Biodiversity links above and below the marine sediment–water interface that may influence community stability

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Abstract. Linkages across the sediment–water interface (SWI) between biodiversity and community stability appear to exist but are very poorly studied. Processes by which changes in biodiversity could affect stability on the other side of the SWI include carbon transfer during feeding, decomposition of organic matter, nutrient recycling, organism recruitment and structural stabilisation of sediments. The importance of these processes will clearly vary among habitats. Direct disturbance to communities on one side of the SWI, such as created by overfishing, habitat destruction, and species invasions, has the potential to impact communities on the other side of the SWI through the many functional links. Hypotheses are proposed to suggest further areas of research to fill the large gaps in our knowledge concerning the nature and intensity of such linkages. The linkage between benthic and pelagic diversity is likely to be tighter where there is a close energetic connection between the domains, such as polar and shallow coastal waters, and where communities are dominated by selective detritivores. The quantity of carbon reserves in the sediment and the predominant mode of larval development of sediment communities probably influence the stability of below SWI communities in the face of changes in above SWI diversity. The organisms, including hyperbenthos, that are found at the SWI may be of crucial importance to the linkage and stability of above and below SWI communities.

Key words: benthos, biodiversity, fish, links, pelagic, plankton, sediment–water interface, stability

Abbreviation: SWI – sediment–water interface

Introduction

In the last few decades, we have acquired a much greater understanding of the processes of disturbance and productivity that control marine biodiversity over large

ecological scales (Huston 1994) and how these processes are expressed through small-scale heterogeneity (Grassle 1989). Some research has also demonstrated how various ecological processes appear to link the domain below the sediment–water interface (SWI) with that above and this has been recently reviewed by Snelgrove et al. (2000). The importance of biodiversity to these processes and the relationships between biodiversity above and below the SWI are relatively poorly studied areas of marine ecology. Nonetheless, there are major ecological processes that link biodiversity above and below the SWI including productivity (or carbon transport), decomposition processes and nutrient regeneration, and recruitment and stabilisation of sediment. The review by Snelgrove et al. (2000) focussed on the mechanisms of the ecological processes. The present review builds from that of Snelgrove et al. (2000) to examine (1) how changes to the processes linking biodiversity above and below the SWI may be critical to stability in either system and (2) how changes in the diversity of organisms living either above or below the SWI may be critical to stability in the other system. Intuitively, where mechanisms exist that link biodiversity above and below the SWI, disruption of the biodiversity will disturb these links and hence affect the stability of above and below SWI communities. Yet the strength and nature of the interactions between above and below SWI communities will vary in different habitats and among different communities so that some communities will be more stable than others or show different attributes of stability. It is these facets of the relationships between above and below SWI biodiversity and stability that we have attempted to explore. We have reviewed the rather limited available evidence of such relationships from which hypotheses have arisen that might be tested to clarify the issues and help to establish the importance of biodiversity links to community stability.

Another review (Smith et al. 2000) has focussed on the impacts of anthropogenic influences, particularly global change, on the links between above and below SWI biodiversity. This review differs in that it concentrates on natural differences between habitats and natural changes that would affect community stability. Examples of anthropogenically-induced changes are used only to indicate how changes in biodiversity in one marine component, either above or below the SWI, can affect stability and biodiversity in the other component.

As with the review by Snelgrove et al. (2000) the term biodiversity is used in its broadest sense, in keeping with common usage and the Convention on Biological Diversity, to encompass the variability of nature in terms of genetic, species and habitats, and even ecosystems. This usage is kept deliberately broad and is not confined to a unit as such; some of the examples that we will summarise are only known to directly involve one or a few species but we feel they do, nonetheless, represent an aspect of biodiversity. In more specific terms, species richness refers to number of species in an area while (composite) diversity refers to measures of species diversity that incorporate both species number and the apportioning of individuals among species

(evenness). The use of different measures in different studies makes comparisons sometimes difficult. Additionally, a change (or lack of change) in one measure does not always mean there is no change in another aspect of diversity.

The link between diversity and stability

One of the ecological arguments justifying the need to maintain and conserve marine biodiversity depends on establishing a link between biodiversity and ecological stability. Attempts to do this have lead to conflicting views that have recently been reviewed by McCann (2000) and which we briefly summarise here. Before the 1970s, empirical observations suggested to ecologists that complex, species-rich communities were more stable than simple, species-poor ones. However, mathematical modelling of randomly constructed communities with randomly assigned interaction strengths (e.g. May 1973) suggested that diversity did not increase stability. Yet, continuing observations still indicate that diversity tends to be positively correlated with ecosystem stability. It has been proposed more recently that community-level stability is dependent on the different responses of species or functional groups to variable abiotic and biotic conditions. Additionally, modelling of food web interactions has suggested that weakly interacting species stabilise community dynamics by dampening the effects of disruptions of strong interactions between consumers and their resources. If the interaction strengths within a community are strongly skewed towards weak interactions the community will be more stable. The few available descriptions of the distributions of interaction strengths amongst complex communities suggest this is the case and therefore support this recent theory. These more recent ideas do not contradict May's mathematical observations since it is the differential responses of the species to changing conditions combined with an increasing number of weak interactions as diversity increases which increase community stability, rather than the diversity itself.

However, there may be considerable functional redundancy in the marine environment (Snelgrove et al. 1997; Clarke and Warwick 1998) with many species seeming to occupy similar ecological niches. What is less clear is to what extent the ecological similarity of many benthic species will mitigate the loss of any one species, and whether a benthic habitat that loses biodiversity is still able to provide the same sorts of ecological services as one with a greater number of species. The Baltic Sea provides an example of an ecosystem that functions despite low benthic species diversity compared to most subtidal marine habitats (Elmgren and Hill 1997). Even within the Baltic there are contrasting areas, some of which are richer in functional group diversity than others (Bonsdorff and Pearson 1999). Is the Baltic fundamentally less stable and can its capacity to function at low diversity be generalised to more diverse systems that lose biodiversity? An advance in the marine biodiversity debate would be to examine the importance of biodiversity to ecosystem resistance, resilience, and

stability. Ecosystem resistance refers to the systems capacity to resist perturbation, whereas resilience refers to its rate of recovery from perturbation. Stability encompasses both terms and in the context of this review refers to a systems capacity to maintain its diversity and continue its ecological functions in the face of natural and human-induced perturbation.

In the marine environment, particularly within the pelagic domain, large-scale ecological research has been predominantly process based, with little concern about which, or whether, species (rather than functional groups) are critical to a given process. Likewise, links between the pelagic realm and the seabed have been viewed primarily from the viewpoint of ecosystem processes where it is clear that the pelagic and benthic realms are linked and that each is dependent on the other. Again, the roles of individual species and biodiversity are rarely considered.

As the marine environment becomes increasingly impacted by human activities (fishing, habitat destruction, pollution, etc.) the biodiversity in different components of the marine ecosystem is being altered. An understanding of the resistance and resilience of the different components to change in the diversity of other parts of the marine ecosystem is therefore becoming critical. There are a variety of ecosystem functions and changes in diversity may have different effects on each of them. Similarly, changes in either the above or below SWI domain could impact the various components of the ecological community in different ways. For example, within the sediment, microbial and macrofaunal diversity will respond differently to changes in the quantity of plankton sedimentation. Some ecosystem functions or some components of the community may be impacted by changes in diversity of particular components of above or below SWI communities whilst others are not. It is not presently possible to determine the relative importance of impacts of biodiversity change on overall ecosystem stability. Thus, it is rarely possible in this review to refer to stability of the whole system but rather we refer to stability of different components of the system.

The marine habitats reviewed

For this review we have considered the same three broad marine sedimentary habitat categories that were used by Snelgrove et al. (2000):

1. Intertidal and shallow sedimentary systems, which may have emergent vegetation and encompassing mangrove swamps, salt marshes, seagrass beds and algal mats.
2. Non-vegetated shallow water coastal systems in which wind and hydrodynamics mix the water column all the way down to the SWI during at least part of the annual cycle.
3. Open ocean systems in which mixing does not penetrate to the interface and light does not penetrate to the bottom in sufficient intensity to support photosynthetic organisms.

The third category is spatially the most extensive marine habitat globally, but the first and second are arguably more important in terms of the key marine ecosystem services that take place within them.

We have divided organisms into those that occur above or below the SWI, treating organisms that live predominantly on or above the sediment surface (e.g. diatoms, algae, seagrasses, saltmarsh plants, pelagic organisms, epifauna, hyperbenthos etc.) as 'above'. In making this simple and somewhat artificial distinction we acknowledge that many benthic species have a pelagic reproductive dispersal stage and some 'above' species have a 'below' component (e.g. saltmarsh grass roots, resting eggs and cysts). As will become apparent, some of these above SWI communities effectively form a relatively permanent structural layer between the sediment and the water at the benthic boundary layer such that it is an artificial concept to ascribe them as confined to either 'above' or 'below' biodiversity. In addition, this discussion will concentrate on sedimentary benthic systems, which constitute the vast bulk of marine seafloor habitats.

Practical and theoretical implications of an aqueous medium

Marine systems have few obvious physical boundaries. The oceanic pelagic system, in particular is vast, so pelagic organisms tend to be dispersed over great distances. The fluidity of the pelagic water medium, its spatial extent, and its temporal and spatial variability makes modelling specific linkages between the pelagic and benthic systems in terms of problematic biodiversity.

Because of the mobility of the organisms in the pelagic medium and the general perception of uniformity of that medium over large spatial scales, processes relating the pelagos and benthos have been determined mostly at large biogeographic scales (10–100 km or more). Yet this approach ignores the large amount of spatial variability of both systems that can be observed at much smaller spatial scales which is considered to be an important structuring feature of benthic and pelagic biodiversity (for selected benthic examples see e.g. Grassle 1989; Morrissey et al. 1992; Rice and Lambshead 1994; for selected pelagic examples see e.g. Pinellaloul 1995; Gallagher et al. 1996; Mann and Lazier 1996; Abraham 1998; Longhurst 1998). Thus, using the conceptual framework of Whittaker (1972) we should examine biodiversity relationships above and below the SWI in terms of both gamma diversity (total diversity of a region) and alpha diversity (small area or sample diversity). There is clearly a problem in determining equivalent spatial scales in the two realms to encompass these terms. Additionally, there is temporal variability in biodiversity in both domains, particularly where the communities are seasonally structured, which is due to inter-annual variations in recruitment success.

For most of the marine environment, primary production occurs among small planktonic organisms. Combinations of lateral (advection) and vertical (sinking)

transport can move these organisms considerable distances before they reach the SWI (Macquart-Moulin and Patriti 1996). Also, these primary producers may be considerably transformed by passage through several guts in the pelagic system before reaching the seabed, particularly in the open ocean where living phytoplankton occur thousands of meters above the sea bed. These factors tend to decouple any obvious biodiversity patterns above and below the SWI (Figure 1).

As a rough approximation primary production is more tightly connected with the sediment both closer to the shore in shallower water than it is in deeper waters (Figure 1), and closer to the poles than in lower latitudes. At higher latitudes primary production occurs in highly seasonal blooms that produce large amounts of sinking material which exceed the feeding capacity of the pelagic community (Høpner Petersen and Curtis 1980). In shallow waters the layer of water in which primary production takes place impinges directly on the seabed. Towards the poles there is only a short productive season when temperature and light levels are sufficient for phytoplankton production to take place. In the Antarctic, in particular, the summer fluxes are amongst the highest ever recorded while the winter fluxes are amongst the lowest (Karl et al. 1996). The short period limits the pelagic seasonal succession (Lindley 1998) preventing the build up of an above SWI food web so that ultimately a greater proportion of the phytoplankton reaches the seabed directly.

We can predict that the biodiversity above will have less influence on the stability of biodiversity below the SWI where the energy flow between the benthic and pelagic species is indirect i.e. where there is a well-developed pelagic food web, as in deep water and tropical coastal systems. Conversely, we would expect temperate shallow water and polar regions to show the greatest connection between diversity in one domain and stability in another. This hypothesis is based on the assumption that the amount and composition of material flux is critical in terms of linkage. However, it might also be argued that higher plankton diversity towards the tropics and in the open ocean could provide a more diverse food source for benthos and therefore impacts diversity through food composition and quality rather than abundance. The problem for ecologists exists in determining at which spatial and temporal scales biodiversity above and below the SWI might be linked.

Summary of mechanisms linking above–below sediment–water interface biodiversity

Current knowledge of the mechanisms involved in linkages between above and below SWI biodiversity has been recently reviewed (Snelgrove et al. 2000) and is summarised here. Organisms within the sediment transport carbon to and from water overlying the sediment through their feeding activities. Suspension feeding removes material from the overlying water. Some infaunal organisms move to the sediment surface or the water column and are predators of above sediment organisms.

Materials are transported to the sediment by sinking, e.g. plankton settling and flocculation, and by predation, particularly from bottom feeding organisms such as fish and also from epibenthic and hyperbenthic organisms. Many macrofaunal organisms have temporary planktonic larvae (known as meroplankton although this term also includes plankton with larval stages in the benthos such as jellyfish). Meroplankton will compete with the permanent plankton (holoplankton) for food. Additionally, some meroplankton are important predators or prey of holoplanktonic organisms.

Within the sediment, nutrients are recycled via decomposition. Microbial groups are responsible for ammonium nitrate regeneration, denitrification, aerobic respiration, phosphate release, and sulphate and metal reduction. Particle shredding caused by meio- and macrofaunal activity, and microbial stripping by protists, meio- and macrofauna facilitate these microbial activities. Bioturbation and bioirrigation, largely by macrofauna, move sediment and fluids predominantly within the sediment and in doing so promote exchange of fluids and materials at the SWI.

Many benthic organisms, particularly macrofauna, spend part of their lifecycle above the SWI usually as eggs and larvae although some adult benthic organisms migrate seasonally or daily into the water to spawn or to feed (Armonies 1988, 1994). Some planktonic organisms, such as copepods, diatoms and dinoflagellates, have eggs or cysts that can sink to the sediment and remain dormant there. Sediment dwelling macro- and meiofauna may consume these eggs and cysts. The movement of larval and adult infaunal organisms into the water column and cysts and eggs from pelagic organisms into the sediment varies seasonally and often fluctuates annually. This variation will in turn impinge upon other organisms in the pelagos or benthos.

The presence of emergent vegetation or tubiculous animals immediately above the sediment alters water flow patterns and hence changes rates and patterns of sedimentation and sediment stability which can affect infaunal organisms.

Physical transport processes at the benthic boundary layer

At the interface between the sediment and the overlying water there is a benthic boundary layer in which water movement is reduced (Mann and Lazier 1996). This interface is probably of crucial importance in facilitating processes whereby organisms on either side of the SWI interact. In some of the processes linking above and below SWI diversity it is the impact of communities on the physical transport of materials to and from the sediment which is key to the linking process. Physical transport of particles and nutrients between the overlying water and the sediment is strongly affected by the structure of the benthic boundary layer (Nowell and Jumars 1984; Snelgrove and Butman 1994; Paterson and Black 1999). Mechanisms of vertical transport across this boundary include (1) sinking, (2) random turbulence and (3) shear. Outside of the benthic boundary layer the ratio between sinking and random turbulence determines the sinking rate of particles (Bouma et al. 2001). Within the benthic boundary layer,
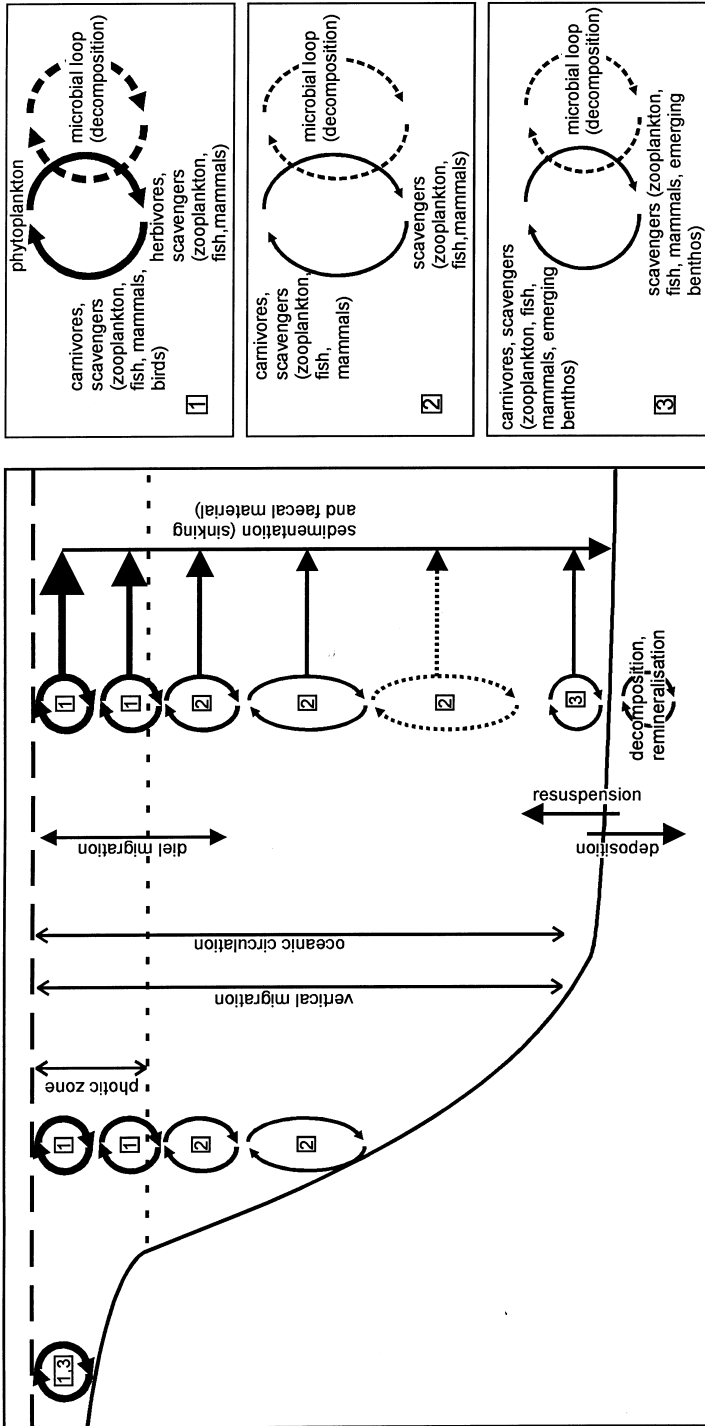
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Figure 1. Schematic simplification of trophic cycling in the marine environment demonstrating lower connectivity between above and below SWI diversity with increasing water depth. Arrows indicate direction of energy/material flow, which decreases with increasing depth as denoted by line thickness. As water depth increases the amount of trophic cycling between the water surface and the SWI increases. Trophic cycles are not discrete events, as depicted here for simplicity, but are interlinked. The organisms involved in trophic cycling change with increasing depth as shown in the numbered boxes on the right-hand side.

shear forces become increasingly important because of the gradient in current velocity with approach to the bed (fluid in direct contact with the seabed is in fact stationary). Flow within the boundary layer can be modified by biogenic structures e.g. tubes and siphons protruding above the sediment and pits and burrows within the sediment; by bivalve, algal and microbial mats and secreted extracellular polymeric substances which may increase sediment roughness; and by bivalve feeding currents (Nowell and Jumars 1984; Ertman and Jumars 1988; Butman et al. 1994; Cummings et al. 1998; Green et al. 1998; Paterson and Black 1999). Flow over soft sediment may also penetrate into the sediment and in permeable sediment flow of dissolved and small particulate material can be influenced by biota (Huettel and Gust 1992). Flow within as well as across the benthic boundary layer directly influences sediment composition and sediment stability.

Processes across the sediment–water interface which could affect biodiversity stability

Carbon transfer through feeding activities

Carbon exchange can be selective or relatively non-selective (i.e. organisms may feed very selectively or relatively non-selectively across the SWI). Where the feeding is extremely selective, e.g. where detritivores are focussing on particular species of phytoplankton settling to the seafloor, the link between biodiversity and stability is likely to be much stronger than when feeding is relatively non-selective.

Infaunal organisms (e.g. many meiofauna and microbes such as flagellates) graze on epibenthic diatoms in the intertidal and shallow subtidal zones. There is evidence that in these habitats grazing rates rarely exceed primary production and the below SWI grazers are not food limited (Sundbäck et al. 1996). Differential utilisation of food resources by meiofauna (e.g. harpacticoid copepods) may prevent interspecific competition both amongst the meiofauna and their prey. Seasonal cycling of autotrophs and resultant detritus levels is well known, thus phasing and differential use of these food resources by the meiofauna could regulate aspects of their biology and their contribution to the productivity of the benthos (Hicks and Coull 1983). There is a seasonal switch from diatom grazing to bacterial feeding by the meiofauna (Sundbäck et al. 1996) but whether this relates to changes in meiofaunal diversity is unknown. Within estuarine sediments, the diversity of meiofauna is relatively large compared to that of the macrofauna. We speculate that this diversity has evolved with the diversity of autotrophic food species such that stability of the estuarine meiofauna community is now dependent on the diversity of above SWI autotrophs. Similarly, selective grazing by meiofauna could maintain autotroph diversity. Comparing the spatial and seasonal changes of the diversity of estuarine meiofauna and microphytes could test this.

Infauna may aggregate discordantly (e.g. Rice and Lambshead 1994) and this discordance may be more marked with seasonal increases in carbon supply from above the SWI. It is not clear whether this is an indication that different 'types' of food attract different organisms, that there is succession within the communities as the 'food' ages regardless of the 'type' of food, or that some other process (e.g. differential settling responses, selective predation, aggregation near mates) is operating. Patterns in data from the deep sea suggest that all may be true (Snelgrove et al. 1992, 1996). Carbon supply from above the SWI to the sediment can be highly seasonal or pulsed in oceanic habitats and in coastal waters at temperate and higher latitudes because of plankton blooms. We hypothesise that sediments with large reserves of carbon, i.e. high levels of aged detritus, should be less susceptible to this seasonality because they are preadapted to dealing with a large carbon loading. Some below SWI organisms will exhibit stability in the face of this seasonality by consuming aged detrital material already present in the sediment through subduction (Levin et al. 1997). Others may be dependent on consumption of fresh material and we hypothesise that these will show less resistance to increases in variability or seasonality of inputs. In instances where carbon loading from above the SWI is sufficient to create hypoxic conditions in the sediment, response by opportunists may swamp any partitioning by benthic organisms of food resources based on composition or age. In areas subject to highly variable pulses of organic enrichment we hypothesise that the community of opportunistic species will be quite resilient at scales exceeding those of the patch. In deep waters, subduction of freshly deposited organic matter deeper into the sediment can be quite rapid (Levin et al. 1997). Thus, even in the deep ocean, fresh detritus may be reaching the sediment and could influence diversity of selectively feeding benthic organisms. With organic enrichment delivered to the sediment in pulses, there tends to be a reduction in diversity but also a different suite of species within the enriched patches (Snelgrove and Smith, in press) which may increase overall benthic diversity of an area by increasing heterogeneity.

Carbon input to the sediment may occur in large quantity pulses due to the formation of plankton blooms or may be a small but constant input. As discussed earlier the timing and quantity of the input will vary according to environmental factors influencing the plankton community but it will also depend on the species composition of the community. The ability of an infaunal community to resist change in magnitude or form of carbon delivery from above the SWI can depend on the timing of such change. For example, intertidal estuarine meiobenthic nematode assemblages were more resistant to a large input of carbon if it was delivered as a series of pulses over a short period rather than as a single massive dose (Schratzberger and Warwick 1998). A similar pattern may be hypothesised for macrofauna.

Development and reproductive success of all organisms may be dependent on the presence of sufficient carbon in an assimilable form. Some plankton species may be more assimilable than others or more readily broken down at the sediment to become

bioavailable. Infauna commonly have a diversity of life stages and juvenile forms are often more sensitive to carbon supply than adults (Levin et al. 1996). They may be sensitive to an increased flux of carbon to the sediment from above the SWI, particularly when hypoxia or anoxia is associated with the carbon input. Because some infaunal organisms are more sensitive to low oxygen than others (Cook et al. 2000), high carbon flux associated with low oxygen is likely to severely disrupt below SWI biodiversity.

The diversity of benthic microbes is likely to be linked to the taxonomic/biochemical composition of the above SWI organisms that eventually impact the sediment (Snelgrove et al. 2000). Microbial community structure might therefore have little resistance to alterations in the composition of material settling to the sediment. However, the quantity of organic inputs is probably ultimately more important than their quality because of the effects on oxygen availability and other aspects of sediment geochemistry. Changes in quantity of organic inputs will probably have more effect on relative microbial population size rather than absolute diversity.

Within intertidal and shallow subtidal areas organic enrichment often results in an increase in fixed and drifting green algae (Raffaelli et al. 1998; Pihl et al. 1999). Different components of the benthic fauna have different responses to the presence of algal mats but the response appears to be consistent regardless of the species of alga or whether the mats are fixed or drifting (e.g. Norkko and Bonsdorff 1996; Raffaelli et al. 1998; Thiel and Watling 1998). These effects are sometimes also evident after the algae has dispersed and have been attributed to an increase in food resources due to in-site burial and decomposition of macroalgae, the latter also affecting communities by creating hypoxic conditions. Some components of the macrofauna show little resistance to the changes caused by the presence of algal mats yet recovery appears to be quite rapid after the mats have gone (Raffaelli et al. 1998) suggesting higher resilience. However, the response of the benthic community varies according to the quantity and persistence of the mats. The sedimentary microbial populations that break down aged algal detritus can be quite specific (Snelgrove et al. 2000) and may linger in the sediment after visible algae on the sediment surface have disappeared (Hansen and Kristensen 1998). The effects of algal mats on benthic diversity feedback to the above SWI predators including birds and these effects are species specific (Rafaelli et al. 1998). This emphasises that mat forming organisms such as algae, but also including seagrasses, diatoms, bivalves and reef forming organisms, are an intermediate community at the SWI affecting the stability of communities both above and below it.

Seagrass beds and algal mats can provide refuge for benthic organisms from fish predation. Increases in algal mats due to eutrophication may alter trophic relationships between above and below interface organisms hence affecting biodiversity links (Isaksson et al. 1994). In a South-western Australian harbour, eutrophication-induced growth of green algae lead to an 82% decline in seagrass cover between 1960 and 1988 (Wells et al. 1991). There was also a crash in a suspension feeding, benthic

bivalve (*Katelysia* sp.) in this harbour between 1985 and 1992 (Peterson et al. 1994). Combined with observations of differences in benthic community within and outside of sea grass beds (Wells et al. 1991), this is indicative that in these shallow waters a substantial change in the above SWI community results in equally substantial and probably persistent changes in the infaunal community.

Competition for food resources between holo- and meroplankton and predation between these components of the plankton might be quite species specific and could affect the stability of both above and below SWI communities (Figure 2). The meroplankton which feed on microphytoplankton are usually too scarce to be food limited as a result of intraspecific competition (Strathmann 1996). This implies that the meroplankton has no impact on the phytoplankton and does not compete with holoplankton for resources but the holoplankton could outcompete the meroplankton for food. Changes in the holoplankton community could affect recruitment and hence stability of below SWI organisms. A contradictory view arises from results of experiments with the larvae of two benthic polychaete species that suggest planktonic larvae in shallow waters could cause an impact on nanophytoplankton populations (Martin et al. 1996). Grazing by polychaete larvae in the water column also appeared to disrupt the grazing control exerted by heterotrophic nanoflagellates on pelagic bacteria resulting in increased bacteria in the presence of the polychaete larvae. There were differences in grazing rates between the two species of polychaete studied. Species specific increases in meroplankton abundance and changes in its diversity could affect stability of the holoplankton communities directly as a result of increased competition for food and indirectly by affecting the organisms that control bacteroplankton community structure.

Such changes have been observed in long time series data in the North Sea where the presence of planktotrophic larvae from benthic organisms is variable. There was an increase in echinoderm larvae during the 1980s and early 1990s and these became the dominant planktonic taxon in the region, this coincided with an increase in adult abundance within the sediment (Lindley et al. 1995). The increased abundance of these larvae could have arisen from decreased predation on echinoderm adults (due to overfishing of demersal fish), from favourable impacts of increased sediment disturbance caused by trawling, as a consequence of climate change or from a combination of some or all of these factors.

Mesocosm experiments, demonstrated increased mortality of the holoplanktonic copepod *Acartia hudsonica* that could only be attributed to interactions with below SWI fauna (Sullivan and Banzon 1990). It was not clear whether the principle cause of the increased mortality was due to predation by benthic suspension feeders or by meroplankton. Competition for phytoplankton food resources did not appear to be a factor in these experiments. Other planktonic copepods within the mesocosm were also reduced in abundance when a within sediment component was included in the mesocosm. Clearly further research on the dynamics of interactions between the mero- and holoplankton is required before we can be certain if above and below
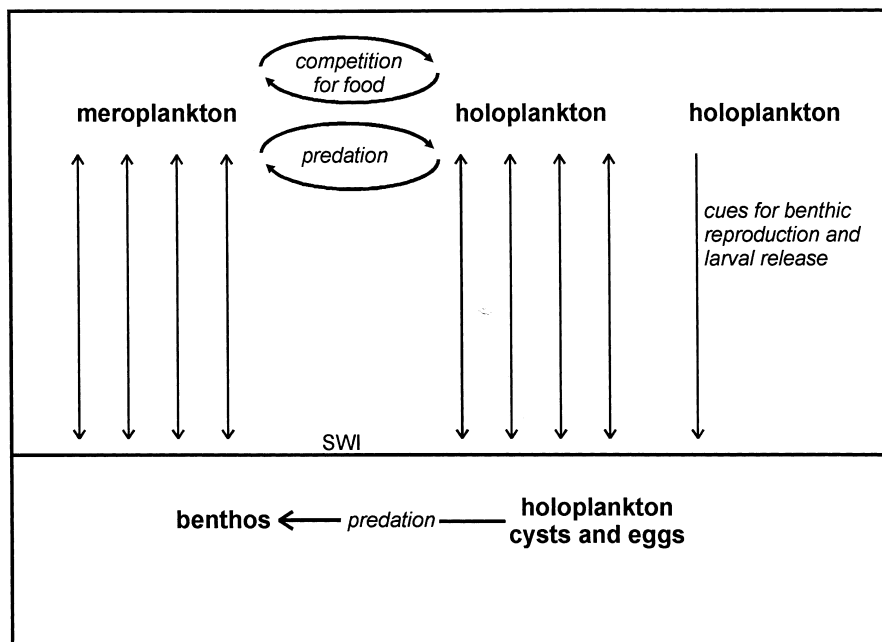
Figure 2. Schematic diagram indicating relationships between holoplankton and meroplankton and between permanent and temporary benthos.

SWI organisms impact on each other at the species level within the plankton let alone whether such interactions are likely to affect community stability.

Changes in the structure of the pelagic predator communities will also have repercussions on the stability of the below SWI community. Overfishing on Georges Bank, off the east coast of North America, has reduced stocks of cod, flounder and haddock, and a fish community dominated by sharks and rays has taken over with a subsequent alteration of trophic flow (Fogarty and Murawski 1998). Similarly, the large-scale removal of cod from Newfoundland waters has coincided with an explosion of shrimp and crab. Although experimental studies to explicitly test the impacts of these changes on infauna are lacking, it is very likely given the way these different species feed that there have been significant impacts.

The invasion of sediment in San Francisco Bay by large numbers of the shallow burrowing Asian clam *Potamocorbula amurensis* provides one of only a few documented examples of how changes in the structure of the community below the SWI can destabilise the community above it. *Potamocorbula amurensis* is a voracious, suspension feeder and has dampened the seasonal summer phytoplankton bloom over successive years since its invasion and annual primary production in the water column is now considerably reduced (Alpine and Cloern 1992). This change in benthic community structure appears to have resulted in a persistent change in pelagic community dynamics.

A contrasting example of a possible reversible change or of non-stable community dynamics between above and below SWI organisms has been observed in the high tidal reaches of the Potomac River Estuary (Phelps 1994). Over a 10 year period an invasion by the suspension feeding Asiatic clam, *Corbicula fluminea*, resulted in decreased water turbidity, increased submerged aquatic vegetation and associated increases in fish and bird populations. A subsequent decline in populations of the clam coincided with a decrease in submerged aquatic vegetation and bird populations to previous levels and an increase in *Microcystis* blooms which had been common before the invasion by the clam.

Decomposition and nutrient cycling

Particularly in shallow coastal waters or near the poles, many of the decomposition processes of nutrient recycling/regeneration of above SWI material occur predominantly within the sediment. There is a feedback of organic and inorganic material flux from the sediment, where it has been remineralised, back into the water column where it then fuels further primary production. The decomposition processes are regulated by the benthos and help to maintain material globally. Keystone functional processes include ammonium production, nitrification, denitrification, sulphate reduction and oxidation and DON or DOC exchanges between the sediment and overlying water. Benthic macrofauna impacts on the rates of these processes through their sediment reworking activities, which bring oxygen deeper into the sediment and irrigate the sediment (for their own respiration). The oxygen fuels a variety of processes including sulphide and metal oxidation, nitrification and aerobic respiration and the irrigation promotes exchange of dissolved nutrients between the sediment and the overlying water (Henriksen et al. 1983). Different species have different modes of reworking and of bioturbation so that the diversity of the bioturbators directly impacts on the rates of the decomposition processes (Henriksen et al. 1983; Pelegri and Blackburn 1995). Some organisms actively pump water and dissolved nutrients to and from the sediment as part of their feeding and respiratory activities. Other organisms passively alter the sediments chemical properties through the bulldozing effects of their locomotion within the sediment. High irrigation activity relative to burrow surface area, or increased nitrification potential of the sediment surface due to selective feeding on the fine particle fraction of the sediment causes increases in nitrate fluxes (Henriksen et al. 1983). Yet, deeper burrowing species with low irrigation activity relative to burrow surface area tend to decrease the nitrate flux from the sediment relative to non-bioturbated sediment. Algal mats can also have an important direct impact on the nutrient dynamics of the marine ecosystem by acting as an effective 'filter' for the flux of nutrients between the sediment and the water column (Boucher et al. 1994; Hansen and Kristensen 1998; Rafaelli et al. 1998).

The extent to which decomposition processes and nutrient fluxes are dependant on the diversity of benthic organisms is not well understood, although there is evidence

that certain organisms are of key importance (e.g. Thayer 1983; Nedwell and Walker 1995; Levin et al. 1997). We are aware of just one study linking functional diversity of benthic organisms, natural material flux and the diversity of above SWI organisms. Chavaud et al. (2000) have suggested that a combination of the hydrodynamic features of the Bay of Brest, feeding activity of a diverse community of benthic suspension feeders and an increase in the suspension feeding gastropod *Crepidula fornicata* have enhanced silicate retention within the Bay. This has prevented a decrease in Si:N ratios that would otherwise have occurred due to increased anthropogenic inputs of nutrients over a 20 year period. The timing of phytoplankton blooms and production levels have altered but, as a consequence of the benthic activity, the community structure of the spring and summer phytoplankton blooms has remained resistant to change. Relationships between the biodiversity of below SWI organisms, decomposition processes and nutrient fluxes and the diversity, and its stability, of above SWI organisms could be an interesting area of study for future research.

Recruitment

Above SWI vegetation structure facilitates benthic larval recruitment to seagrass beds giving increased resistance and resilience to benthic populations. In seagrass beds, vegetated sites have more diverse and abundant benthic communities than nearby unvegetated sites (Peterson 1979; Summerson and Peterson 1984; Hutchings et al. 1991). However, the diversity of the seagrass plants themselves may not be of importance. The fauna associated with different seagrass species within sites shows more similarity in community structure than the fauna found amongst the same species but at different sites (Hutchings et al. 1991). The creation of a 3D structure by the seagrass community appears to be the important factor, density and height of the seagrass are important for recruitment of fish and decapods and presumably benthos (Bell and Westoby 1986). As indicated in the section above on physical transport processes, this is probably due to modification of water flow by biogenic structures causing deposition of particles, which also include larvae and small juveniles (Fonseca et al. 1982; Gambi et al. 1990).

The presence of a planktonic larval stage in many benthic organisms may confer a greater element of community resilience since there is more likely to be a potential supply of recruits to adult populations that have been affected by adverse conditions. Some pelagic organisms have plasticity of life histories which similarly increase the resilience of the population to unfavourable conditions (e.g. dinoflagellate cysts which lie dormant in the sediment). Organisms with both benthic and pelagic life stages often exhibit strong seasonal and annual fluctuations. These organisms may have low resistance to adverse conditions, i.e. their biphasic life history may expose them to the double jeopardy of deleterious conditions in both the water column and at the seafloor. The factors responsible for this are still being debated but potentially include variable (a) advective losses in the water column, (b) larval settlement

success, and (c) post settlement mortality. All these may be in part a function of physical factors such as local current conditions operating over the seafloor (Olafsson et al. 1994; Snelgrove and Butman 1994; Olivier and Rétière 1998; Thiébaut et al. 1998).

We do not know whether meroplankton survival is influenced by the species composition and abundance of available food in the plankton. It may be critical to the survival of feeding planktonic stages of benthic organisms that their presence in the pelagic zone is synchronised with availability of suitable planktonic food resources. Larval release in a deep-water crab may be linked to settlement of phytodetritus (Starr et al. 1994). Chemical exudates and physical contact by sinking phytoplankton may be important spawning cues (Starr et al. 1991, 1992; Tamburri et al. 1996). Do many species with feeding larval stages respond to cues from settling plankton and are these responses specific to cues from different plankton species? Resilience of the benthos is dependant on ongoing recruitment; intuitively interactions between mero- and holoplankton (e.g. predation and competition) will impact larval availability and hence resilience of the below interface community (Figure 2).

Benthic organisms with planktonic larval stages are often considered to be either planktotrophic or lecithotrophic. Planktotrophic species broadcast eggs into the plankton that are relatively underdeveloped and have a only a small yolk food supply. Lecithotrophic species broadcast fewer but more developed and larger eggs with a larger yolk food supply. Lecithotrophic larvae generally spend shorter periods of time in the plankton than planktotrophic larva. In the deep sea and at higher latitudes there is a greater proportion of lecithotrophic than planktotrophic larval development within the benthos (Knudsen 1979; Lindley 1998). For example, at abyssal depths up to 75% of bivalve species have lecithotrophic larval development (Knudsen 1979). This has a number of implications, including a lesser impact of meroplankton–holoplankton interactions on stability in these habitats. Isotopic evidence suggests that these larvae stay near the bottom. Planktonic larvae are smaller than lecithotrophic larvae and have higher dispersal rates. We might predict a higher proportion of lecithotrophic larval development to confer a greater resistance of the community to environmental change, because of the reduced effect of planktonic impacts, but less resilience, because planktonic larvae provide a refuge against benthic impacts.

Structural stabilisation of sediments

Sediment stabilisation is most relevant in littoral and shallow sub-littoral sediment. Vegetation such as seagrasses, mangroves, algal and diatom mats, and large epifaunal organisms with tubes or hard shells can act as structuring agents or ecosystem engineers creating a new interface between the sediment and the overlying water. These biogenic structures can modify local water movement, stabilise sediments and trap nutrients (see section on physical transport processes above and also Holland et al. 1974; Hutchings and Saenger 1987; Boucher et al. 1994; Blanchard et al. 1997).

In vegetated habitats it is unclear whether the diversity of the above interface vegetation or of the organisms associated with it are important to below interface organisms, let alone whether diversity affects stability. Diversity of the mangrove tree species or seagrass species within a mangrove area or a seagrass bed is often rather low but in mangrove areas particularly the trees are 'structural' species which support a diverse species assemblage (Howard et al. 1989; Ellison and Farnsworth 1996).

Within the sediment the diversity of meiofaunal communities varies in the presence of mangrove leaf litter but it is unaffected by the diversity of mangroves themselves (Gee and Somerfield 1997; Somerfield et al. 1998). Loss of structure, be it mangroves, seagrasses, large bivalves etc. modifies local water flow patterns. This completely changes the sediment characteristics leading often to rapid erosion and changes in the infaunal community. Once these above SWI structural species are lost they may not return and nor do the below interface communities associated with them, indicating the lack of resilience (Hutchings et al. 1991). This in turn affects above interface communities. Anthropogenic disturbance in the Caribbean and the Asia-Pacific region during the 1980s reduced mangrove areas by between 0.2% and 1.7% per year (Ong 1995; Ellison and Farnsworth 1996). Commercial fisheries for shellfish and fin fish are declining at a similar rate as many species use the mangrove for nurseries and/or refugia.

Beds or mats of epifaunal bivalves such as mussels and oysters and of tubiculous polychaetes can modify the biodiversity of infauna living in the sediment below in various ways either inhibiting or enhancing it (e.g. Gruet 1986; Dittman 1990; Gherardi and Cassidy 1994; Mettam et al. 1994; Porras et al. 1996; Crooks 1998; Crooks and Khim 1999). Often suspension feeders in particular are reduced within sediments beneath these epibenthic rafts whilst deposit feeders increase. Through modification of water flow in the boundary layer the rafts can increase sedimentation and often also increase organic enrichment through biodeposition of faeces and pseudofaeces. As with vegetative structures the effect of the structure above the SWI on stability of below SWI organisms appears to depend on its extent and persistence rather than the diversity of the raft forming organisms. Small faunal rafts can increase microhabitats and enhance below interface diversity. Large rafts particularly reduce water flow directly over the sediment resulting in increased deposition that can cause the underlying sediment to become anoxic and have negative effects on below SWI diversity. The raft forming epifauna are usually suspension feeders that can outcompete infaunal suspension feeders and physically obstruct their feeding mechanisms and also impede recruitment on below SWI organisms with planktonic larval stages through predation and physical obstruction. The mats vary in persistence over time and it is unknown whether these effects are lasting and therefore whether the underlying infaunal communities can be considered to be stable. Some mats such as those of the Asian mussel, *Musculista senhousia*, are virtually annual. Others may persist for many years.

These examples suggest that above SWI structure that stabilises sediments can increase resistance of below SWI organisms but if it is removed then the below SWI

system shows little resilience. The degree of resistance depends on the quantity of above sediment structure (for example diatoms have less influence than macrovegetation), or on problems associated with the structure such as hypoxia and anoxia associated with green algal mats (discussed above).

Gaps in knowledge

We do not know the spatial and temporal scales at which above and below SWI biodiversity are related, particularly for non-vegetated coastal and oceanic habitats. Of the limited amount of work done already, most has either been at either very small spatial and temporal scales involving specific communities and/or species, or at a large, broad scale – i.e. looking at processes such as carbon flow. It is not clear how, or if, we can extrapolate between these scales. We need more detailed knowledge of the mechanisms that link above and below SWI biodiversity before we can say with certainty how far changes in the biodiversity either above or below the SWI will affect the stability of the biodiversity or of ecosystem functioning in the other system. We do not have a clear idea of the levels of organisation that are critical to the processes linking above and below SWI biodiversity – i.e. there is a lack of definition of the functional groups involved, their relative importance and the levels of redundancy within them.

Within the marine environment, the SWI is a rather indistinct boundary, particularly in shallow coastal situations where there is vegetation or structural fauna. Clearly many of the organisms that we have designated as above SWI are benthic. Often they act as a further interface between the sediment and the water. These organisms will have their own interactions with both above and below SWI organisms but in terms of biodiversity relationships such specialised relationships are poorly studied. The hyperbenthos are the mobile fauna inhabiting the zone just above the SWI. They include organisms that undergo diel migrations from the sediment into the water column (e.g. mysids and some polychaetes) or from the water column to the sediment (e.g. some chaetognaths). Hyperbenthos are the subject of increasing research but they are difficult to study from a logistical point of view and their role in linking biodiversity above and below SWI still requires further investigation. (Armonies 1994; Mees and Jones 1997; Dauvin et al. 2000).

It has been suggested that benthic fauna, particularly the meiobenthos, could affect plankton community dynamics by differential predation on the resting cysts and eggs of phyto- and zooplankton within the sediment (Figure 2; Marcus and Boero 1998) but, as far as we are aware, this has not been investigated.

How can we fill these gaps?

The gaps in our knowledge identified in this review require new research directions. Specifically, increased collaborations are needed between biodiversity researchers in

pelagic and benthic realms (this has also been highlighted by Boero et al. 1996), particularly studying relationships between diversity and ecosystem function across the two environments. Increased use of modelling will help define biodiversity relationships, particularly in concert with increased collection and parallel analysis of long term plankton and benthic data sets. Further developments of field studies to test relationships are also required, including manipulative experiments. Carefully designed mesocosm experiments could provide a controlled environment to test specific aspects of the relationships, which could then be verified in further field studies. Both field and mesocosm studies should be conducted at sufficiently large scales to integrate pelagic and benthic systems.

Summary of hypotheses

There is clearly so little known about how links between biodiversity above and below the SWI affect stability that we have ended up with few clear conclusions but instead the series of hypotheses summarized here:

   (i) Biodiversity above the SWI will most influence stability of biodiversity below the interface where there is a close energetic connection between the two domains e.g. in temperate shallow water and polar regions.
  (ii) Sediment systems with low reservoirs of carbon will be most influenced by changes in pelagic diversity.
 (iii) Sediment systems with a large reservoir of carbon will be resistant to change in pelagic diversity but are likely to be less resilient once the reservoir is exhausted.
  (iv) The linkage in stability of biodiversity between domains is likely to be stronger in those communities dominated by very selective detritivores.
   (v) Reduction in the diversity of autotrophic food species will reduce the relatively high diversity of meiobenthos in estuaries.
  (vi) Diversity of the benthos will influence nutrient cycling and hence affect stability of plankton diversity
 (vii) Infaunal communities with a higher proportion of lecithotrophic larvae should be more resistant but less resilient to changes in above SWI biodiversity.
(viii) Selective feeding by benthos on plankton cysts and eggs will alter planktonic diversity.
  (ix) Changes in hyperbenthic communities will affect both above and below SWI communities.

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