



The structure and replenishment of rocky shore intertidal communities and biogeographic comparisons

David R. Schiel*

*Marine Ecology Research Group, School of Biological Sciences, University of Canterbury,
Private Bag 4800, Christchurch, New Zealand*

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Abstract

Marine scientists have made many recent advances in understanding the connections between the structure of benthic communities, replenishment of populations through dispersal processes, and interactions with the nearshore water mass. In this review, some of the themes and models relating to these processes and interactions are discussed. Benthic–pelagic coupling models are in the early stages of development, but encompass oceanic processes such as upwelling and downwelling, the transport of larvae and their arrival back to shore to settle. Most current knowledge of these processes is based on a few taxa, especially barnacles and mussels. This is discussed with reference and comparison to macroalgae, which dominate much of the intertidal zone on temperate rocky shores, and have quite different life histories, transport and settlement processes. The role of key, habitat-dominating species is discussed, particularly their early life histories, with reference to the differences in community composition, nearshore dynamics and settlement processes in different countries. Finally, some suggestions are made for future work to fill gaps in understanding about rocky shore communities.

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1. Preamble

Almost 18 years ago, two Australian ecologists asked in the title of a paper, do intertidal communities have different ecologies or different ecologists? ([Underwood and Fair-](#)

* Tel.: +64-3-364-2031; fax: +64-3-364-2590.

E-mail address: d.schiel@zool.canterbury.ac.nz (D.R. Schiel).

weather, 1986). They referred specifically to studies on species that were common in different countries but which had different trophic relationships. They also questioned how advances in understanding of marine ecosystems could be made if different methodologies and philosophies were applied in different places.

With increasing frequency in recent years, ecologists have explored the relationships between localised and broader-scale processes within and among coastlines of different countries in a search to understand not only local variation but also global processes (e.g., Jenkins et al., 2001; Menge and Branch, 2001). Inevitably, these studies involve a wide range of differences in biological, chemical and physical variables, including community composition, life histories of different taxa, trophic dynamics, coastal physics and nutrient inputs. We know a great deal about each of these individually, but more so in some ecosystems than in others. The interrelationship between these variables is less well known. Furthermore, there may be biases in perception that are only slowly being corrected, driven at least partially by the highly productive and influential literature from US scientists which, at least until recently, has tended to cite mostly north American studies (Wardle, 1995). As the realisation of global problems and an awareness of the need for more scientific information and access to it to help solve them increase (Annan, 2003; Lubchenco and Iwata, 2003), it is timely to re-visit the question posed by Underwood and Fairweather (1986).

The history of marine ecological research is rich, extensive and varied, and there have been numerous recent, thoughtful reviews of most topical issues. These include special features in *Ecology* discussing the underlying philosophy of scientific progress in ecology (Graham et al., 2002, et seq. [6 reviews]), long-range dispersal (Kinlan and Gaines, 2003), issues relating to marine reserves (Lubchenco et al., 2003, et seq. [17 reviews]), a special issue of the *Journal of Experimental Marine Biology and Ecology* (Gibson et al., 2000, et seq. [12 reviews]), and a book covering most facets of marine ecology (Bertness et al., 2001, 19 chapters). Our field has been well-served by excellent syntheses of the complex issues facing marine ecologists as we grapple with natural ecosystems. Despite the wealth of literature, however, we are also subject to “bandwagon” issues (Paine, 2003) and are prone to drawing analogies from the ecosystems we are most familiar with, perhaps like Miss Marple, Agatha Christie’s famous home-grown detective who found all facets of the world within her own small village. This leads to several questions. How well do models developed elsewhere apply to local ecosystems? How important are local variations in community composition and dynamics to achieving a broad understanding of structure and function? How do ecologists reconcile local issues relating to particular ecosystems with broader issues when there are great differences in taxa, usage patterns and management structures? And how can the predictive power of research and advice, which are both a measure of the relevance of our science and its usefulness (cf., Peters, 1991a,b), be increased?

Given the numerous recent reviews, it seems that no paradigm has been left unexplored. Rather than plumbing the same waters, therefore, I address some of the above questions not as a thorough review, but from a perspective of an ecologist who has worked extensively on the rocky shores of New Zealand, where several models relating to benthic community structure have been tested. This special edition of the *Journal of Experimental Marine Biology and Ecology* provides an opportunity to put forth such a perspective and

highlight both commonalities and divergences between widely separated rocky shore ecosystems.

2. Introduction

One of the most important areas of research in ecology in recent times involves the interactions of benthic communities with the nearshore and open ocean environments, so-called “benthic–pelagic coupling” (cf., Menge et al., 1997a,b). This topic encompasses virtually every facet of marine biology involved in the physics of the coastal water mass, the life histories of coastal species, larval supply, settlement, recruitment, and trophic interactions. Conceptually, little of this is new (cf., Sinclair, 1988, Graham and Dayton, 2002 for review), but there are new methodologies and a greater focus on multidisciplinary studies that have opened new possibilities of understanding complex processes and interactions (Paine, 2002; Palumbi et al., 2003). Inevitably, this involves considerations of spatial and temporal scales, and how to design and implement meaningful experiments (Underwood, 2000). Seemingly simple questions like “how connected are populations?” have absorbed fisheries ecologists and managers for over 100 years (Sinclair, 1988; Peters, 1991a,b) but have assumed increasing importance to coastal ecologists more recently. Understanding connectivity is crucial for marine reserve designs (Palumbi, 2003; Shanks et al., 2003), gene flow between populations (Palumbi, 2001), recovery from disturbances (Sousa, 2001) and the potential impacts of invasive alien species (Ruiz et al., 1999).

Unfortunately, our knowledge of the interactions of the nearshore water mass with benthic communities is currently based on relatively few species and even fewer types of organisms. This has been highlighted in several recent reviews. For example, although Grantham et al. (2003) compiled a list of >1000 species, documenting their larval life history characteristics and potential distances of dispersal, most species were plankton feeders and the great majority had an obligate period in the plankton. Kinlan and Gaines (2003) derived dispersal distances of 95 species. Most of these were invertebrates with an obligate developmental period and only 10 were larger macroalgae, the fucoids and laminarians that dominate many habitats. Menge (2000a) reviewed top-down and bottom-up processes and community regulation in marine rocky intertidal habitats. In his first table of examples of top-down control, 17 of 20 examples involved barnacles and/or mussels. In prominent examples of larval supply and benthic processes, all of the examples are barnacles and mussels (Gaines and Roughgarden, 1985; Menge et al., 1999; Connolly and Roughgarden, 1998). Given the importance of these taxa to our current understanding of rocky intertidal dynamics, it is worth asking to what degree they are representative of nearshore processes and dynamics.

A recent (Bertness and Callaway, 1994; Bruno et al., 2003) and controversial (Menge, 2000b) issue has been a re-focus on facilitation and positive interactions within marine communities. Are they an essential structuring force, under what circumstances, and how strong is their effect relative to other processes such as trophic dynamics? Many of the cited studies involved plants, particularly large brown algae.

Whether or not facilitation occurs, macroalgae, particularly those in the Order Fucales, are dominant occupiers of primary space in the middle to low intertidal zone of temperate

shores throughout the world (Abbott and Hollenberg, 1976; Schonbeck and Norton, 1978; Clayton and King, 1981; Kautsky et al., 1986; Adams, 1994; Chapman, 1995). Interactions between macroalgae and other taxa in the communities in which they occur are fundamental to local dynamics and are essential components of general models. One focus of this review, therefore, is on macroalgae, which offer many contrasts to filter-feeding invertebrates. Macroalgae do not have an obligate development period in the plankton and tend to have shorter dispersal distances than most invertebrates (Santelices, 1990; Norton, 1992; Reed et al., 1992; Dethier et al., 2003; Kinlan and Gaines, 2003). Consequently, their interaction with the nearshore water mass is far different from filter-feeding invertebrates, and the degree of connectivity of localised populations could therefore be quite different. As for invertebrates, however, the relationship between propagule supply, settlement, recruitment and post-recruitment processes is not well-known for many species. Obviously, relatively inert macroalgal propagules do not display the behaviours of invertebrate larvae (cf., Morgan, 2001; Underwood and Keough, 2001) but nevertheless their ability to settle and attach, particularly in turbulent conditions near rocky shores can be critical to community structure (cf., Brawley and Johnson, 1991).

Finally, most elements of marine ecology come together in biogeographic comparisons. There is a long history of descriptions across biogeographic regions in most countries, usually describing floral and faunal components on the basis of latitude, temperature or degree of wave exposure (e.g., Stephenson and Stephenson, 1949; Dakin, 1960; Morton and Miller, 1968; Ricketts et al., 1985). The history of experimentally testing underlying processes responsible for regional differences is more recent, especially within a framework of top-down (trophic) and bottom-up (nutrients and larval supply) processes (reviewed in Menge, 2000a,b). Environmental gradients of nutrients, productivity, physical harshness and disturbance can have major effects on the types and strengths of community interactions (Connell, 1975; Menge and Sutherland, 1976, 1987; Menge and Olson, 1990). Four distinct regions of the world have been cited in support of the critical interaction of top-down and bottom-up processes in community regulation: the Pacific Northwest of the United States, South Africa, Chile, and New Zealand. A “comparative-experimental” method (McPeck, 1998; Menge et al., 2002) using experiments in widely separated regions has been used to elucidate general principles in the structure of marine communities. Because such studies have involved New Zealand (Paine, 1971; Menge et al., 1999, 2003), which has some shores that are at least superficially similar to those in the northwestern USA, I discuss various structuring processes, often by using specific comparisons to New Zealand to illustrate strengths and deficiencies in nascent nearshore-benthic models.

3. The upwelling hypothesis and community structure

Connolly and Roughgarden (1998) pointed out many of the contradictions in the literature relating to community structure and regulation. Although the roles of competition, predation and disturbance have been elucidated in many countries and regions, these processes can vary considerably within regions and at different scales. They and others (e.g., Underwood and Denley, 1984; Connell, 1985; Gaines and Roughgarden, 1985; Gaines and Bertness, 1992) have argued that if recruitment rates largely determine adult

distribution and abundance patterns, then they may also determine the strength of interactions among species. Furthermore, a primary determinant of recruitment rates is the rate at which larvae arrive to shore through upwelling-related events.

Upwelling occurs when strong equatorward winds blow along a coastline causing the surface layer of water to move offshore (Pickard and Emery, 1990). Colder water, usually laden with nutrients moves up from below the thermocline to replace it, and then moves offshore as winds persist. This not only circulates nutrients into the shallow nearshore zone but also transports larvae in the surface waters offshore (Lalli and Parsons, 1997). A variety of processes, such as relaxation events, can move larvae back towards coastal habitats (Connolly and Roughgarden, 1998). Because of the coriolis effect, upwelling tends to occur commonly along the eastern boundary currents and, hence, west coasts in both hemispheres (Pickard and Emery, 1990; Bearman, 1998). Where upwelling is strong and persistent, therefore, the arrival of larvae back to shore is poor but where it is intermittent, with frequent relaxation events, larvae may be brought shorewards and recruitment can be high (Menge et al., 1997a,b; Connolly and Roughgarden, 1998), leading to different trophic effects.

3.1. *South Africa, Chile*

Although the broad correlations between species' distributions and physical factors such as temperature, wave exposure and upwelling have long been known (Hubbs, 1948; Stephenson and Stephenson, 1949; Dawson, 1950; Lewis, 1964), most evidence for the interaction of trophic and nutrient-derived influences in marine community structure is more recent. The most cited example is for South African shores (review in Menge, 2000a,b) which, along with the west coast of the USA and Peru–Chile, has a major upwelling system. Bustamante and Branch (1996) surveyed 2500 km of shoreline, quantifying and extending earlier observations of the distinct biogeographic provinces along the upwelled Benguela west coast, a southern and an eastern region. Although the west coast had a higher biomass of species in the intertidal zone, it also had only about half the number of species of the south and east coasts, which were influenced by the Indo-Pacific radiation. Within each of these regions, however, were great localised differences in intertidal communities that largely related to the degree of wave exposure (cf., McQuaid and Branch, 1984, 1985). Filter-feeding invertebrates were an order of magnitude more abundant on exposed than on sheltered shores around Cape Peninsula. Intertidal algae were also far less abundant on sheltered shores than in exposed and semi-exposed places. Bustamante et al. (1995) referred to the “subsidy” of intertidal grazer biomass by drift kelp fronds that came ashore on the west coast and sustained much larger populations of intertidal limpets than did *in situ* algal productivity alone. This had trophic consequences because the abundant grazers controlled the standing crop of benthic intertidal algae. It appeared, therefore, that it was not just the highly productive subtidal mass of kelp that sustained intertidal invertebrate populations but the delivery of kelp fronds to shore in more exposed conditions.

Other work from South Africa shows that kelp beds occur nearshore throughout the provinces and yet this does not necessarily imply large herbivore and filter/suspension-feeder populations were present (Field and Griffiths, 1991; Branch et al., 1994). Hence, the

question is begged, is it more the productivity per se that drives the “subsidy” (i.e., a nutrient-derived, bottom-up process, leading to increased production) or the degree of wave exposure (a delivery process) interacting with intertidal dynamics that drive these intertidal invertebrate populations? The answer is not clear for many coastal ecosystems. However, because of the great importance of wave exposure to community structure, the explanation could be more physically based than nutrient-based. The relative contributions of plankton and subtidal, macroalgal-derived energy to benthic community structure and regulation are of some importance but are little understood.

The processes that tip the balance between dominance by filter-feeders and algae are not always clear, yet they form a major focus in intertidal studies examining both broad and localised scales of community organisation. For example, along the coast of Chile, Broitman et al. (2001) did extensive surveys and noted a distinct discontinuity in community structure at about 32°S latitude. Mussels were rare north of this latitude but tended to increase in abundance to the south in the mid-intertidal zone. This was presumed to coincide with an oceanographic feature. The low tidal zone was dominated by kelps, which also became more abundant to the south, while ephemeral and crustose algae were more abundant in warmer northern waters. They characterised some of their many study sites as undergoing occasional upwelling, but they found no trend of increased abundances of filter-feeders at these locations. While the abundances of major taxa showed clear trends with latitude and its correlate sea-surface temperature, there was no clear trend that could be ascribed to upwelling or productivity.

The western coast of the USA is probably the most studied nearshore region of the world. There has been considerable analysis of biogeographic boundaries and within-region variation in community structure relating to oceanographic features, particularly upwelling. This involves a complex interaction of many variables and is still in the early days of experimentation, which I discuss below.

3.2. Pacific coast of the USA

The mechanisms influencing upwelling, the transport of larvae, and effects on community structure and processes in the Pacific northwest have been examined and discussed in several papers (Ebert and Russell, 1988; Roughgarden et al., 1991; Wing et al., 1995; Connolly and Roughgarden, 1998; Largier, 2003). In this region, upwelling is more intense towards the south and is particularly intense around major headlands (Huyer, 1983; Ebert and Russell, 1988). Connolly and Roughgarden (1998) used transect data from many exposed rocky intertidal benches in California and Oregon to determine the relationship between sessile invertebrate cover and bare space and how they are related to upwelling intensity. They found less free space in Oregon than in central and northern California, less primary algal cover in Oregon, and a greater cover of the mussel *Mytilus californianus* and acorn barnacles (*Balanus glandula*) in Oregon. They concluded that there was less free space and greater cover of competitively dominant filter-feeders in the area of weakest upwelling. They considered a “predation gradient” to be an unlikely cause of these patterns because the areas surveyed were above the lower limit of mussel beds where predation by sea stars mostly occurs. They further argued that the wide area of the continental shelf in California and the persistence of upwelling led to fewer invertebrate

larvae reaching the shore to settle, compared to the narrower shelf and frequent relaxation events in Oregon that allow more larvae to reach shore. Consequently, their model and the work on which it was based (e.g., [Roughgarden et al., 1988](#)) provide an oceanographic circulation-modulated driver of recruitment variation that leads to variations in the intensity of trophic interactions.

Clearly, complex oceanography intersects with upwelling, larval transport and settlement events. Based on SST and long-term trends in wind stress, there are distinct regions along the US west coast, with transitions near Point Conception in the south and Cape Mendocino in the north ([Mendelssohn and Schwing, 2002](#)). These headlands coincide with the southern limits of many northern species and the northern limits of southern species, respectively ([Morris et al., 1980](#)). These areas, therefore, have biogeographic as well as structural importance for benthic communities. Within these regions, however, there is great variability. For example, [Connolly et al. \(2001\)](#) argue that because recruitment by competitively dominant filter-feeders is not saturating in central and northern California, mesoscale processes within this region are more important than larger-scale trends in upwelling as determinants of community structure.

These arguments for benthic–pelagic coupling have considerable strength in linking together most aspects of the nearshore environment, community structure and regulation. Importantly, they also provide a predictive framework for testing critical processes. The major strengths are in clarifying mechanisms for recruitment variability and its causes and the trophic effects that result from recruitment variation, thereby coupling pre- and post-recruitment processes and broad and local-scale events. Nevertheless, there are critical processes in the supply and delivery process, and considerable variability in benthic processes that include not only predation and grazing but also disturbance variability and intensity, successional events, competitive hierarchies, and community composition that can play a more dominant role than upwelling in determining community structure (e.g., [Foster et al., 2003](#); [Chapman and Underwood, 1998](#)). Clearly, there are problems in testing large-scale processes related to upwelling, and much of the evidence is correlational. So, how general are the predictions of upwelling events and effects on community structure and organisation?

3.3. New Zealand and comparisons to other regions

Bruce Menge and his collaborators have been insightful and instrumental in realising that a comparative-experimental approach can be used across continents and hemispheres to evaluate the generality of processes in widely separated ecosystems. Their recent work comparing Oregon and southern New Zealand is based on the similarity in latitude and composition of exposed shores that are dominated by filter-feeders ([Menge, 2000a](#)). Major findings are that there are significant differences in settlement and trophic interactions between the east and west coast of NZ that are largely driven by oceanographic conditions, particularly upwelling on the west coast and downwelling on the east coast ([Menge, 2000a,b](#); [Menge et al., 1999, 2003](#)). They found that predation rates were higher, recruitment of barnacles and mussels was greater, there were more large predators (sea stars), and that grazing was more intense on west coast sites. [Menge et al. \(2003\)](#) concluded that because the concentration of phytoplankton (as measured by chlorophyll-*a*)

and particulates was similar on both coasts, that “larval transport and oceanic productivity are decoupled in New Zealand”, unlike results from Oregon (Menge et al., 1997a,b). These are complex issues involving the interactions of nearshore processes with community structure and ecological processes. Here, I discuss these issues within the broader context of NZ shores.

3.3.1. New Zealand community structure

In many ways, New Zealand serves as a microcosm of processes affecting temperate communities: it has a complex hydrography, large rivers affecting coastlines, prominent headlands, a complex continental shelf, and a large suite of endemic species. New Zealand has been described as an archipelago in space and time (Nelson, 1994). With three main islands and around 600 islands and islets (Molley and Dingwall, 1990), NZ spans 13° of latitude and is influenced by complex oceanography (Heath, 1985; Fig. 1).

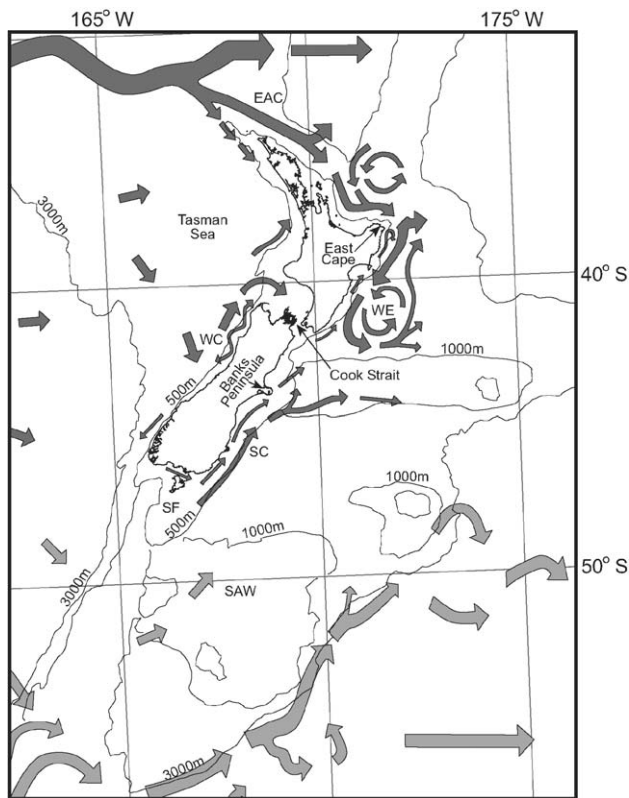


Fig. 1. The currents and continental shelf around New Zealand. Note position of subantarctic waters to the south (SAW); subtropical waters to the east; the Southland Front (SF), the Southland Current (SC), the warm-core eddy (Wairarapa Eddy) on the east coast; the currents around East Cape (central right, North Island); the tropical front and East Australian Current in the north; the Westland Current (top right, South Island). Depth contours of continental shelf are shown. Further details in the work of Heath (1985). Redrawn from map by National Institute of Water and Atmospheric Research.

The major land masses extend from the subtropical north (34.5°S) to the cool temperate south (47.5°S), but territorial waters are extended considerably by the subtropical Kermadec Islands, the Chatham Islands to the east, and the subantarctic islands in the far south. Along the mainland of the North and South Islands, the annual average sea-surface temperature (SST) varies from 17.5° in the far north to 11.5° at the tip of the South Island, with surprisingly little variation at equal latitudes between the east and west coasts (e.g., Uddstrom and Oien, 1999; Murphy et al., 2001). Biogeographic provinces have long been recognised, although these varied depending on taxa (Moore, 1961; Pawson, 1961; Dell, 1962). The west coast has a mixed coastal flora and fauna, with a historically recognised breakpoint just south and west of Cape Reinga (at the top of the North Island) and in the south in the vicinity of Fiordland (southwest coast of the South Island). Discontinuities have been noted on the east coast at East Cape for many invertebrates and south of Cook Strait (between the North and South Islands) for many algae (Moore, 1961). Nelson's (1994) analysis of large brown algal distributions found distinct elements in the northern part of the North Island, but no clear separation from the region of Cook Strait south. Very distinct elements of communities were noted at the widely separated subantarctic islands and the Chatham Islands, and the Three Kings Islands, 57 km north of the North Island, all of which have a high degree of endemism. Nelson reiterated reservations (e.g., Lang, 1895) about the explanatory power of dispersal as the prime influence shaping the composition of the NZ algal flora and stressed geological, oceanographic, climatological and ecological influences that have interacted over millions of years.

On intertidal rocky shores, two of the most striking features are that barnacles and mussels dominate most west coast sites but are found primarily on headlands on the east coast, whereas large brown algae dominate most east coast sites but few on the west coast (Schiel, unpublished database). Of particular note is that smaller fucal species (less than about 1 m in length as adults), especially the endemics *Carpophyllum maschalocarpum*, *C. angustifolium*, *Cystophora torulosa*, and *Hormosira banksii*, are abundant along much of the east coast but give way to the giant southern bull kelp (Order Fucales) *Durvillaea antarctica* (Hariot) in the more exposed waters south of Cook Strait. Bull kelp can reach >80 kg/m², can have considerable whiplash effects that limit the taxa able to survive in nearby areas (Santelices et al., 1980) and often occurs just below mussels, especially on east coast headlands. This zone on the west coast is usually occupied by tough red algae (corallines and *Gigartina* species) that can withstand the considerable sand scour on low tidal benches.

Across sites of different wave exposures on both coasts in the South Island, mussels (both *Perna canaliculus* (Gmelin) and *Mytilus galloprovincialis*) are found commonly on sheltered shores (mostly within harbours and behind headlands), and on exposed shores (i.e., average wave force 40–60 Newtons), mostly in the mid intertidal zone. Therefore, one of the most important associations between barnacles and mussels is that on exposed shores they tend to co-occur with bull kelp on the east coast but not on the west coast. It should be noted that the intertidal sea star *Stichaster australis* occurs abundantly on the west coast, but is found only in small numbers on the east coast itself but often on wharf pilings in harbours when mussels are abundant (cf., Morton and Miller, 1968, p. 362).

3.3.2. New Zealand coastal environment and upwelling

The nearshore environment around New Zealand is complex, yet understanding its nature is fundamental to determining how it affects onshore community structure and the validity of comparisons to elsewhere. The currents, continental shelf, positions of persistent eddies, productivity patterns, amount of sedimentation and geomorphology form an intricate interwoven picture (Bradford-Grieve et al., in press). On average, the entire west coast (other than within harbours and fiords) is considered very exposed with almost continual pounding of oceanic swells. The east coast is mostly semi-protected north of East Cape but more exposed on outer coasts sites from there southwards. Most east coast sites are composed of softer sedimentary rocks, except for headlands such as Banks Peninsula (cf., Menge et al., 1999) which are harder volcanic or metamorphic rock, while west coast reefs are composed mostly of hard metamorphic rock. The broad relationship between rock types and exposure may affect community structure; few mussels are found on the softer sedimentary rocks, mostly because they do not attach well (although this has not been tested). For example, mussels are uncommon on the Kaikoura peninsula (composed mostly of mudstone and friable limestone), although they are common on harder reefs to the south and north. Reefs composed of softer rocks rarely occur where wave-exposure is great, and are usually dominated by fuclean seaweeds, such as *H. banksii*, *Cystophora* spp. and *Carpophyllum* species.

Hydrographically, NZ is surrounded by several distinct water masses (the surface Subtropical and Subantarctic waters, and from the surface down, Antarctic Intermediate Water, Deep Water, and Antarctic Bottom Water; Fig. 1). Major currents are the subtropical East Australian Current in the north, the Westland Current in the southwest, and the Southland Current that flows from the south-western end of the South Island and northwards up the east coast (Heath, 1985; Vincent et al., 1991; Chiswell and Schiel, 2001). Around the middle of the South Island, a mixture of water from the Southland Current is deflected eastwards along the continental shelf, but some northward flow is evident intermittently through a submarine saddle (Shaw and Vennell, 2000) (contrast with Menge et al., 2003; Fig. 1). Upwelling occurs intermittently from at least the central west coast of the South Island northwards to Cook Strait (Vincent et al., 1991; Stanton, 1971, 1976) and also along the northeast coast of the North Island.

There is some debate about how frequently upwelling occurs along the west coast and whether sudden decreases in seawater temperatures as recorded by onshore sensors (frequently used in intertidal studies; cf., Menge et al., 1999) are indications of upwelling or of freshwater input. There is considerably higher rainfall on the west coast than the east coast (e.g., average annual rainfall is around 2200 vs. 600 mm; NIWA meteorological records) and there are two large rivers that may have caused the cold water plumes seen in some studies. Vincent et al. (1991) found cold-water plumes extending offshore from the coast in the vicinity of river mouths but argued they were unlikely to be a direct effect of cold riverine input because of dilution and because differences between seawater and river temperatures were not large at the time of their study. However, Stanton (1972) showed there can be a salinity anomaly near rivers, and Vincent et al. (1991) also found that the colder water had reduced salinity. In areas where river discharge significantly affects surface salinity values, as along the west coast of South Island (Stanton, 1976; Bradford, 1983) and the west coast of the US, upwelling episodes may, in fact, result in higher

salinity waters being brought to the surface, which may not be nutrient-rich as they do not represent below-thermocline waters (Pickard and Emery, 1990). Productivity along the west coast of NZ, therefore, may not be due to upwelling alone but to freshwater input of nutrient-rich water, a “benthic-terrestrial” rather than a “benthic–pelagic” coupling (cf., Menge et al., 1999). These sorts of issues need considerably more work because they entail far different mechanisms for benthic processes. Analyses of stable isotopes may help resolve the sources of nutrient inputs.

Circulation around the east coast of the South Island is also complex. Murphy et al. (2001) showed that the highest concentrations of chlorophyll-*a* around NZ occurred off the southern region of the South Island and to the east along the continental shelf. Rather than upwelling-driven productivity, it appears that this is due to mixing of the warmer coastal waters, poor in macronutrients but iron-rich, with the macronutrient-rich but iron-poor subantarctic waters (Abraham et al., 2000; Boyd et al., 2000). These waters are driven up the east coast by the Southland Current, although this process is not well-understood (Murphy et al., 2001). Whatever the combination of processes driving coastal productivity and benthic community structure, it is undoubtedly more complicated than upwelling and downwelling, and we are only in the early stages of understanding.

4. Alternative hypotheses for replenishment of populations

All studies on benthic–pelagic coupling highlight the importance of phytoplankton production, larval transport, the interface with the nearshore environment, and recruitment limitation, which affects community processes. Where organisms with an obligate period in the plankton are concerned, it is trivial to conclude that larval transport and recruitment are linked to coastal oceanography (including circulation and nutrient concentrations). As Menge et al. (2003) note, it is coupling between processes and their various strengths that require understanding. Furthermore, larval behaviours and retention can be important factors in larval transport (Morgan, 2001; Warner and Cowen, 2002). Here I discuss other hypotheses relating to larval transport and early life histories.

4.1. Coastal circulation, larval pool and retention

As Largier (2003) points out, coastlines are not usually straight or smooth, and consequently water flows can separate from the coast and form eddies. Furthermore, cross-shore flow is an integral part of larval dispersal. Results from intensive, yet temporally limited studies indicate relatively poor recruitment of mussels and barnacles on the east coast compared to the west coast of the South Island of New Zealand (Menge et al., 1999), but the influence of large-scale circulatory flows vs. localised influences is not clear. For example, study sites on the north side of Banks Peninsula on the east coast have unique localised influences which may be far different from other east coast sites. The strong, permanent, northwards-flowing current that sweeps past the peninsula often creates large eddies that meander into the bay on the north side of the peninsula (Shaw and Vennell, 2000), probably transporting larvae away from shore. Although downwelling can influence larval transport, there is little evidence that it is strong or even exists nearshore,

let alone is a dominant process affecting communities along the east coast. However, the presence of eddies, the width of the continental shelf, and the great distances between large mussel populations are likely to have a reduction effect on larval abundance. The nearest large mussel patches to this peninsula (other than on the peninsula itself) are >50 km to the north and south, where small headlands and reefs occur. Therefore, the regional pool of larvae may be quite small and diffuse, compared to the west coast where mussel populations occur on most reefs from the far north to the far south.

For any group of taxa, it seems unlikely that we can be sure of the influence of physical factors affecting settlement unless we have a reasonable idea of what the local and regional pool of larvae may be for those taxa (Meidel and Scheibling, 2001). Where mussel and barnacle populations are ubiquitous along a coastline, such as the Pacific northwest, this larval pool may be large, but this is less likely in areas with widely spaced, sparser populations (Warner and Cowen, 2002).

The larval pool may be maintained by retention near adult populations. There is considerable evidence that even long-lived larvae may not be dispersed great distances and that local retention may be considerably more prevalent than previously thought (Warner and Cowen, 2002). Larvae have numerous sensory capabilities and behaviours that detect variations in the water column and help them find suitable settlement sites (Kingsford et al., 2002). By moving vertically, larvae of many species are able to take advantage of different characteristics of the water column. Sponaugle et al. (2002) concluded that physical factors resulting in departure from unidirectional water flows that are uniform with depth (characteristics of most heterogeneous coastlines) provide the opportunity for larval retention, and therefore self-recruitment of populations.

4.2. Dispersal, habitat-forming seaweeds

There have been excellent recent reviews on dispersal in marine organisms, which recognise the critical importance of this process to all facets of marine community structure (Warner and Cowen, 2002; Kinlan and Gaines, 2003; Shanks et al., 2003; which I will not review here). Overall, however, marine algae, especially habitat-forming large brown algae are poorly represented. Because seaweeds are such a dominant component of nearshore subtidal and intertidal communities, are associated with many other organisms and processes and have been central to the often intense debate about the nature and extent of community structure and dynamics (Foster, 1990, 1991; Paine, 1991; Underwood, 2000), it is crucial to understand their place in models involving dispersal.

Reviews of dispersal in seaweeds have highlighted both knowledge and shortcomings in this critical process (Santelices, 1990; Norton, 1992; Johnson and Brawley, 1998). Algae have small propagules that when released into a turbulent coastal environment are at the mercy of the water mass. Laminarian spores are motile and may swim for many hours (Reed et al., 1999), but they are only around 6–10 μm in length and actively travel only very small distances. Successful colonization of kelps requires around 1–10 spores per mm^2 to ensure fertilization (Reed, 1990a; Reed et al., 1991, 1997). Furoid algae, the most common intertidal large brown algae, produce non-motile eggs that are not of neutral density (so they sink) but move largely with the water mass (Clayton, 1992; Chapman, 1995; Gaylord, 1999; Gaylord et al., 2002). To colonize habitats, therefore, large brown

algae must achieve several processes: fertilization, dispersal to appropriate substrata, initial attachment and subsequent recruitment, often in high-energy, turbulent shores where water velocities can reach several metres per second (Denny, 1995). These processes are, to some extent, density-dependent and also different from most invertebrates, the larvae of which can display complex behaviours and respond to settlement cues (e.g., Keough, 1989; Raimondi, 1990; Gaines and Bertness, 1992).

Most fucoid and some laminarian algae are capable, at least potentially, of dispersing both as propagules and as adults, in contrast to attached invertebrates, which are confined to dispersing in their early life stages only (Fig. 2). The relative importance of these two dispersal stages can be surmised for a few algal species, but is probably species-specific. For example, the notoriously invasive fucoid *Sargassum muticum*, when still attached to the substratum, drops the vast majority of its propagules within 5 m of parent plants, yet populations have spread widely and quickly once introduced to a new areas because of detached, drifting adult plants (Deysher and Norton, 1982; Chapman, 1995 for review). Although most detached seaweeds probably get cast ashore, some can survive for extended periods as drift plants (Norton and Mathieson, 1983). Species such as *S. muticum*, *S. sinclairii* (in New Zealand) and *Cystoseira osmundacea* (California) have a form of parental care in that germlings, complete with sticky rhizoids, are attached to receptacles of drifting plants and are capable of quick attachment after they drop from parents, descend through the water column and contact a surface (Norton and Fetter, 1981; Deysher and Norton, 1982; Schiel, 1985, 1988).

Drifting adult plants have the potential to disperse long distances. For most species, however, the ability of drift plants to remain reproductively viable is simply assumed, but unknown. For example, southern bull kelp (*D. antarctica*) and *H. banksii* make up a significant portion of coastal drift and beach-cast seaweed along the east coast of southern

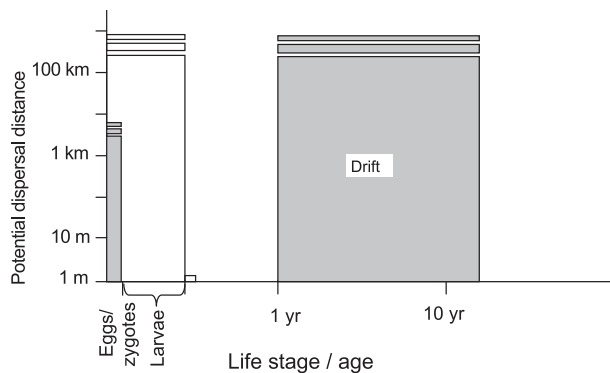


Fig. 2. Stylised diagram comparing potential dispersal of laminarian and fucoid algae (shaded bars) with sessile invertebrates (open bar) at different stages of development. Most fucoids and some laminarians float when detached; “drift” represents detached, reproductive plants, which may be >10 years old. Furthermore, reproductively active fronds can detach from perennial fucoids over many years. Although potential dispersal distances can be high, it is largely unknown how important and effective long-range dispersal is to population replenishment over generational time.

New Zealand, but whether these drifters are capable of effectively seeding onshore rocky habitats has never been tested.

It was generally thought that the major form of longer-range dispersal for large subtidal algae was through detached, drifting adult plants (e.g., Anderson and North, 1966; Dayton et al., 1984) but recent work has shown that the early life stages are also capable of dispersing at least several kilometres. Reed et al. (1992) showed that spores have the capacity to survive for long periods and germinate in the water column, providing a possible means of dispersal. Gaylord et al. (2002) showed that spores of giant kelp, released near the bottom of plants, are capable of successful dispersal, fertilization, settlement and development up to several kilometres away from adults. This depends on the period of competence, flow conditions, turbulence, sinking speed of propagules and their proximity to the substratum (McNair et al., 1997; Gaylord et al., 2002).

When spores and zygotes are released directly into the water column, the synchrony of release and the presence of a spore cloud may significantly aid in providing the densities required for fertilization and colonization (Norton, 1992; Reed et al., 1997), although these processes are unknown for most seaweeds. Intertidal fucoids face special challenges by releasing eggs into often turbulent onshore waters. Although egg release can occur during low tide in some species (Brawley et al., 1999), the speed and strength of propagule attachment are critical before the onslaught of tide and waves (Vadas et al., 1990; Taylor and Schiel, 2003). Furthermore, because of the presence of a viscous sub-layer near the benthos that varies with water motion (Schlichting, 1979; Gaylord et al., 2002), the ability of propagules to penetrate this, attach and develop can vary. There is great diversity of types of algal propagules and how they adhere (Fletcher and Callow, 1992) and also of their constituent mucilage, reactions and rates of curing (Vreeland et al., 1998). Gaylord et al. (2002) highlighted the need to understand the physics of algal propagule dispersal and its relationship to water flow to achieve an understanding of algal dispersal in hydrodynamically complex waters.

4.3. Propagule abundance, settlement, recruitment

4.3.1. Algae

The arrival of settlers in high numbers is crucial for fucoid algae, but for reasons other than fertilization. Not only is post-settlement mortality of zygotes and embryos high due to various stresses at low tide (e.g., Brawley and Johnson, 1991) but high densities of recruits may be required for viable adult populations to form. Plant morphology can be related to density (Schiel and Choat, 1980; Ang and DeWreede, 1992; Reed, 1990b). Dense adult stands of fucoids can help lessen desiccation at low tide because of the layering of fronds (e.g., Schonbeck and Norton, 1978, 1979), as well as reducing water flow, providing shade and microhabitat to areas below that can affect community structure (Bruno et al., 2003). For example, the most common intertidal fucoid in New Zealand (*H. banksii*) requires >1 recruit (ca. 2 mm in length) per cm² to produce a closed canopy in the absence of grazing, and the number of settlers needed to produce these recruits is much greater (ca. 250–750 per cm²; Schiel, unpublished data).

Dense algal populations are one of the commonest features of temperate intertidal reefs worldwide and their critical dynamics seem, at this stage, to be only loosely connected to

larger scale processes such as upwelling and downwelling. Algae have complex ways of extracting resources from the surrounding water mass across different hydrodynamic environments (Hurd, 2000), they do not have obligate planktonic development, and most of their mass of propagules do not seem generally to go far. Most intertidal fucoids and laminarians are highly tuned to the disturbance regimes in which they form dense populations. Understanding the interaction of their heteromorphic life histories, especially their early life stages, with turbulence, water flow and substratum characteristics is at least as essential as trophic dynamics to general models of community structure.

4.3.2. *Invertebrates*

Establishing the relationship between larval abundance, settlement and recruitment is notoriously difficult, usually requiring pumping, netting or trapping of larvae, counting microscopic settlers and recruits. Capturing settlers often involves artificial samplers, the use of which has a long history in marine ecology (e.g., Coe, 1953; Foster and Sousa, 1985, for review). One such sampling device is the “tuffie”, a spun plastic pot scrubber on which mussels readily settle (e.g., Connolly et al., 2001; Menge et al., 2003). This is similar to the furry ropes used commercially in NZ to catch mussel spat (Meredyth-Young and Jenkins, 1978). Tuffies are a standard size, so allow comparisons between sites and times, and are therefore a useful experimental unit. Recently settled mussels on tuffies have been used as a measure of recruitment in several important recent publications (e.g., Menge et al., 1999, 2003; Connolly et al., 2001). But is it “recruitment”? Although this term can be loosely defined (Connell, 1985), whatever these artificial collectors catch is a large step away from recruitment to a natural rock surface. Although tuffies can be a valuable tool in providing a standard measure of mussel settlement among sites, it is not clear how this relates either to larval abundance or to replenishment of populations. The relationships between larval abundance and recruitment can be modified by settlement patterns, larval behaviour, larval competence and condition, the nature of the substratum and post-settlement mortality (Morgan, 2001, for review).

To determine the relationships between larval abundance, settlement (i.e., <1 week old) and recruitment, Hayden (1995) did simultaneous sampling over 3 years in a mussel-growing centre in central NZ. She found there was usually a significant correlation between larval abundance and settlement (15 out of 20 sites, where weekly larval abundance and settlement were measured; significant r -values ranging from 0.56 to 0.94; minimum $n=12$) but that the relationship failed altogether in one of the years. At two sites, the correlations were negative. There was also usually a significant correlation between settlement and 8-week-old recruits (13 out of 20 weekly samples; significant r -values ranging from 0.41 to 0.75; minimum $n=12$), but the relationship between settlement and 12-week-old recruits was much weaker (only 3 of 10 correlations were significant; significant r -values ranging from 0.43 to 0.58). Some relatively poor settling sites had good recruitment while other sites had high mortality of settlers. It is hardly surprising that there is variability in these relationships but they highlight that it cannot be assumed that the numbers that appear on collectors necessarily relate to the numbers at earlier or later stages.

Estimating these relationships is not easy (cf., Gaines and Roughgarden, 1985), and is made more complicated by the highly variable nature of the plankton, identification of

larval stages of invertebrates of particular interest in benthic communities, and capturing settlers for species other than barnacles and mussels. Nevertheless, understanding these linkages for more key taxa is essential for elucidating the mechanisms linking the pelagic and onshore environments, and replenishment of benthic populations (cf., [Roughgarden et al., 1984](#)).

4.4. Wave exposure

The degree of wave exposure is a crucial predictor of community structure and processes ([Menge and Sutherland, 1976, 1987](#)) and has long been used as one of the main categorizers of marine communities (e.g., [Stephenson and Stephenson, 1949](#); [Dakin, 1960](#); [Morton and Miller, 1968](#); [Ricketts et al., 1985](#)). It also affects the activity of mobile predators, and thus top-down interactions and community structure. However, separating the effects of the various large-scale physical effects from smaller scale processes on biological communities is challenging. For example, El Niño events are associated with large-scale nutrient depletion that leads to reduced giant kelp populations, but they are also associated with frequent and intense storm activity that removes kelp plants ([Dayton and Tegner, 1984](#); [Dayton, 1985](#); [Dayton et al., 1999](#)). Populations of giant kelp in more sheltered areas away from the open coast can survive El Niño events, presumably because they are protected from severe wave action and because there may be localised variation in nutrient depletion ([Foster and Schiel, 1993](#)). There is also a positive correlation between the degree of wave exposure and other physical variables such as sedimentation, which may affect community structure ([Kendrick, 1991](#); [Airoldi, 1998](#); [Schiel et al., in review](#)).

One of the most important effects of wave exposure is on the ability of organisms to attach and stay attached. There are limits to the forms of benthic invertebrates on wave-exposed shores ([Denny et al., 1985](#)) that allow them to stay attached in waves that can travel at >10 m/s ([Denny, 1995](#)). Seaweeds such as *Fucus gardnerii* have smaller prostrate forms in exposed conditions and poorer survival than in more protected sites ([Blanchette, 1997](#)). However, much less is known about effects on early life stages. The ability to attach in sufficient numbers to form a viable population may be one of the more important discriminators in community structure, especially for seaweeds, the propagules of which have little or no ability to swim ([Santelices, 1990](#); [Norton, 1992](#)).

Several studies have shown that the propagules of habitat-forming algae have a differential ability to remain attached to substrata across different wave climates. For example, [Vadas et al. \(1992\)](#) found that 99% of zygotes of *Ascophyllum nodosum* (L.) LeJolis that had been settled for 15 min were removed by a single low-energy wave. In New Zealand, [Taylor and Schiel \(2003\)](#) tested the ability of zygotes of an exposed-coast species, *D. antarctica*, and a sheltered-coast species, *H. banksii*, to remain attached across wave exposures. They found that in most wave exposures, 80–100% of *Durvillaea* zygotes survived a full tidal cycle, regardless of wave exposure or the post-settlement time that zygotes were attached. However, *Hormosira* zygotes that had been settled for 1 and 6 h had no more than 8% survival, and then only in very sheltered conditions. Given 12 h of post-settlement time before being exposed to field conditions, *Hormosira* survival was still only 20–40% in sheltered conditions and <5% in exposed sites after one tidal cycle. In most conditions, only *Durvillaea* was able to attach firmly and quickly. They concluded

that at least some fuclean species may be precluded from forming populations on exposed shores where conditions are mostly unsuitable for their attachment.

Settlement of large, habitat-forming seaweeds involves a series of complex physical, biological, ecological and chemical processes at a micro-scale, from the release of propagules by reproductive adults, arrival at suitable substrata, initial adhesion to a surface, permanent attachment and development (Norton, 1983; Reed, 1990a; Brawley and Johnson, 1992; Vreeland and Epstein, 1996). The timing of release of propagules can also be critical to attachment. For example, propagules that are released from parent plants during low tide may avoid the problems associated with turbulence, at least for the critical period of initial attachment. Microsites are known to be important in the ability of propagules of many species to survive (Eckman, 1990; Amsler et al., 1992; Crimaldi et al., 2002) but their relationship to the physics of attachment and detachment of large brown algae is unknown. The integration of these factors will advance our knowledge of how these processes combine to produce “windows” of recruitment. We especially need a greater knowledge about microscopic-scale processes to attain a more comprehensive understanding of marine community development, and the feedbacks between resident populations, dispersal and recruitment processes across wave climates (Caley et al., 1996), which are so crucial to understanding the downstream effects of disturbances and potential for recovery (Sousa, 1984, 2001).

4.5. Sedimentation

Sedimentation can have adverse effects on benthic organisms (Abelson and Denny, 1997), but is unlikely to be independent of other factors, especially wave exposure. Coarse sediments such as sand and gravel can abrade tissue from organisms or remove them from reefs, thereby affecting community structure. For example, some red algae are resistant to sand abrasion and can survive where few other species can (D’Antonio, 1986). Sediments can interfere with settlement, cause a reduction in light penetration in the water column and be associated with nutrient enrichment (Kautsky et al., 1986; Jonsson and Carmen, 1994; Heiskanen and Tallberg, 1999), affect the light environment of settled early stages (Devlinny and Volsse, 1978), or create anoxic smothering conditions (D’Antonio, 1986).

Most studies of sediments on rocky shores have noted the variable arrival and departure of sediments, and consequently the variable effects on reef organisms (e.g., Littler et al., 1983; Stewart, 1983; Airolidi et al., 1996). In heavily sedimented areas of the Mediterranean Sea, the growth patterns and biomass of algal turf assemblages are affected by the degree of sedimentation (Airolidi and Virgilio, 1998; Airolidi et al., 1996). In one study in southern California, sand cover changed from 0 to 55% during winter, which affected the relative abundances of an anemone, a sand tube worm and macroalgae (Taylor and Littler, 1982). One of the most frequent effects on larger algae, however, may be on settlement. Kelp spores may fail to attach to primary substratum when a layer of sediment is present and may not develop if covered by even a light dusting of fine sediment (Devlinny and Volsse, 1978; Norton, 1978; Vadas et al., 1992; Chapman and Fletcher, 2002). For example, Schiel et al. (in review) found that a light dusting of fine sediment reduced attachment of *Durvillaea* and *Hormosira* zygotes by up to 70% compared to clear substratum, and that a complete cover of sediment prevented attachment altogether.

There can also be interactive and indirect effects of sediments. For example, on sheltered shores in Britain, the removal of an *Ascophyllum* canopy resulted in a loss of the understory turf assemblage and a reduction in silt (Jenkins et al., 1999). This led to an increase in the abundance of limpets and eventually to recruitment of *Fucus* species. In New England, the removal of the snail *Littorina littorea* resulted in algal recruitment, the accumulation of sediment and eventual recruitment of invertebrates characteristic of soft sediments (Bertness, 1984). In each of these cases, the local character of the assemblage and trophic interactions were changed at least partly by sedimentation.

The interaction of sediments and reef biota clearly may contribute to the renowned patchiness of benthic communities, can operate on a fine scale at specific settlement sites and concavities within reefs (Airolidi, 1998), and at greater scales where sediments accumulate over large areas (Norton, 1978). Increases in sedimentation along the coastal strip, particularly in less exposed areas, from changes in land use, urbanization, forestry, farming, and coastal dredging are seen as major threats to benthic communities in many places, including New Zealand (cf., Heiskanen and Tallberg, 1999; Lotze et al., 2000; Madsen et al., 2001). Understanding how sedimentation may affect the early life stages, in particular, of benthic organisms may prove to be crucial in elucidating influences on community structure and the interaction of wave exposure gradients.

4.6. Predation

The intensity of predation is a key component of models on community organisation (Paine, 1974; Connell, 1975; Menge and Sutherland, 1976, 1987; Menge et al., 1994) that can be affected by high recruitment of filter-feeding benthic invertebrates (Connolly and Roughgarden, 1999a,b). Where mussels are involved, predation by sea stars can set the lower vertical limit of mussel populations on a shore as well as create or maintain patches within mussel beds that allow a wide diversity of other species to persist without being overgrown by competitively superior mussels (Paine, 1974; Paine and Levin, 1981; but see Lohse, 1993). In studies in several countries, the abundance of predators is positively correlated with the abundance of filter-feeders, and these tend to occur mostly on exposed shores (Bustamante and Branch, 1996; Menge et al., 1999; Connolly and Roughgarden, 1998). Furthermore, it has been argued that predation intensity is one of the key trophic interactions in benthic–pelagic coupling, whereby the increased recruitment of filter-feeders and increased productivity in areas affected by upwelling also have increased intensity of predation (Menge et al., 1997a,b). Given the overall importance of this process, it is worthwhile to assess its generality.

The size and types of predators and invertebrates that have been used to test for predation clearly have an influence on its intensity and importance to community organisation. For example, Menge et al. (2003) experimentally tested predation on mussels that were 30–40 mm in shell length and found that they were differentially affected between coastlines of New Zealand. Predation rates were higher on the west coast, which was due to the predacious sea star *Stichaster australis*. They suggested that predation intensity was upwelling-related because of differences in larval supply of sea stars to the different coasts. Mussels in this size range are at least 6 months old (i.e., post-settlement; Fox, 2003), which leaves a considerable gap in time between the sizes caught on tuffies as

a measure of recruitment and those used to measure predation intensity. What about the earlier life stages?

In New Zealand, one of the most important predators of recently settled mussels is the labrid fish *Notolabrus celidotus*. Hayden (1995) showed experimentally that the dense populations of this fish around the mussel-growing areas of central NZ were a major cause of spat loss on commercial farms. *N. celidotus* could completely strip lines of mussels less than ca. 1 cm in length. This fish and the related *N. fucicola* are the commonest fish species along eastern NZ coastal sites (Hickford and Schiel, 1995; Schiel and Hickford, 2001), where they feed on a wide range of small invertebrates (Denny and Schiel, 2001). Like lobsters in southern California that move up during high tide to feed in intertidal mussel beds (Robles, 1987; Robles et al., 1995), these fish readily forage for invertebrates at high tide. Furthermore, they tend to have relatively restricted territories on nearshore reefs and do not move far from these areas to feed (Jones, 1984). They may well be the cause of poor recruitment of mussels at reef-associated sites, which are particularly common along the east coast (Rilov and Schiel, unpublished data). Therefore, it is not necessarily the case that predation intensity is greater where recruitment is high.

In summary, there is often a significant gap in time between settlement, recruitment to populations, and the stages on which predation experiments are done. If larger prey are used for experiments, the actual strength of this process in community structure may be underestimated, thereby altering our perception of how different oceanographic regimes affect important top-down trophic interactions. The incorporation of the earlier post-settlement stages into experiments and a greater understanding of the role of mobile subtidal predators are crucial to the development of benthic–pelagic models.

4.7. Key species and recovery from disturbance

Disturbance is a constant feature of nearshore rocky reefs and especially for intertidal communities, which are subjected to waves, desiccation and, increasingly, human impacts of various types. Following a disturbance, there is often a bloom of ephemeral algae, such as *Ulva*, that may slow the development of longer-lived perennials (Sousa, 1979, 2001). In some circumstances, facilitation may occur. For example, Farrell et al. (1991) found that barnacles facilitated algal development in Oregon, but Foster et al. (2003) did not find this to be the case at sites in central and northern California. Perceptions of crucial processes may be both site and zone-dependent. For example, in the high intertidal zone, algal abundance is a function of grazing and of the suitability for algal growth (Foster, 1982; Cubit, 1984), but relatively little is known about variation in the latter for most places (Foster et al., 2003).

Depending on resident communities and their location, there may be vastly different responses to disturbance. For example, a recent study on the high shore at six sites along the California coast used complete clearances in two seasons (spring and autumn) to determine recovery relative to controls (Foster et al., 2003). The quick appearance of ephemeral algae at two sites was associated with delayed recovery of perennial algae. At two other sites, autumn clearances resulted in a different dominant alga (*Mastocarpus papillatus*) than the spring clearings (*Endocladia muricata*). Slower recovery occurred in the plots cleared in autumn but, nevertheless, five of the six plots recovered to control

conditions by the end of 6 years. Overall, the main differences between controls and disturbed plots were in abundance and not composition of species. Foster et al. (2003) also reported that the amount of bare space was high and concluded it was unlikely to be a limiting resource for settlement. Although the number of grazers was high (>100 limpets per 0.19 m²), peaking after 2–3 years, the importance of their role was lessened because their abundance, combined with calculations of species-specific consumption rates, was only weakly correlated with recovery. Recovery, therefore, varied among sites, between seasons at some sites, and had no consistent relationship to latitude. They concluded that their results were remarkably similar to those of Chapman and Underwood (1998) on wave-exposed shores of New South Wales.

Recovery from episodic disturbances, however, can take many years, particularly if they are large. When large-scale events such as El Niño affect widespread areas, there is a relationship between the dispersal of propagules and spatial heterogeneity during the recovery process. Reed et al. (2000) showed that in 27 sedentary marine species within kelp forest communities, those with limited dispersal showed high variation among sites but became more evenly spread over several years after severe disturbance whereas species with long-range dispersal retained the same variability among years. These results seem to reflect the proximity of disturbed areas to sources of propagules.

Underwood (1998, 1999) followed the recovery of a population of *H. banksii* after a large disturbance from a severe storm and through a series of experiments. Virtually all *Hormosira* plants were removed by a large storm in 1974, but the recovery process was complex and the full original assemblage did not recover (Underwood, 1998). Recovery of the *Hormosira* populations took up to 5 years, but this depended on the initial degree of damage at each site. Underwood (1999) also showed experimentally that a series of direct and indirect interactions affected recovery. Recovery was far quicker if only fronds and not holdfasts were removed because plants could regenerate from fronds. Molluscan grazers affected recovery, delaying it by around 9 months where holdfasts were left intact and for up to several years where entire plants had been removed. Furthermore, there was a series of indirect effects. The barnacle *Chamaesipho tasmanica* (Foster and Anderson) recruited into areas where the *Hormosira* canopy was removed by the storm but there was also a change in predator abundance and activity associated with this. Underwood (1999) showed experimentally that whelks had little influence where the canopy of *Hormosira* was sparse and furthermore that barnacles survived well under intact *Hormosira* canopies when whelks were not present.

Several contrasts to other studies were noted by Underwood (1999). The whiplash effects by dominant algae seen in many other studies (Dayton, 1971; Menge, 1976; Santelices et al., 1980; Hawkins, 1983) did not occur. This may well be a consequence of the unique buoyant, beaded form of *H. banksii* plants that tend to stay off the substratum during submergence. Second, because the whelks rely on *Hormosira* for shelter, the interaction of barnacles and whelks depended on the presence of the algal canopy, a form of indirect interaction. Finally, there was also a modifying interaction (cf., Wootton, 1993, 1994) because the influence of whelks on barnacles was modified by the size and extent of the algal canopy.

Experiments done on the same species in southern New Zealand showed similar slow recovery of *H. banksii* after disturbance but through a quite different process (Schiel and

Taylor, 1999; Schiel, unpublished). No limpets or barnacles ever recruited into any of the frond-removal or full clearances done quarterly at six sites over 2 years and followed for 5 years. The major grazing mollusc within the *Hormosira* beds, *Turbo smaragdus* Gmelin, had an effect on reducing ephemeral algae such as *Ulva* and *Adenocystis utricularis* (Bory Skottsberg and the perennial articulated coralline *Jania micrarthrodia* Lamouroux, but little or no effect on *Hormosira* (Walker, 1998), even though this grazer can affect recruitment of fucoids in northern New Zealand (Creese, 1988). Recovery in cleared areas was mediated almost entirely by recruitment processes of *Hormosira*, which occurred more quickly in the lower portion of the *Hormosira* zone than in the upper portion.

On New Zealand shores, at least one of the major structuring factors for the mid-intertidal assemblage is that *H. banksii* is the only perennial large brown algae capable of forming large beds. Ultimately, therefore, patches cleared of this species are likely to be re-occupied. This stands in contrast to studies such as Foster et al. (2003) that had several species capable of dominance and where switches occurred after disturbance. In other systems, such as the Pacific northwest, where space can be dominated by barnacles, mussels and several species of algae, the structuring processes are bound to be more complex.

These studies are only a few examples of many that illustrate complex pathways of direct and indirect interactions intersecting with life histories. Even comparing the same species (*H. banksii*) across nearby countries reveals different associated assemblages, different interactive processes involving grazers and predators, considerable site-to-site variation, and different pathways to recovery from disturbance, especially when they are large or involve many species (Povey and Keough, 1991; Underwood, 1998, 1999; Schiel and Taylor, 1999). As pointed out by others, predictability is not likely to be great unless these complex pathways are clarified in detailed experimental analyses within particular assemblages.

5. Conclusions

Searching for general principles that lead to predictive capacity in marine communities is fraught with the difficulties of dealing with often unique assemblages, great site to site variation in both composition and structuring processes, largely unknown life histories (especially early life stages) of most species, inadequate knowledge of the interactions with the nearshore water mass and the extent to which populations are open or closed (cf., Cowen et al., 2000). Nevertheless, progress towards understanding all facets of marine benthic communities has never been so dramatic as in the past several years. Most aspects of marine ecology have been reviewed recently and major, and often contentious, views have been brought into sharp focus. I conclude here by offering a perspective on some of these issues for future work.

5.1. The role of key species

On both conceptual and practical grounds, a better understanding is required of the dynamics of key species, especially habitat-forming foundation species, and not just

keystone species. For many years, there has been an emphasis on trophic interactions and the role of top predators (e.g., Paine, 1980) and the ways they may affect communities and ecosystems (e.g., Paine, 2002) but in the absence of strong keystone interactions (c. f., Menge et al., 1994), the demographics and population dynamics of dominant space-occupiers are of some importance. Bruno et al. (2003) highlighted the role of facilitation or positive interactions in community structure. One of the most important distinctions they made was between species that were primary and secondary holders of space. So, for example, where algae or mussels are removed, the species that live on, under and among them may disappear or be greatly reduced in abundance (e.g., Dayton, 1971, 1975; Witman, 1985; Dean and Connell, 1987; Lohse, 1993). They provide modified models relating to environmental stress and disturbance that incorporate the positive interactions of species across gradients. Although the relative importance of positive interactions compared to other processes in community structure has been questioned (Menge, 2000b; Shouse, 2003), these interactions are undoubtedly important in many cases, particularly in the more stressed habitats higher on the shore (Bertness et al., 1999; Bruno et al., 2003).

Marine algae in the low to mid-intertidal zone provide many examples of such key foundation species (Bruno et al., 2003). Although not discussed in this context, Underwood (1998, 1999) clearly showed that a furoid alga (*H. banksii*) is such a species in New South Wales. Its loss triggered a series of direct and indirect interactions in the community. Also of interest was that even though there were strong interactions involving barnacles, whelks and ephemeral algae, *Hormosira* returned to dominance within several years. Presumably, despite all of the interactions, this species and others such as *A. nodosum* (Jenkins et al., 1999) have a large pool of propagules, repeated reproduction, and enough escapes from grazers to swamp areas and eventually to recover populations.

It seems likely that if such key species prove to be vulnerable to increased temperature through climate change, there could be dramatic shifts in community structure. For example, seaweeds have thermal limits for their survival, growth or reproduction (Van den Hoek, 1982). Several studies have presented evidence of long-term changes in communities associated with seawater warming (Southward et al., 1995; Holbrook et al., 1997; Sagarin et al., 1999). Schiel et al. (in press) showed that increased seawater temperature from a thermal outfall in central California resulted in the virtual disappearance of dominant red algae (*Mazzaella* spp.) and a replacement by low-lying turfs, ephemeral algae and grazing gastropods. Understanding the structuring processes of these sorts of species that in many cases do not seem to be restricted by strong trophic interactions will be crucial.

These studies merely highlight the fact that while progress is dramatic, our knowledge of important species in different parts of the marine ecosystem is quite narrow, that there are important localised differences, and that interactions and their strengths will vary among locations.

5.2. Algae vs. filter-feeders

What tips the balance between domination by filter-feeders and algae across shores? It appears that one of the important dichotomies in perceptions about the importance of various processes is in the roles and interactions of the two primary space occupiers, plants

and filter-feeding invertebrates. Within mussel beds, for example, mussels are competitive dominants and predators play a key role in creating and maintaining primary space in which other species can live (Paine, 1966, 1971; Dayton, 1971; Menge, 1976). Connolly and Roughgarden (1998) suggest that higher algal abundances in northern California compared to Oregon are because of competitive release from mussels, which do not recruit well into these southern sites. In models derived from these and similar studies, therefore, the major driver is whether or not competitively superior invertebrates recruit in sufficient numbers. Foster et al. (2003), however, highlight the importance of understanding the dynamics of the algal populations, especially their variation in demographic features of dominant plants, their fecundity and reproduction and, presumably their ability to swamp areas near adults with propagules. They point out that most of the intertidal zone throughout much of the west coast of the USA is dominated by algae. Furthermore, many species of algae are capable of living on and among filter-feeding invertebrates (Lohse, 1993) and are therefore not excluded entirely. Foster et al. (2003) call biotic variations that result from facilitative interactions and variations caused by consumers “small ripples on the large waves of variation” caused by site-specific demographic attributes of dominant marine plants.

Experiments within mussel beds show that patches within them are created and maintained by physical disturbance and predation (e.g., Paine and Levin, 1981). Species such as the sea palm *Postelsia palmaeformis* Ruprecht can establish within these patches but are eventually excluded as mussels re-establish and outcompete them for primary space (Paine, 1979, 1988). On many reefs dominated by algae, however, mussels do not play a prominent role (Foster, 1990; but see Paine, 1991). Reciprocal transplant experiments would help clarify the roles and capabilities of these dominant taxa in areas of their abundance. If, for example, mussel domination is mediated by recruitment limitation (cf., Connolly and Roughgarden, 1998, 1999a,b), experimental placement of mussels within algal beds should be able to test competitive interactions and establish under what circumstances mussels or algae are competitively superior.

5.3. Early life history

The emphasis in marine ecology has clearly shifted to early life histories of coastal species and the processes affecting dispersal, return to shore, settlement and recruitment. There is considerable recognition of the importance of these processes and how they vary among species (Dewreede and Klinger, 1988; Menge and Branch, 2001; Morgan, 2001; Underwood and Keough, 2001) but many challenges lie ahead in understanding the interactions with the nearshore water mass, the mechanisms of attachment in turbulent coastal waters and survival to recruitment. Before models of dispersal and recruitment mechanisms can be generalised, we will need a better understanding of a greater range of species and habitats.

Experimental manipulations of different densities of the microscopic stages of habitat-forming species have been a useful tool since the early days of experimental marine ecology (Connell, 1961). Current hypotheses relating to facilitation (for example, by algal canopies), the influence of gradients of environmental variables (for example, wave exposure), disturbance and recovery in different habitats, and the role of density-

dependence in settlement are eminently testable using transplants of habitat-forming species (e.g., [Brawley and Johnson, 1993](#); [Reed, 1990a](#)) and should help complete the loop from release of propagules to viable adult populations.

5.4. *Effect of the nearshore water mass*

Although processes such as upwelling and downwelling can affect larval transport to shore ([Connolly and Roughgarden, 1998](#)), the relationships between oceanic conditions, larval arrival and settlement processes are far from clear. Satellite images showing, for example, warm water intrusions into the coast that coincide with settlement (e.g., [Menge et al., 1997a](#)) are suggestive, but offer only a few points of a correlation of wide-ranging processes. Questions arise: how often is high settlement of potentially long-range dispersers such as barnacles and mussels associated with relaxation events in upwelling? Conversely, how often are relaxation events associated with high settlement (i.e., how good is the correlation between them)? How do the intensities of these different processes relate to each other?

Achieving a greater understanding of oceanographic-onshore linkages is difficult and will increasingly involve multi-disciplinary studies and more extensive use of remote sensing. For example, improved algorithms and better satellite imagery will be a great aid in achieving more accurate data on SST and productivity. [Murphy et al. \(2001\)](#) point out some of the problems of calibration that can arise in coastal waters, such as degraded signals, validation of signals from (for example) chlorophyll vs. fine sediments in coastal waters, and differences in signals in different water masses and different parts of the globe. It is also clear that molecular techniques provide powerful tools to discern genetic structure, dispersal and gene flow within and among populations ([Grosberg and Cunningham, 2001](#)). As pointed out by [Palumbi et al. \(2003\)](#), physical patterns do not always predict biological connectivity and, because it is impractical to gather precise information for thousands of species, it may be possible to test predictions from oceanographic models using a range of species with different dispersal traits. Achieving this for a wider range of taxa and oceanographic conditions will be a significant step in the process. Mapping results from these sorts of studies onto oceanographic features, and the use of onshore experiments at more replicate sites grouped within a greater range of factors (such as strong and weak upwelling) will provide new insights into structuring processes of benthic communities.

5.5. *Human impacts*

Invasive alien species, pollution, urbanization, coastal development, and extraction of species will be an increasing challenge to marine ecologists and managers ([Ruiz et al., 1999](#)). [Thompson et al. \(2002\)](#) forecast for 25 years and discuss potential impacts and their differences between industrialised and developing nations. They argue for strategic research that integrates field experiments and monitoring programmes to verify management regimes.

Not only is the problem of transporting species across borders, particularly through shipping, of critical importance, but also our knowledge of how species take hold and spread once they do arrive ([Ruiz et al., 1999](#)). Effects on native flora and fauna, human

impacts on benthic communities, and facilitative processes and trophic interactions are all testable (e.g., Moreno et al., 1984; Castilla and Duran, 1985; Bruno and Bertness, 2001).

5.6. Cross country comparisons

Underwood (2000) called for (among other things) larger-scale analyses using careful integration of the comparative-experimental approach at smaller scales nested within larger scales, and to ensure that analyses at larger scales are commensurable with similar studies in other places and habitats. Menge et al. (2002) have been at the forefront of such experimental procedures. These sorts of experimental comparisons are fraught with difficulties because of different species' pools, variable oceanographic regimes, coastal sedimentation, etc. (factors that operate at the local scale) but nevertheless are powerful tools in working towards general principles of community dynamics. Given the great local variation, site selection and replication within and between major sources of variation are crucial.

The caveats for these sorts of studies are that we simply do not have enough knowledge about more than a few species and their interactions with the complexities of the nearshore water mass. Whether nutrients are actually limiting in nearshore waters, the degree of availability of nutrients and phytoplankton because of thermal or freshwater stratification, and the composition and abundance of the local species pool could all affect perceptions about the importance of other mechanisms such as upwelling and downwelling (some of these discussed in Menge and Branch, 2001; Menge et al., 2003).

Despite its problems and shortcomings, experimental marine ecology is not only thriving but also playing a more prominent role than previously in ecological theory and in addressing global problems. An awareness of increasing threats to the marine environment presents a challenge to all of us: to grapple with the localised problems in our own ecosystems (i.e., the “back-yard” issues that we all face); to do the broad-ranging, underpinning science that leads to basic understanding of marine ecosystems; and to help ensure that our science is useful and gets translated into management policy.

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