H. diversicolor* across field plots did not cause the dominant *C. volutator* to decline in density (i.e. the intended shift in species dominance was not achieved; see *Field experiment* within the 'Experimental procedure' and 'Data analysis' sections of Materials and Methods). One gram of dried *U. intestinalis* was added to each of the above treatments. Two control treatments were also used: 9) *U. intestinalis* addition but no fauna addition, and 10) no *U. intestinalis* addition and no fauna addition. These treatments provided a baseline from which to measure the effects of species densities and allowed the influence of *U. intestinalis* addition on nutrient concentration to be determined. Each treatment was replicated six times.

Microcosms were created by filling opaque cylindrical vessels (10 cm diameter, 40 cm height) with 0.75 l of homogenised sediment (10 cm depth) and 1.50 l of overlying water (30 psu; 20 cm depth), which had been pre-filtered through 1.2 µm mesh. After a settling period of 24 hours, macroinfauna were transferred from aquaria into microcosms to produce the experimental treatments. After two days the water was replaced to remove excess nutrients associated with assembly. One gram of dried *U. intestinalis* was added to each vessel and allowed to settle onto the sediment surface. Microcosms were aerated throughout the 12-day experiment period (starting at macroinfauna addition) and kept at a constant temperature of 16°C under artificial lighting.

Duplicate samples of overlying water (5 ml) were taken at the end of the experiment and sediment contained within each microcosm was sieved through 0.5 mm mesh. Additional sieves of 0.355 and 0.235 mm mesh were stacked below to capture fragments of *U. intestinalis* that passed through the 0.5 mm sieve. The wet biomasses of *C. volutator* and *H. diversicolor* were immediately weighed to provide comparable measurements to the start of the experiment. Retained *U. intestinalis* was dried at 70°C and re-weighed. Organic matter consumption was indicated by the loss of mass of *U. intestinalis* (*sensu* Godbold et al. 2009b). Ammonium (NH_4-N) and nitrate (NO_3-N) concentrations in the water samples were measured using a Seal Analytical AutoAnalyser 3 HR, calibrated using Analar Grade solid ammonium sulphate and potassium nitrate dissolved to 100 ppm stock standards, and summed to give the dissolved inorganic nitrogen (DIN) concentration (*sensu* Caliman et al. 2012). Variation in DIN concentration among microcosms was taken to indicate variation in the level of nutrient flux.

Due to the large total number of microcosms (n = 60) the experiment was temporally staggered across six experimental runs, each consisting of a single block of ten microcosms (one replicate of each treatment). The experiment began on the 1st of September 2014 and an experimental run was initiated every 7 days. Within each block, all microcosms were created using the same batch of homogenised sediment, seawater, macroinfauna, and *U. intestinalis*.

Field experiment

At the time of the field experiment (June-July 2014), macroinfaunal biomass at the study site was dominated by *C. volutator* (mean density = 45 g m^{-2}) followed by *H. diversicolor* (mean density = 10 g m^{-2}). As previous studies suggest that high densities of *H. diversicolor* cause the density of *C. volutator* to decline (e.g. Ólafsson & Persson 1986; Rönn et al. 1988), *H. diversicolor* was added to experimental plots (approximately 0.03 m^2) at initial densities of 1 g (32 g m^{-2}), 2 g, 3 g, 4 g, 6 g, 8 g and 0 g (as a ‘no addition’ baseline) with the aim of creating a progressive shift from *C. volutator* dominance to *H. diversicolor* dominance. This range of treatments included superficially high initial densities, as a trial experiment showed that an addition of 8 g of *H. diversicolor* was required to produce a density that was approximately equal to the average density of *C. volutator* after 14 days. Each of the seven *H. diversicolor* density treatments was replicated three times. Plots were laid across the shore in three blocks at an elevation of 1 m above mean sea level. Each block contained one replicate of each of the seven density treatments.

The field experiment was set up between the 21st and the 23rd of June 2014. One block was set up on each day during this period. Sediment containing *H. diversicolor* was collected from the study site, sieved through 0.5 mm mesh in a bath of seawater, and retained individuals were incubated as described above for the microcosm experiment. The density treatments were weighed out in the laboratory and transported to the experiment site within plastic containers filled with water from the aquaria used for incubation. *H. diversicolor* individuals were transplanted onto the sediment surface within circular plots (20 cm diameter) after creating small holes (using a metal rod; 0.5 cm diameter) to encourage individuals to burrow within the plot area. A corer (2 cm diameter, 2 cm depth) was used to collect a single surface sediment sample from the centre of each plot immediately prior to transplantation. Any macroinfauna contained within these samples were removed using forceps. Samples were then frozen at -15°C for later analysis of total carbon (C) and total nitrogen (N) content.

At the end of the experiment, individual surface sediment samples were again collected from the centre of each plot for analysis of total C and total N, as described above. The plots were then sampled in their entirety using a cylindrical corer (20 cm diameter, 20 cm depth). Samples were sieved through 0.5 mm mesh and the residue preserved in 70% ethanol. Retained fauna were identified to the lowest taxonomic level possible and their fresh biomasses weighed after soaking in freshwater and draining through filter paper for 30 minutes.

After freeze-drying the surface sediment samples, % total C and % total N were calculated using a Carlo Erba NC 2500 Elemental Analyser, calibrated using High Organic Standard OAS (Elemental Microanalysis Ltd) (C = 7.17% ± 0.09%; N = 0.57% ± 0.02 %). The change in total C from the start to the end of the experiment was used as a measure of organic matter consumption. A greater net loss of total C (initial % total C – final % total C) was taken to indicate a greater consumption of organic matter. I therefore assumed that any deposition of C and any loss of C through non-consumptive processes was equivalent across all plots within a block. Change to the C:N ratio was used as an index of nutrient flux (*sensu* Godbold et al. 2009b). A greater increase in C:N during the experiment (final C:N – initial C:N) was taken to indicate a greater loss of total N relative to changes in total C (associated with organic matter consumption or deposition) and therefore a greater flux of nutrients into the overlying water.

Data analysis

Statistical analyses were performed using R statistical software (version 3.2.1, R Core Development Team 2015). Higher-order terms were deleted before testing lower-order terms in general lineat models. Null hypotheses were rejected at $p < 0.05$. Assumptions of homoscedasticity and normality of residuals were checked by inspecting plots of residuals against fits and normal quantile plots, respectively. Data were ln-transformed, when required, to meet test assumptions.

Microcosm experiment

General linear models were used to assess how organic matter consumption (loss of mass of *U. intestinalis*) and nutrient flux (DIN concentration) varied in relation to the densities of *C. volutator, H. diversicolor* and their interspecific interactions (*C. volutator***H. diversicolor*). Density-dependent intraspecific effects (*C. volutator*^{2} and *H. diversicolor*^{2}) were also included in the models to account for any influence that intraspecific competition for food and/or space may have on functioning, but were removed if statistically insignificant.

As nutrients are remineralised by the break-down of organic matter (Nixon 1981), and these nutrients may be released into the overlying water when detritus is consumed by benthos (and therefore not be attributable to the burrowing activities of macroinfauna), the relationship between DIN concentration and the loss of mass of *U. intestinalis* was tested using a general linear model, with Block included as a factor. Similarly, a general linear model was used to compare DIN concentration in the two control treatments and assess the influence of *U. intestinalis* addition and decomposition on nutrient flux in the absence of macroinfauna, with Block again included as a factor.

In one replicate containing *U. intestinalis*, a mass of the detrital alga was found floating within the microcosm at the end of the experiment and had therefore not been available to benthic organisms. The resulting observation for organic matter consumption lay > 3 standard deviations from its expected value. The replicate was therefore removed from all analyses as the desired treatment had not been achieved. However, robust linear regression using MM-estimation (Venables & Ripley 2002, section 6.5; implemented in the R package **rlm**), without removing the outlying observation, produced almost identical coefficients to the least squares linear models, with the observation removed, for both organic matter consumption and nutrient flux.

Results are presented based on species densities recorded at sampling (i.e. final densities; see Table 1), to allow for consistency with field experiment analyses. Performing analyses using either the initial densities or the means of initial and final densities had little quantitative effect on the results (see Supplementary Material, Tables 5.3 & 5.4, respectively).

Field experiment

The densities of *H. diversicolor* and *C. volutator* at sampling were plotted against the transplanted density of *H. diversicolor*. This allowed assessment of whether the experimental treatment had: 1) raised *H. diversicolor* density beyond ambient conditions, and 2) resulted in a shift in species dominance. A general linear model was also used to assess the relationship between the densities of *C. volutator* and *H. diversicolor* at sampling, with ‘Block’ included as a factor in the model. Although the attempt to induce a shift in species dominance was unsuccessful, and there was no significant relationship between the densities of the two species (general linear model: $F_{1,18} = 0.490$; $p = 0.4930$), the density of *H. diversicolor* was successfully raised beyond ambient conditions and the density of *C. volutator* was highly variable among plots (Fig 5.2). This allowed the influence of the densities of the two species (and their interactions) on function delivery to be assessed.

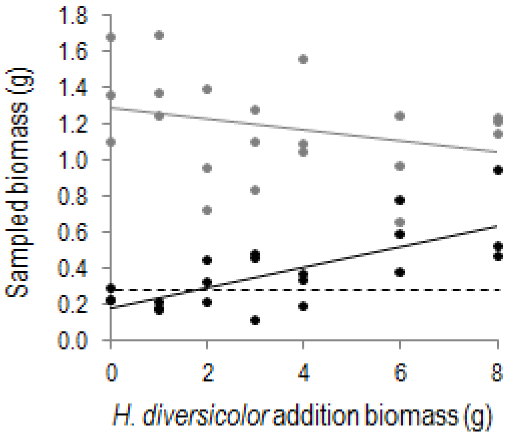

Fig 5.2. Variation in the sampled biomass (12 days after experiment initiation) of *Hediste diversicolor* (black; linear regression, $R^2 = 0.59$) and *Corophium volutator* (grey; linear regression, $R^2 = 0.09$) in relation to the addition biomass of *H. diversicolor* in field plots. The dashed line marks the maximum density of *H. diversicolor* recorded in plots with no experimental additions.

General linear models were used to test how organic matter consumption (initial % total C – final % total C) and nutrient flux (final C:N – initial C:N) varied in relation to the densities of *C. volutator*, *H. diversicolor*, *C. volutator*H. diversicolor*, *C. volutator*^{2} and *H. diversicolor*^{2}. Squared density terms were removed from the models if statistically insignificant. The densities of the other macroinfauna (*Macoma balthica* and *Tubificoides* spp.) and Block were also included to reduce residual variation. All terms except Block were treated as quantitative variables.

RESULTS

Microcosm experiment

Organic matter consumption (the loss of mass of *U. intestinalis*) varied significantly in relation to *C. volutator*H. diversicolor* (Table 5.1). *C. volutator* density had a consistently positive effect on organic matter consumption, whereas the effect of *H. diversicolor* density on organic matter consumption went from minimal to positive as the density of *C. volutator* increased (Fig 5.3a). The effects of *C. volutator*^{2} and *H. diversicolor*^{2} were not significant ($p > 0.05$; Table 5.1).

Nutrient flux (ln-transformed dissolved inorganic nitrogen (DIN) concentration) also varied significantly in relation to *C. volutator*H. diversicolor* (Table 5.1). The effect of increasing *H. diversicolor* density on nutrient flux went from positive to minimal as the density of *C. volutator* increased (Fig 5.3b). As the density of *H. diversicolor* increased, the effect of increasing *C. volutator* density on nutrient flux went from positive to slightly negative (Fig 5.3b). The effects of *C. volutator*^{2} and *H. diversicolor*^{2} were not significant (Table 5.1).

Nutrient flux (ln-transformed DIN concentration) did not vary significantly in relation to organic matter consumption (the loss of mass of *U. intestinalis*) among microcosms (general linear model: $F_{1,46} = 0.446$; $p = 0.5077$). In control microcosms, DIN concentration was significantly lower when detrital *U. intestinalis* was added (ANOVA: $F_{1,4} = 17.91$; $p = 0.0134$; see Supplementary Material, Fig 5.4), indicating that, in the absence of macroinfauna, decomposition of *U. intestinalis* caused DIN to decline.

Table 5.1. Effects of the densities of *Corophium volutator* and *Hediste diversicolor* on organic matter consumption (*Ulva intestinalis* consumed) and benthic-pelagic nutrient flux (ln-transformed dissolved inorganic nitrogen concentration) in laboratory microcosms. Squared density terms, which were included to assess potential effects of intraspecific competition, were removed from the models when statistically insignificant. All remaining relevant higher-order terms, regardless of statistical significance, were deleted before testing the lower order terms. significant *p*-values (< 0.05) are in bold.

		Organic matter consumption		Nutrient flux	
Term	d.f.	*F*	*p*	*F*	*p*
Block	5,44	13.386	**< 0.0001**	3.698	**0.0070**
Corophium volutator	1,45	86.287	**< 0.0001**	13.161	**0.0007**
Hediste diversicolor	1,45	17.663	**0.0001**	17.639	**0.0001**
C.volutator^2	1,42	2.859	0.0983	0.342	0.5616
H.diversicolor^2	1,42	0.001	0.9824	1.104	0.2994
*C. volutator *H. diversicolor*	1,44	4.290	**0.0442**	6.208	**0.0166**

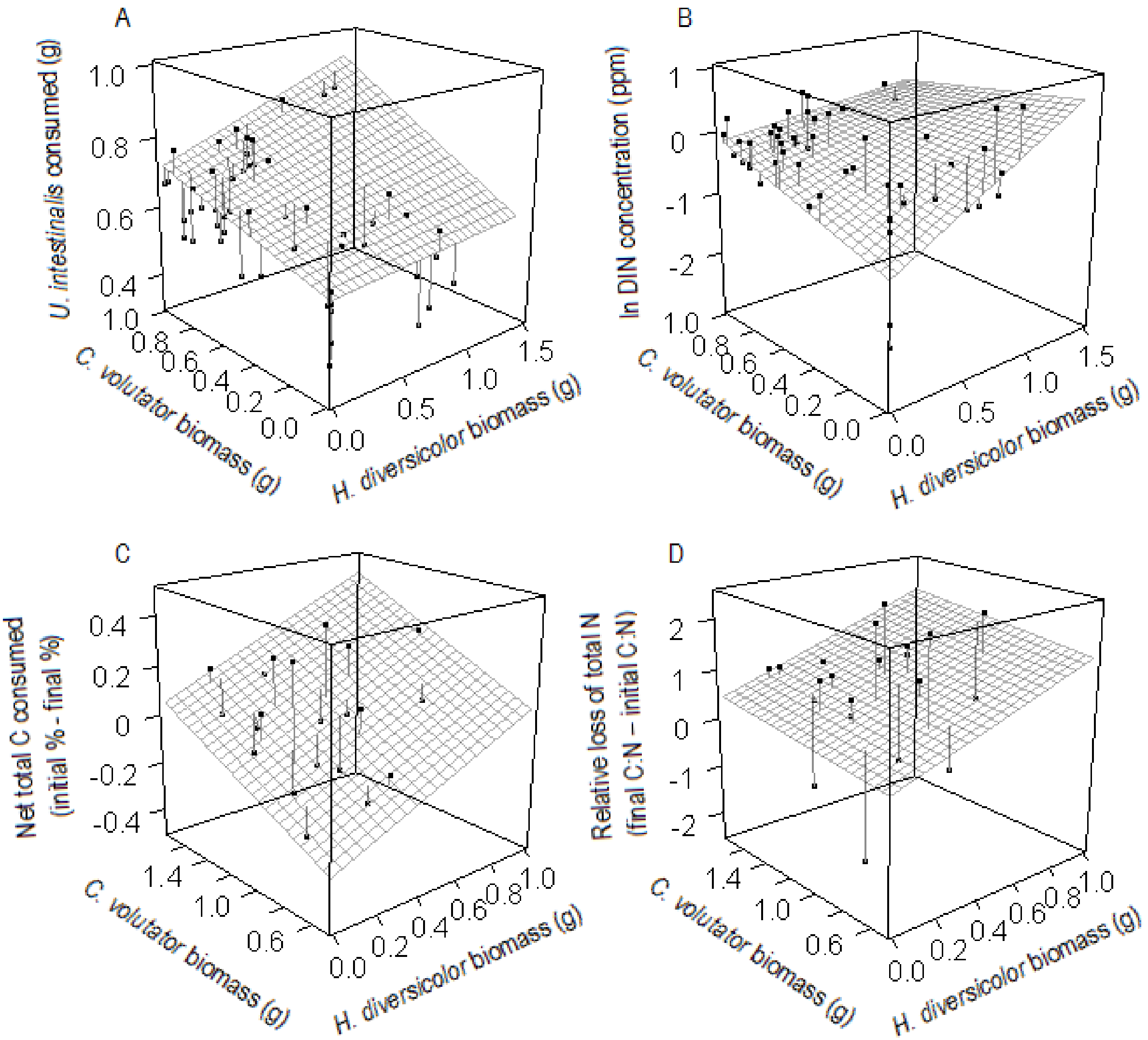

Fig 5.3. Variation in organic matter consumption and benthic-pelagic nutrient flux in relation to the densities of *Corophium volutator* and *Hediste diversicolor* in laboratory microcosms (A & B, respectively; DIN = dissolved inorganic nitrogen) and field plots (C & D, respectively). The 3D surfaces are based on the predicted values from the relevant linear models, with Block set to ‘block 1’ (i.e. the first experimental run), other significant terms set to their means, and other non-significant terms excluded. The points represent the actual observations and the lines connecting the points to the 3D surface represent the size of the residuals. The interaction between *C. volutator* and *H. diversicolor* is included in plots A and B, as this term was significant ($p < 0.05$) in both of these models. The interaction was not included in plots C and D, as this term was not significant in these models ($p > 0.05$). The surface for D was plotted with respect to the densities of *C. volutator* and *H. diversicolor* to show the trend of the data; however, neither term was significant. Both terms plotted in C were significant.

Field experiment

Organic matter consumption (initial % total C – final % total C) increased significantly with increasing densities of *C. volutator* and *H. diversicolor* (Table 5.2; Fig 5.3c). *C. volutator***H. diversicolor*, *C. volutator*^{2} and *H. diversicolor*^{2} were not significant (Table 5.2).

Nutrient flux (final C:N – initial C:N) did not vary significantly with respect to the densities of *C. volutator, H. diversicolor, C. volutator***H. diversicolor, C. volutator*^{2} or *H. diversicolor*^{2} (Table 5.2; Fig 5.3d).

Table 5.2. Effects of the densities of *Corophium volutator* and *Hediste diversicolor* on organic matter consumption (Total C before the experiment – total C after the experiment) and benthic-pelagic nutrient flux (C:N after the experiment – C:N before the experiment) in field plots. Squared density terms, which were included to assess potential effects of intraspecific competition, were removed from the models when statistically insignificant. All remaining relevant higher-order terms, regardless of statistical significance, were deleted before testing the lower order terms of interest (*C. volutator* and *H. diversicolor*). significant *p*-values (< 0.05) are in bold.

		Organic matter consumption		Nutrient flux	
Term	d.f.	*F*	*p*	*F*	*p*
Block	2,14	0.090	0.7686	0.115	0.7391
Corophium volutator	1,15	6.346	**0.0236**	0.004	0.9500
Hediste diversicolor	1,15	6.942	**0.0188**	0.237	0.6332
C.volutator^2	1,12	0.446	0.5167	0.011	0.9173
H.diversicolor^2	1,12	0.165	0.6920	3.679	0.0792
C. volutator **H. diversicolor*	1,14	1.264	0.2799	0.120	0.7340
Macoma balthica	1,14	0.003	0.9591	0.922	0.3532
Tubificoides spp.	1,14	4.117	0.0619	0.518	0.4834

DISCUSSION

Experimental tests of how biodiversity change influences ecosystem functioning have focussed mainly on the impacts of species loss (Hooper et al. 2005; Tilman et al. 2014). Few studies have tested the impacts of shifts in species densities, despite this pattern of biodiversity change being common compared to extirpations (Dirzo et al. 2014). The present study found that concurrent changes in the densities of two common benthic invertebrates affected organic matter consumption and benthic-pelagic nutrient flux in a soft-sediment marine ecosystem. The microcosm experiment indicated that interspecific interactions altered density-function relationships for both ecological functions. In field plots, density-function relationships appeared to be unaffected by interspecific interactions for organic matter consumption, whereas for nutrient flux no significant density-function relationships were observed. The results reaffirm that changes to species densities can impact key ecological functions (see Chapin et al. 1997; Gaston 2010), but also suggest that the impact of density changes in one species may depend on the composition of the assemblage with which it interacts. An effect of interspecific interactions on functioning was, however, only detected under homogenous environmental conditions and not within a natural heterogeneous ecosystem.

Within the two-species microcosm experiment, trait-specific predictions of relationships between function delivery and species density (Fig. 5.1, black lines) were supported only when the density of the second species was low. As the density of the second species increased, interspecific interactions caused density-function relationships to depart from trait-specific predictions in two ways: 1) a relationship emerged that was not predicted; e.g. *Hediste diversicolor* density had a positive effect on organic matter consumption only at high *Corophium volutator* densities, and 2) a relationship was not observed when one was predicted; e.g. the positive effect of *H. diversicolor* density on nutrient flux disappeared at high *C. volutator* densities (Fig. 5.1, dashed lines). As postulated *a priori*, I suggest that the above interactions for both functions are explained by *C. volutator* causing *H. diversicolor* to switch from suspension-feeding to deposit-feeding (see Scaps 2002 for review of feeding plasticity in *H. diversicolor*) in response to reduced suspension-feeding efficiency due to sediment resuspension by *C. volutator* (see de Deckere et al. 2000). Other macroinfaunal species commonly used in biodiversity-ecosystem functioning experiments also cause sediment resuspension, e.g. the gastropod *Peringia ulvae* (see Orvain et al. 2006) and the bivalve *Macoma balthica* (see Widdows et al. 1998), which may partly explain why nutrient flux has often been found to be highest in microcosms containing only *H. diversicolor* (e.g. Emmerson et al. 2001; Godbold et al. 2011).

Aside from the proposed mechanism, there are other possible explanations for the significant interspecific interactions observed in the microcosm experiment. One possibility is that *H. diversicolor* caused *C. volutator* to increase its rate of deposit-feeding and reduce the rate at which it flushes its burrows. However, I am unaware of a mechanism through which this could occur. The activities of two species within the sediment may also have interacted to promote microbial decomposition of organic matter (Kristensen 1988), which in the absence of macroinfauna caused DIN concentration to decline (Fig. 5.4) and thus may also explain the negative interaction observed for nutrient flux. Irrespective of the exact mechanism, the influence of interspecific interactions on ecosystem functioning can be considered as facilitative with regard to organic matter consumption and antagonistic with regard to nutrient flux. From an ecosystem functioning perspective, the nature of interspecific interactions (i.e. facilitation or antagonism) may therefore be dependent on the particular function considered.

Regarding the field experiment, there are various possible explanations for why results differ from those of the microcosm experiment and why no significant interspecific interactions were observed. First, it is noted that *C. volutator* density was higher than *H. diversicolor* density in almost all field plots (see Fig 5.2). The chance of detecting the significant interaction observed for organic matter consumption within microcosms may therefore be comparatively small in the field, as the low densities of *C. volutator* at which *H. diversicolor* did not affect organic matter consumption within microcosms were not re-created in field plots. This may also explain why no significant effect of *H. diversicolor* density on nutrient flux was detected in the field, as this relationship was most positive when the density of *C. volutator* was low within microcosms (Fig 5.3b). The same may also apply regarding the lack of an effect of *C. volutator* on nutrient flux in the field. However, there were some plots in which *H. diversicolor* biomass was close to zero in the field (Fig 5.2), which is the condition under which a positive effect of *C. volutator* on nutrient flux would be expected based on microcosm experiment results (Fig. 5.3b). If the above explanations are valid, then the results of the field experiment may essentially be consistent with those of the microcosm experiment.

With the possibility of congruence between microcosm and field experiment results considered, there are reasons why we might expect to observe different results under the different experimental contexts used in this study. For example, the effect of the abiotic environment on functioning may have masked biotic effects in the field (see Srivastava & Vellend 2005). Indeed, the effect of interspecific interactions on functioning appears to increase over time in natural ecosystems (**Chapter 4**), and my experiment may have been of insufficient duration to detect their influence in the presence of environmental heterogeneity. Previous studies have reported that *C. volutator* is sensitive to oxygen depletion (Gamenick et al. 1996) and tends to move away from organically enriched patches of sediment whereas *H. diversicolor* moves toward them (Bulling et al. 2008; Godbold et al. 2011). It is therefore possible that confinement of species to enriched sediment within my microcosm experiment caused *C. voluator* to irrigate its burrows more regularly than usual in order to prevent hypoxia, thus resuspending more sediment and enhancing the effects of interspecific interactions compared to what would occur within a natural, open ecosystem (assuming that the mechanism proposed to explain the observed interactions in the microcosm experiment was actually in effect). It is also possible that environmental heterogeneity in the field reduced the strength of interspecific interactions, as has been observed in fungal (Tiunov & Scheu 2005) and bacterial communities (Jousset et al. 2011), or that interactions with other taxa present at the field site influenced the results. Finally, I reiterate that direct measurements of functions were taken within microcosms whereas proxy measurements were taken within field plots, which may have made us less likely to detect effects in the field. Therefore, while the results provide no evidence for interspecific interactions affecting density-function relationships within a natural ecosystem, they should not be considered as an indication that such interactions were not occurring.

To assess the impacts of ongoing biodiversity change requires that we can map specific changes in species assemblages to the delivery of ecological functions (Strong et al. 2015). Biological traits (i.e. morphological, behavioural and life history characteristics) are the main medium through which individual species affect functional delivery, and therefore represent a tool through which the impact of biodiversity change on the functioning of ecosystems can be indirectly inferred (Bremner 2008; Mouillot et al. 2011). As trait-based predictions of species density-function relationships were supported in the microcosm experiment only when the density of the other species was low, this suggests that interspecific interactions may impede our ability to accurately predict the impacts of biodiversity change in natural ecosystems based on simplistic assumptions about trait expression.

Whereas a switch in the feeding mode of *H. diversicolor* in the presence of *C. volutator* may explain the density-function relationships observed in my microcosm experiment, other recent studies have demonstrated that species can switch feeding modes depending on environmental conditions (Cesar & Frid 2012; Törnroos et al. 2015). Methods used to infer functioning from traits, e.g. Biological Traits Analysis (BTA; Bremner et al. 2003; **Chapter 3**), generally account for such trait plasticity using fuzzy-coding, whereby the degree to which species exhibit different strategies is approximated (e.g. 50% deposit-feeder, 50% suspension-feeder; Chevenet et al. 1994). My results, and the results of the aforementioned studies, suggest that for BTA to predict even the direction of changes to function delivery with confidence, biotic and abiotic context should be considered when classifying the traits of each constituent species. The possibility that changes to abiotic conditions may alter the nature of biotic interactions (i.e. facilitative vs antagonistic; Maestre et al. 2010), and that the activities of biota can modify abiotic conditions (Hale et al. 2014), makes this task even more daunting. Nevertheless, it appears that an incorporation of species-species and species-environment interactions is required if we are to be able to accurately predict changes to functioning associated with ongoing biodiversity change.

ACKNOWLEGEMENTS

I thank Shannon White for her assistance with fieldwork and Les Connor and Sabena Blackbird for their assistance with laboratory analyses.

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SUPPLEMENTARY MATERIAL

Table 5.3. Effects of the initial densities of *Corophium volutator* and *Hediste diversicolor* on organic matter consumption (*Ulva intestinalis* consumed) and benthic-pelagic nutrient flux (ln dissolved inorganic nitrogen concentration) in laboratory microcosms. Squared density terms, which were included to assess potential effects of intraspecific competition, were removed from the models when statistically insignificant. All remaining relevant higher-order terms, regardless of statistical significance, were deleted before testing the lower-order terms. Significant *p*-values (< 0.05) are in bold.

		Organic matter consumption		Nutrient flux	
Term	d.f.	*F*	*p*	*F*	*p*
Block	5,44	15.371	**< 0.0001**	2.468	**0.0469**
Corophium volutator	1,45	74.215	**< 0.0001**	12.681	**0.0009**
Hediste diversicolor	1,45	9.687	**0.0032**	16.737	**0.0002**
C.volutator^2	1,42	0.408	0.5264	0.211	0.6482
H.diversicolor^2	1,42	0.001	0.9723	0.390	0.5357
C. volutator **H. diversicolor*	1,44	3.293	0.0764	5.012	**0.0303**

Table 5.4. Effects of the mean (of initial and final) densities of *Corophium volutator* and *Hediste diversicolor* on organic matter consumption (*Ulva intestinalis* consumed) and benthic-pelagic nutrient flux (ln dissolved inorganic nitrogen concentration) in laboratory microcosms. Squared density terms, which were included to assess potential effects of intraspecific competition, were removed from the models when statistically insignificant. All remaining relevant higher-order terms, regardless of statistical significance, were deleted before testing the lower-order terms. Significant *p*-values (< 0.05) are in bold.

		Organic matter consumption		Nutrient flux	
Term	d.f.	*F*	*p*	*F*	*p*
Block	5,44	15.297	**< 0.0001**	3.297	**0.0129**
Corophium volutator	1,45	84.760	**< 0.0001**	14.261	**0.0005**
Hediste diversicolor	1,45	15.288	**0.0003**	19.985	**< 0.0001**
C.volutator^2	1,42	1.213	0.2770	0.101	0.7528
H.diversicolor^2	1,42	0.039	0.8441	0.125	0.7255
C. volutator **H. diversicolor*	1,44	4.840	**0.0331**	5.541	**0.0231**

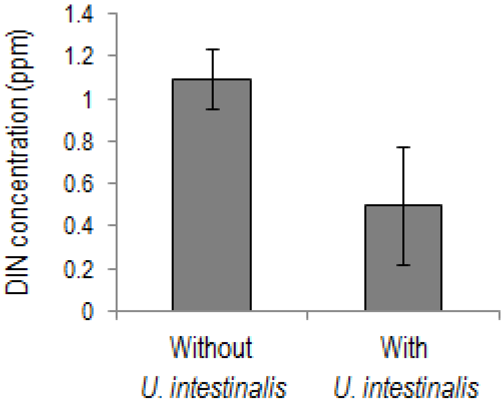

Figure 5.4. Mean dissolved inorganic nitrogen (DIN) concentration (with 95% confidence intervals) in microcosms containing no macroinfauna with and without the addition of detrital *Ulva intestinalis*.

Chapter 6

General Discussion

The goal of this thesis was to address some of the gaps in knowledge regarding the causes of variation in biological assemblages and its consequences for ecosystem functioning, with a specific focus on the marine benthos.

My analyses have shown that the long-term dynamics of a North Sea macroinfaunal assemblage were explained by variation in pelagic primary production (hence detrital input to the seabed) and sea surface temperature (SST) (**Chapter 2**). A shift in composition of the assemblage occurred midway through the time series and persisted thereafter, thus potentially altering the functioning of the ecosystem. However, effect trait composition did not differ significantly between periods that preceded and followed this compositional shift (**Chapter 3**), implying that ecosystem functioning was maintained despite extrinsic factors driving long-term changes to species composition. Interestingly, the only period when effect trait composition changed significantly (1986-91; **Chapter 3**) was the period during which a subset of the assemblage tracked an increase in detrital input to the seabed, culminating in the community shift (**Chapter 2**). This suggests that ecosystems may function differently while undergoing perturbations, but could ultimately be resilient to changes to functioning despite shifts in species assemblages, due to density compensation by functionally redundant taxa. The rate of functional recovery to the pre-perturbation state appears to be enhanced in systems that are regularly subjected to disturbance (**Chapter 3**), which suggests that the effects of disturbance on functioning may increase when applied to systems that are closer to pristine. Overall, the results of the first section of this thesis (**Chapters 2** and **3**; see Fig. 1.1**)** suggest that it is possible for ecosystems to sustain their long-term functioning despite externally-driven compositional shifts. This finding offers some hope that ecosystems will continue to deliver the services they currently provide (e.g. food production and climate regulation) in the face of environmental change.

The experiments conducted in the second section of the thesis (**Chapters 4** and **5**; see Fig. 1.1) have shown that species density-function relationships can be predicted using the biological traits of marine macroinfaunal species. However, trait-based predictions were not consistently supported in either of these chapters, with both highlighting an influence of interspecific interactions on functioning. Changing the density of one species affected functioning by causing the density of a second, functionally dominant, species to change

(**Chapter 4**). Such an indirect effect of species over functioning has previously been given little consideration within the biodiversity-ecosystem functioning (BEF) field, which opens up the possibility that species with little apparent direct influence over function delivery may be more functionally important than previously suggested. Interspecific facilitation was implied by the analyses of **Chapters 4** and **5**, and its influence over the functioning of a natural ecosystem appeared to increase over time, as predicted (**Chapter 4**). The nature of interspecific interactions (i.e. facilitation *vs.* antagonism) was found to depend on the function considered (**Chapter 5**), and there was some indication that intraspecific interactions may shape function delivery in natural ecosystems (**Chapter 4**). This thesis has therefore provided some new insights into biotic influence over the functioning of ecosystems; pointing to the capacity for trait-based predictions of changes to function delivery, but also pointing to a role of biological interactions as an important determinant of functioning.

The first step toward predicting future ecological change and potentially mitigating anthropogenic impacts is identifying its underlying causes. If changes to detrital input to the seabed do indeed affect the benthos, as suggested by **Chapter 2** of this thesis, and by other observational studies ranging from the northern Baltic Sea (Weigel et al. 2015) to the northeast Pacific (Ruhl and Smith 2004), then what does this mean for the benthos of the future? Pelagic primary production has been increasing in response to oceanic warming in some regions (high latitudes, possibly as a direct effect of warming) and decreasing in others (mid-low latitudes, as thermal stratification reduces nutrient availability) over the last century (Behrenfield et al. 2006; Boyce et al. 2010). Widespread changes to the benthos are therefore likely to have occurred during this period as a result of changes to primary production, and will likely continue with ongoing climate change. If predictions regarding the effects of warming on pelagic primary production are accurate, then the impacts on the benthos (and other ecosystem components) in high latitude regions could be exacerbated should the increase in production be accompanied by an increase in fishery exploitation. Similarly, a decrease in production in mid-low latitude regions may have negative consequences for food availability in regions where a majority of the global human population resides, thus potentially also resulting in the more intensive and extensive fishing pressure in these regions. Such possibilities reaffirm the importance of being able to predict future ecological change, so that societies can respond to projections and mitigate impacts ahead of time.

Although modern climate change is widely accepted to be human derived (Cook et al. 2013), global warming is projected to proceed even if anthropogenic ‘greenhouse gas’ emissions were to be abruptly ended (Wigley 2005). Associated ecological impacts therefore cannot be prevented or reversed by directly manipulating the driver. If the increase in atmospheric greenhouse gas concentrations is curtailed, however, then this may mitigate impacts on pelagic primary production, the benthos and other biological components; many of which constitute essential ecosystem goods (e.g. fish; Blanchard et al. 2012). Adding (or removing) nutrients that are essential for phytoplankton growth could potentially allow oceanic pelagic primary production to be manipulated in the desired direction (D'Elia et al. 1986; Martin et al. 1990). Ocean fertilisation has previously been proposed as a means for increasing phytoplankton-driven carbon sequestration to mitigate global warming (Gribbin 1988). If successful, such an approach could offset reductions in mid-low latitude pelagic primary production both directly and indirectly by curtailing an increase in the factor that is causing it to change. Such interventions are, however, by no means guaranteed to be successful, and the ecological consequences could turn out to be negative rather than positive (Buesseler et al. 2008).

The results of **Chapter 3** bring into question whether mitigating ecological change is something about which to be concerned. If ecosystem functioning is ultimately resilient, then does it matter if species assemblages change over time? The answer to this question, from an ecosystem functioning perspective, would necessarily be no. However, there are a few things that need to be considered before making this assertion. The first is to reiterate that the Biological Traits Analysis (BTA; Bremner et al. 2003), as applied in **Chapter 3,** assesses potential changes to functioning based on our current understanding of marine BEF relationships, i.e. the link between biological traits and functions. This understanding is constantly being developed, with **Chapters 4** and **5**, for example, suggesting that biotic interactions are also important. It is therefore possible that my analyses did not detect potential changes to functioning despite such changes actually occurring. Second, the datasets used in **Chapter 3** come from just two sites in one region of the world. The generality with which these results apply is not yet known, although there are some consistent findings from other northeast Atlantic benthic systems (Neumann & Kröncke 2011; Veríssimo et al. 2012). The third point is that species assemblages differ among sites due to natural and anthropogenic influences. Changes to trait composition, and thus functioning, over time might be more likely to occur in relatively pristine systems, or systems subjected to different extrinsic forcing than was the benthos at Stations M1 and P over the study period. Rather than asserting that ecosystems will retain their functioning into the future, it is therefore only defensible at this point to say that ecosystems possess some capacity to buffer changes to functioning as community composition changes over time.

One of the main aims of this thesis was to experimentally test hypotheses that would increase our understanding of BEF relationships. The finding that a species' influence over functioning can occur via its effect on other species implies that the decline or loss of a population could potentially enhance function delivery (**Chapter 4**). While counter-intuitive and interesting in a basic sense, this finding also opens the door, albeit controversially, to the possibility of removing organisms from ecosystems as a means of engineering favourable ecosystem functioning. Indeed, the species that had an indirect negative effect on function delivery in **Chapter 4**, *Scrobicularia plana*, is a local cuisine in Charente-Maritime, France (Davidson 2014). Therefore, harvesting this species could provide a commercial product, while also potentially enhancing functioning and the provision of associated ecosystem services. The complexity of ecosystems should, however, be noted when considering such a possibility. I conducted the experiment covered in **Chapter 4** at a single site, which was low in species richness. At other sites, with higher biodiversity, removing species could have knock-on effects on many populations, which could in turn have a variety of conflicting effects on function delivery. The aggregate impact of these changes may depend on the function considered (**Chapter 5**; Byrnes et al. 2014), and any such interventions should therefore be carried out with extreme caution. What can be generally taken from this result, however, is that the potential indirect functional importance of species should be considered by environmental managers. Moreover, if interspecific facilitation does enhance functioning, as suggested by **Chapters 4** and **5**, then maintaining diverse species assemblages may be the best way to ensure that we avoid undesirable ecological change.

In moving forward in our attempt to understand biotic influence over the functioning of ecosystems, there is a need for manipulations of natural assemblages to supplement the findings of controlled laboratory experiments (see Gamfeldt et al. 2015). I aimed to do this as part of the research contained within this thesis (**Chapters 4** and **5**) and subsequently new insights into BEF relationships have emerged. A possible next step is to conduct experiments across more sites and assess the generality of the results obtained here. Ultimately, manipulations of species-rich subtidal systems, which constitute the majority of the seabed, are needed to shed light on the broader impacts of benthic biodiversity change. Manipulating biodiversity in subtidal systems is technologically challenging and expensive, and was therefore outside the scope of this thesis. Intertidal sediments, on the other hand, are accessible on foot, contain species that can survive transplantation between sites, and are therefore an ideal system for moving marine BEF experiments to the field. Testing specific predictions derived from ecological theory (e.g. how species will influence functioning based on their traits) will maximise the insights from such experiments and increase the wider applicability of findings.

Assessing the generality of long-term time series studies, such as those analysed in **Chapters 2** and **3**, is constrained by the availability of such data across sites of the same habitat type. A combination of experimentation and the analysis of broad-scale surveys are therefore needed to compensate for the paucity of high-resolution monitoring studies. Using response and effect traits of species will aid our ability to establish links between extrinsic drivers and functional impacts (see Lavorel & Garnier 2002). A consideration for how species exhibit plasticity in their effect traits depending on abiotic (Cesar & Frid 2012; Törnroos et al. 2015) and biotic context (**Chapter 5**) will allow BTA to more accurately assess potential changes to functioning. Taking simple proxy measurements of ecosystem functioning (e.g. redox potential discontinuity depth or pore water nutrient concentrations) whilst carrying out surveys will further our understanding of BEF relationships in natural ecosystems. Such data would, for example, allow the predictive capacity of BTA to be tested and refined, thus potentially producing a tool through which the levels of a suite of functions can be accurately approximated.

Previous experiments suggest that marine BEF is underpinned by the roles of individual species, with particular biological traits (i.e. identity effects) (Gamfeldt et al. 2015; Strong et al. 2015). This implies that conservation might be best focussed on functionally dominant species in order to sustain high levels of function delivery. The results presented here highlight the role of biological interactions in determining function delivery – through facilitation, antagonism and the coupling of species densities – and suggest this role may vary depending on the function considered. Predicting the impacts of biodiversity change on function delivery therefore appears to be more complicated than previously suggested, and management decisions based around single species or functions might have undesirable and unpredictable consequences. A precautionary approach to biodiversity conservation is therefore advisable while our understanding of BEF continues to develop.

This raises the question of how managers should prioritise the conservation of species vs. functioning if we one day have a complete understanding of BEF. I argue that it is our responsibility to not let our actions drive species to extinction, regardless of their functions and utilities. Relying heavily on BEF over ethics to defend this position will open the door to BEF being used to defend actions that cause species to go extinct but do not impair ecosystem functioning. However, humans will always depend on ecosystems and will thus always exert some degree of impact on biota. The challenge is to minimise this impact so that functioning is sustained, while also ensuring that species are not driven to extinction. Succeeding in this challenge will require that managers prioritise the localised protection of species, coupled with the broad-scale protection of ecosystem functioning.

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