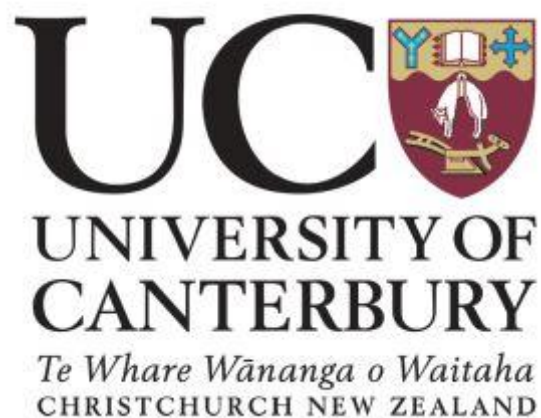


**Impacts of altered physical and biotic conditions in
rocky intertidal systems: implications for the structure
and functioning of complex macroalgal assemblages**

A thesis submitted in partial fulfilment of the requirements for the Degree of
Doctor of Philosophy at the University of Canterbury,
New Zealand

Tommaso Alestra

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Abstract

Complex biogenic habitats created by large canopy-forming macroalgae on intertidal and shallow subtidal rocky reefs worldwide are increasingly affected by degraded environmental conditions at local scales and global climate-driven changes. A better understanding of the mechanisms underlying the impacts of complex suites of anthropogenic stressors on algal forests is essential for the conservation and restoration of these habitats and of their ecological, economic and social values. This thesis tests physical and biological mechanisms underlying the impacts of different forms of natural and human-related disturbance on macroalgal assemblages dominated by furoid canopies along the east coast of the South Island of New Zealand.

A field removal experiment was initially set up to test assemblage responses to mechanical perturbations of increasing severity, simulating the impacts of disturbance agents affecting intertidal habitats such as storms and human trampling. Different combinations of assemblage components (i.e., canopy, mid-canopy and basal layer) were selectively removed, from the thinning of the canopy to the destruction of the entire assemblage. The recovery of the canopy-forming furoids *Hormosira banksii* and *Cystophora torulosa* was affected by the intensity of the disturbance. For both species, even a 50% thinning had impacts lasting at least eighteen months, and recovery trajectories were longer following more intense perturbations. Independently of assemblage diversity and composition at different sites and shore heights, the recovery of the canopy relied entirely on the increase in abundance of these dominant furoids in response to disturbance, indicating that functional redundancy is limited in this system. Minor understory furoids, which could have provided functional replacement for the dominant habitat formers, had reduced rates of growth or recruitment when the overlying canopy was disturbed.

I then used a combination of field and laboratory experiments to test the impacts of physical and biotic stress sources on the dominant fucoids *H. banksii* and *C. torulosa*. The large fucoid *Durvillaea antarctica* was also included in one of the laboratory investigations. I assessed how altered physical and biotic conditions affect these important habitat formers, both separately and in combination. Physical stressors included increased sedimentation, nutrient enrichment and warmer water temperatures. Biotic stress originated from interspecific competition with turfs of articulated coralline algae and ephemeral, fast-growing green and brown algae.

Sediment deposition severely reduced the survival and growth of recently settled *H. banksii*, *C. torulosa* and *D. antarctica* germlings in laboratory experiments. In the field, the recruitment of *H. banksii* on unoccupied substrates was significantly higher than in treatments in which sediments or mats of turf-forming coralline algae covered the substrate. This shows that sediment deposition and space pre-emption by algal turfs can synergistically affect the development of fucoid beds. Further impacts of sediment accumulation in the benthic environment were investigated using *in situ* and laboratory photorespirometry techniques to assess the contribution of coralline algae to assemblage net primary productivity (NPP), both in the presence and absence of sediment. The NPP of articulated corallines was reduced by sediment. Sediment accumulation among the thalli limited the access of the corallines to the light and induced photoinhibitive mechanisms. In the absence of sediment, however, coralline algae enhanced the NPP of assemblages with a fucoid canopy, showing the importance of synergistic interactions among the components of multi-layered assemblages in optimizing light use.

Nutrient enrichment had a less pervasive influence on the dominant fucoids *H. banksii* and *C. torulosa* than sedimentation. In laboratory experiments, nutrients stimulated the growth of *H. banksii* and *C. torulosa* germlings. However, negative impacts of high nutrient

levels were observed for the early life stages of *D. antarctica*. The abundance of opportunistic, fast-growing algae rapidly increased in response to nutrient enrichment both in the laboratory and in the field. Impacts of ephemeral species on furoid early life stages were only evident in laboratory contexts, where green algae of the genus *Ulva* impaired both the settlement of *H. banksii* zygotes and the growth of its germlings. Furoid recruitment in the field was not affected by increased covers of ephemeral algae caused by enhanced nutrient regimes, indicating that *H. banksii* and *C. torulosa* may be resistant to short-term (one year) nutrient pollution.

In the laboratory, increased temperatures within the range predicted for the end of the 21st century caused increased mortality in the *H. banksii*, *C. torulosa* and *D. antarctica* germlings. In a separate experiment, a combination of warmer water temperatures and nutrient enrichment enhanced the growth of ephemeral green algae. These results suggest that opposite responses to altered climate conditions may contribute to shifts from complex biogenic habitats dominated by macroalgal canopies to simplified systems monopolized by a limited number of stress-tolerant species.

This research contributes to a clearer mechanistic understanding of biotic and physical mechanisms shaping the structure of coastal marine hard bottom communities under increasingly stressful conditions worldwide. These findings may provide insights for other studies investigating the complex mosaic of challenges facing marine coastal ecosystems.

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CHAPTER 1

General Introduction

1.1. ANTHROPOGENIC THREATS TO COASTAL ECOSYSTEMS

Located at the interface between the oceans and the mainland, coastal ecosystems are among the most diverse in the world and include a complex mosaic of nearshore terrestrial and aquatic habitats such as sand dunes, mangrove forests, coastal marshes, seagrass and algal meadows, mussel and oyster beds, mud flats and coral reefs (Carter 1988, Burke et al. 2001, MEA 2005). These systems are generally characterized by elevated levels of biodiversity (Gray 1997) and they support key ecological processes such as primary and secondary production, carbon sequestration, nutrient cycling and gas exchanges (Alongi 1998, Gattuso et al. 1998, Barbier et al. 2011). Coastal ecosystems also provide a range of important economic and social benefits to humans, including the provision of food, raw materials and energy resources. In addition, they contribute to the regulation of climate, erosion, wave action and water quality along the coastlines and support tourism and recreational activities (Costanza et al. 1998, Peterson & Lubchenco 1997, Barbier et al. 2011).

Despite their proven ecological, economic and social values, coastal ecosystems are some of the most used and threatened natural systems globally, to the extent that few if any coastal areas in the world remain free from the impact of anthropogenic perturbations (Halpern et al. 2008). Humans have inhabited and modified large areas of the coastline for centuries, and coastal systems are currently exposed to exceptional anthropogenic pressures as a result of recent demographic trends. In 1990, about 23% of the global population, equivalent to 1.2 billion people, lived near the coasts (Small & Nicholls 2003), while this percentage had risen to 41% (2.5 billion) by 2002 (UNDP 2005). Population growth has been accompanied by an increase in the types and intensity of perturbations associated with human activities in both the terrestrial and marine realms. These include disturbances acting at local and regional scales such as habitat and shoreline modification, chemical pollution,

eutrophication, increased sedimentation, harvesting of species, and introduction of non-native species (Burke et al. 2001, MEA 2005, Airoidi & Beck 2007, Halpern et al. 2008).

Escalating human impacts in coastal areas can have catastrophic consequences, as shown by the collapse of entire ecosystems in response to resource overexploitation and degraded habitat quality (Jackson et al. 2001, Rabalais et al. 2002, Bellwood et al. 2004, Lotze et al. 2006). Coastal systems are also influenced by global-scale stressors such as increasing temperature, water acidification, sea level rise, changes in frequency and intensity of extreme weather events, and the alteration of biogeochemical cycles (Vitousek et al. 1997, Harley et al. 2006, IPCC 2007, 2013, Crain et al. 2008, 2009, Halpern et al. 2008). The combination of anthropogenic impacts at local scales and altered physical conditions at a global level poses unprecedented threats to nearshore systems. For example, the interactive effects of overfishing, altered ocean currents and rising water temperatures underpinned the range extension of the sea urchin *Centrostephanus rodgersii* in eastern Tasmania, leading to extreme overgrazing of productive kelp beds (Ling et al. 2009). Other compound impacts of multiple anthropogenic perturbations are also alarming. For example, changing climate conditions may exacerbate fishery impacts by reducing the size and productivity of commercial species, causing the degradation of their habitats and facilitating the spread of competitors and pathogens (Harley et al. 2006, Brander 2007). The loss and transformation of important biogenic habitats may also increase the vulnerability of coastal areas to extreme weather events, the frequency and intensity of which are predicted to increase under altered global climate conditions (Webster et al. 2005, IPCC 2007, 2013, Hawkins et al. 2009). Historical losses of forested wetlands, for example, amplified the impacts of the 2005 Hurricanes Katrina and Rita on the central region of the Gulf Coast in the USA (Day et al. 2007).

The wide ecological implications of the global deterioration and loss of coastal ecosystems and their substantial financial costs are now recognized (Costanza et al. 1998, Barbier et al. 2011). As human pressure on coastal ecosystems continues to grow, researchers, policymakers and managers are increasingly seeking solutions to protect coastal habitats and guarantee sustainable use of natural resources (Burke et al. 2001, MEA 2005, Arkema et al. 2006, Granek et al. 2010). Understanding which threats have the biggest impacts on different systems is critical for the design of management and restoration actions (Halpern et al. 2007, 2008, Crain et al. 2009). This cannot be achieved without a detailed knowledge of biotic and abiotic mechanisms underlying natural and human-driven alterations in coastal areas. Investigating the impacts of complex suites of stressors and the processes driving the responses of the perturbed systems is, therefore, essential for the development of appropriate management and conservation strategies (Hughes et al. 2005, Airoidi et al. 2008, Connell et al. 2008, Crain et al. 2009, Foster & Schiel 2010, Thrush & Dayton 2010).

1.2. IMPACTS ON ROCKY INTERTIDAL HABITATS: REDUCTION OR LOSS OF HABITAT-FORMING MACROALGAE

Intertidal rocky reefs are among the most vulnerable habitats to human impacts because they are easily accessible to people and simultaneously exposed to multiple anthropogenic stressors originating from both the land and the sea (Halpern et al. 2007, 2008). This is particularly concerning, given that intertidal rocky reefs occur throughout the world and host a large variety of benthic communities characterized by different patterns of composition and mechanisms of organization (Dayton 1971, Menge & Lubchenco 1981, Paine & Levin 1981, Bertness et al. 1999, 2006, Menge & Branch 2001, Schiel 2004). Rocky intertidal systems have strong functional linkages with the surrounding seascape and with the land. Hard bottom intertidal assemblages are, for example, integral parts of complex food webs that regulate the

exchange of energy and materials between the ocean and the mainland (Paine 1980, Wootton 1994, Polis et al. 1997). Intertidal reefs are also nursery and foraging areas for many species of fishes and crustaceans of commercial interest (Turner 1977, Rangeley & Kramer 1995) and sustain artisanal and commercial invertebrate fisheries (Castilla & Fernandez 1998, Harley & Rogers-Bennett 2004). Intertidal rocky shores are also important for recreation, tourism and scientific research (Crowe et al. 2000, Thompson et al. 2002).

Rocky intertidal habitats are affected by many anthropogenic perturbations, acting across a wide range of spatial and temporal scales. The impacts of complex combinations of local stress sources and broad-scale changes in the physical environment on intertidal systems vary greatly depending on the composition of the resident assemblages, the level of biological organization and of the spatial and temporal scales investigated (Crowe et al. 2000, Thompson et al. 2002, Schiel 2009). A phenomenon consistently observed on intertidal reefs around the world, however, is the decline in the abundance of structurally complex biogenic habitats created by large canopy-forming macroalgae (Benedetti-Cecchi et al. 2001, Thibaut et al. 2005, Airoidi & Beck 2007, Airoidi et al. 2008, Mangialajo et al. 2008, Bellgrove et al. 2010). Analogous patterns have also been recorded on shallow subtidal reefs (Eriksson et al. 2002, Connell et al. 2008, Foster & Schiel 2010, Perkol-Finkel & Airoidi 2010, Moy & Christie 2012, Tamburello et al. 2012). Fragmentation and loss of macroalgal canopies have generally been attributed to poor habitat quality, especially in the proximity of metropolitan areas. There is, however, growing evidence that canopy-forming macroalgae may also be affected by rising sea water temperatures (Southward et al. 1995, Barry et al. 1995, Wernberg et al. 2010, Andrews et al. 2014, Jueterbock et al. 2014) and increasing storminess along the coastlines (Hawkins et al. 2009, Schiel 2011).

The extensive decline of macroalgal canopies has profound implications for the structure and functioning of intertidal rocky reef communities and for the ecological services

that they provide. Algal canopies exert a pervasive influence on the associated communities by modifying the physical environment and influencing resource availability and species interactions (Schiel & Foster 1986, Jones 1994, Chapman 1995, Bruno & Bertness 2001). In intertidal habitats, in particular, canopy-forming macroalgae maintain high levels of diversity and productivity, despite the extreme physical challenges posed by periodic exposure to the aerial environment (Chapman 1995, Bertness et al. 1999, Schiel 2006). The loss or fragmentation of intertidal algal canopies usually result in dramatic shifts to simplified systems dominated by low-lying turf-forming algae, with long-term impacts on community structure and functioning (Benedetti-Cecchi et al. 2001, Lilley & Schiel 2006, Worm & Lotze 2006, Bellgrove et al. 2010, Schiel & Lilley 2011, Tait & Schiel 2011a,b). Such loss of structural complexity can also affect the exchange of organic material and organisms between intertidal reefs and the surrounding systems. Habitat simplification in the absence of large canopies, for example, can cause a reduction in the diversity and biomass of the invertebrate fauna, particularly of small soft-bodied invertebrates, with potential flow-on effects to the higher trophic levels (Hardwick-Witman & Mathieson 1983, Kendall et al. 2004, Råberg & Kautsky 2007). Similarly, the loss of large macroalgae can also reduce the subsidies provided by intertidal reefs to non-vegetated nearshore habitats (Anderson & Polis 1998, Riera & Hubas 2003) and offshore areas (Fischer & Wiencke 1992, Hill et al. 2006).

1.3. NEW ZEALAND NEARSHORE ENVIRONMENT AND INTERTIDAL HARD BOTTOM COMMUNITIES

The nearshore environment around New Zealand is extremely complex. New Zealand coastlines span from subtropical to sub-Antarctic latitudes and are surrounded by distinct water masses (i.e., the Subtropical and Sub-Antarctic waters on the surface, and below the surface, the Antarctic Intermediate, Deep, and Bottom Water; Heath 1985, Schiel 2004). The

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 along the east coast (Heath 1985, Vincent et al. 1991, Chiswell & Schiel 2001). Upwelling occurs along the west coast of the country, which is also extremely exposed to large oceanic swells. The east coast is, on the other hand, mostly semi-protected north of East Cape in the North Island, but more exposed from there southwards. Downwelling prevails along the east coast, but there is also significant episodic upwelling in many areas (Morton & Miller 1968, Menge et al. 1999, 2003, Chiswell & Schiel 2001, Schiel 2004).

Wave-exposure, substrate type and oceanographic conditions affect the structure of rocky intertidal communities, which differ substantially between the east and the west coast. Invertebrates (particularly mussels and barnacles) dominate intertidal areas along the west coast, but are scarcely abundant along the east coast. Complex algal assemblages are common along the east coast, especially on large intertidal benches. These assemblages are usually dominated by canopies of small furoids (less than about 1 m in length as adults) such as *Carpophyllum maschalocarpum*, *Carpophyllum angustifolium*, *Cystophora retroflexa*, *Cystophora scalaris*, *Cystophora torulosa* and *Hormosira banksii* in sheltered and semi-exposed areas, and by the large *Durvillaea antarctica* in more exposed waters (Morton & Miller 1968, Schiel 2004, 2006, 2011). Subtidal rocky reefs can be relatively small around much of the east coast of the South Island and they usually do not extend far offshore (Schiel & Hickford 2001). Intertidal regions, therefore, provide much of the macroalgal-dominated habitat and account for a significant portion of rocky reef productivity (Tait 2010).

Extensive research has shown that intertidal furoids are the cornerstone of community organization in intertidal assemblages along the east coast of the South Island of New Zealand. Furoid canopies shape the structure and functioning of these assemblages,

facilitating the development of a rich understory comprising juvenile furoid plants, encrusting and turf-forming coralline algae, and a variety of fleshy red, brown and green algae (Lilley & Schiel 2006, Schiel 2006, Tait 2010). Synergistic interactions between understory algae and the dominant furoids haven been shown to enhance assemblage productivity (Tait 2010, Tait & Schiel 2011b). Long-term impacts on the associated understory algae (Lilley & Schiel 2006, Schiel & Lilley 2007, Schiel 2011) and on assemblage productivity dynamics (Tait 2010, Tait & Schiel 2011a) have been recorded following the experimental or natural removal of furoid canopies.

These complex macroalgal assemblages are threatened by numerous anthropogenic sources of disturbances such as human trampling (Schiel & Taylor 1999), increased sedimentation (Schiel et al. 2006), and altered wave regimes (Schiel 2011). Building on the findings of previous studies in this system, and on the extensive body of research addressing the loss of algal beds worldwide, this thesis tests physical and biological mechanisms underlying the impacts of different forms of natural and human-related disturbance on these macroalgal assemblages.

1.4. AIMS AND STRUCTURE OF THE THESIS

I used a suite of manipulative field and laboratory experiments to test the impacts of physical and biotic stressors on the structure and functioning of intertidal algal assemblages dominated by furoid canopies. I tested the responses of individual species, selected combinations of taxa, and entire assemblages to assess both the direct impacts of the experimental perturbations on target organisms and their influence on intra- and interspecific interactions among different assemblage components.

The thesis consists of five chapters describing experimental work (Chapters 2 to 6) and a general discussion (Chapter 7). I first set up a field experiment based on experimental

manipulations at the assemblage level (described in Chapter 2). Building on this first experiment, I then did a series of field and laboratory experiments involving selected groups of taxa (Chapters 3, 4 and 5) and individual species (Chapter 6) whose responses to altered physical conditions may have profound implications for the structure and functioning of these macroalgal assemblages.

Chapter 2 describes a field experiment testing the responses of complex macroalgal assemblages dominated by furoid canopies to simulated disturbance events of increasing intensity. Intertidal assemblages are faced with increasing levels of mechanical disturbance due to growing human presence and stormier conditions along the coastlines. Here I examined the recovery capacity of the dominant furoids and assessed how the associated understory taxa responded to the loss of the canopy, or recovered when removed themselves.

Chapter 3 describes a combination of field and laboratory experiments testing the impacts of turf-forming coralline algae and sediment on the recruitment of a canopy-forming furoid and their influence on assemblage productivity dynamics. The spread of low-lying turfs and increased sediment loads are often associated with the regression of macroalgal canopies. Here I examined the influence of turfs and sediment on key ecological processes which shape the structure and functioning of benthic assemblages dominated by furoid canopies.

Chapter 4 describes a field experiment testing the interactions among furoid, articulated coralline and ephemeral algae under increased nutrient loads. Low lying algal turfs and ephemeral fast-growing algae can both affect the recruitment of slow-growing perennial furoids. Here I examined potential shifts in the interactions among these three groups of algae under altered nutrient regimes.

Chapter 5 describes three laboratory experiments testing the interactions between the early life stages of a habitat-forming furoid and fast-growing, opportunistic green algae. Increased competition with opportunistic, fast-growing species is contributing to the decline of algal canopies. Here I examined the mechanisms underlying the impacts of ephemeral green algae on different stages of the early life history of a canopy-forming furoid and the influence of temperature, nutrient enrichment and grazing pressure on the interactions between the two taxa.

Chapter 6 describes a series of laboratory experiments testing the impacts of different combinations of temperature, nutrients and sedimentation on the early life stages of three habitat-forming furoids. Anthropogenic perturbations rarely act in isolation and their compound effects are causing great concern and stimulating extensive research. Here I examined the combined impacts of anthropogenic stressors of global and local dimensions on critical phases of the life cycle of three important perennial macroalgae.

Chapter 7 provides a general discussion of the experimental results and of their relevance to the increasing body of research investigating the causes and implications of the loss of complex biogenic habitats in coastal areas.

1.5. STUDY SYSTEM

Algal assemblages dominated by furoid canopies, which colonize large intertidal platforms along the east coast of the South Island of New Zealand, were used as a model system. All field experiments were done at Wairepo Flats, a large intertidal reef located in Kaikoura (42°25'S, 173°42'E; Fig. 1.1). The experiment described in Chapter 2 was also replicated at a southern site, Moeraki Point (45°21'S, 170°51'E; Fig. 1.2), located in Moeraki, approximately 400 km south of Kaikoura. These two sites are representative of algal-

dominated intertidal systems which are common along the east coast of New Zealand and were selected because of the great abundance of furoid canopies and their easy accessibility.



Fig. 1.1. Wairepo Reef, Kaikoura, showing extensive cover of the furoid *Hormosira banksii*.



Fig. 1.2. Moeraki Point, Moeraki. Note the extensive cover of *Hormosira banksii* in the foreground. Darker areas in the background consist of a cover of the furoid *Cystophora torulosa*.

Intertidal algal assemblages at both sites present a clear zonal pattern, with canopies of *Hormosira banksii* covering the mid-intertidal zone (0.5 to 1 m above the lowest astronomical tide level), and canopies of *Cystophora torulosa* dominating in the low-

intertidal zone (0.1 to 0.3 m above the lowest astronomical tide level). Other fucooids such as *Carpophyllum maschalocarpum*, *Cystophora retroflexa* and *Cystophora scalaris* are less abundant and are generally found in the low-shore in tide pools and in the understory of *C. torulosa* canopies. Canopies of the large fucooid *Durvillaea antarctica* are abundant at both locations in exposed areas at the intertidal-subtidal fringe.

In the mid-shore region, encrusting and turf-forming articulate coralline algae (mainly *Corallina officinalis*) are the most abundant components of the understory of *H. banksii* canopies. Other less abundant taxa form a mid-canopy layer between the *H. banksii* canopy and the basal layer of corallines. The mid-canopy is generally composed of juvenile fucooids (i.e., small plants of *C. torulosa* and of the dominant *H. banksii*) and small fleshy brown (*Adenocystis utricularis*, *Colpomenia* spp., *Ectocarpus* sp., *Mesogloia intestinalis*, *Scytosiphon* sp., *Tinocladia novae-zelandiae*), green (*Chaetomorpha coliformis*, *Enteromorpha intesinalis*, *Ulva* sp.) and red algae (*Ceramium* spp., *Champia* sp., *Gelidium* spp., *Laurencia* sp., *Lophothamnium hirtum*).

In the low-shore region, encrusting and turf-forming articulate corallines (a mix of *Corallina officinalis* and *Jania* spp.) are the most abundant understory taxa associated with *C. torulosa* canopies. The mid-canopy is usually more abundant and diverse compared to mid-shore assemblages. It includes juvenile fucooids of several species (*C. maschalocarpum*, *C. retroflexa*, *C. scalaris*, *C. torulosa*, *H. banksii*) and a mosaic of small, fleshy brown (*Adenocystis utricularis*, *Colpomenia* spp., *Dictyota* spp., *Ectocarpus* sp., *Halopteris* spp., *Mesogloia intestinalis*, *Scytosiphon* sp., *Tinocladia novae-zelandiae*, *Xiphophora gladiata*, *zonaria* sp.), green (*Chaetomorpha coliformis*, *Enteromorpha intesinalis*, *Ulva* sp.) and red algae (*Ballia* sp., *Bryocladia eriocoides*, *Ceramium* spp., *Champia* sp., *Echinothamnion* spp., *Gelidium* spp., *Gigartina chapmanii*, *Heterosiphonia* sp., *Hymenena* spp., *Laurencia* sp., *Lophothamnium hirtum*, *Lophurella* spp., *Polysiphonia* spp.).

The structure of these furoid-dominated assemblages is mainly determined by non-trophic interactions. As commonly observed along the east coast of the South Island of New Zealand, grazing invertebrates are generally small and do not play a dominant structuring role as in other intertidal systems elsewhere (Lilley & Schiel 2006, Schiel 2006, 2011). The major grazing mollusc within furoid beds in this study system, the trochid gastropod *Lunella smaragdus*, feeds primarily on ephemeral algae (e.g., *Ulva*), but has little impact on the dominant furoids (Walker 1998, Schiel 2006).

Hormosira banksii

Hormosira banksii (Fig. 1.3) is a dioecious furoid common in intertidal areas around New Zealand and south-eastern Australia. Its thalli can grow up to 50 cm and are composed of a series of beaded-like structures containing seawater which make *H. banksii* particularly resistant to heat and desiccation (Morton & Miller 1968, Brown 1987, Adams 1994).



Fig. 1.3. *Hormosira banksii*.

H. banksii reproduces mainly during spring and summer (September-March), but pulses of gamete release occur throughout the year (Osborn 1948, Dunmore 2006). *H. banksii* is the only canopy-forming furoid colonizing mid-shore habitats in New Zealand (Schiel 2006). Small *H. banksii* plants also occur in the low-shore as part of the understory assemblages associated with *Cystophora torulosa* canopies.

Cystophora torulosa

Cystophora torulosa (Fig. 1.4) is a monoecious furoid found around New Zealand and south-eastern Australia. It is abundant in low-shore intertidal areas and in the shallow subtidal zone (Adams 1994, Schiel 2006). Small *C. torulosa* individuals also occur in the mid-shore in the understory of *H. banksii* canopies (Schiel 2006). *C. torulosa* is particularly prone to desiccation and does not survive well if exposed to a hot sun for a prolonged period at low tide (Schiel 2006, Tait 2010). Reproduction occurs in spring and early summer (September-December; Dunmore 2006).



Fig. 1.4. *Cystophora torulosa*.

Durvillaea antarctica

Durvillaea antarctica (Fig. 1.5) is the world's largest furoid alga. It is a dioecious furoid with large buoyant fronds growing up to 10 m in length. It is found along exposed coasts in New Zealand, Tasmania, Chile and the Subantarctic Islands (Santelices 1990, Adams 1994). *D. antarctica* holdfast support high invertebrate biodiversity (Santelices 1990, Edgar & Burton 2000) and can facilitate long-distance dispersal of the associated invertebrate communities through oceanic rafting (Fraser et al. 2011). The reproduction of this species is restricted to a 16 week period during autumn and winter (May-August; Hay 1979).



Fig. 1.5. *Durvillaea antarctica*.

Understory species: turfing and opportunistic algae

Algal turfs and fast-growing, opportunistic algae are known to affect the recruitment and early life history stages of slow-growing perennial furoids (Benedetti-Cecchi 2001, Berger et al. 2004, Steen 2004, Worm & Lotze 2006, Bellgrove et al. 2010). A series of hypotheses related to the influence of degraded environmental condition on the interactions between turfing and ephemeral algae and dominant habitat-forming furoids was tested in this thesis.



Fig. 1.6. Turf-forming geniculate coralline algae.



Fig. 1.7. Opportunistic green (*Ulva* spp.) and brown algae (*Colpomenia* spp.).

In the study system investigated in the thesis, turf-forming algae are the main benthic space occupiers and are represented by geniculate corallines (Fig. 1.6) such as *Corallina officinalis* and *Jania* spp. Along with the dominant canopy-forming furoids, coralline turfs

are the most abundant components of these macroalgal assemblages (Schiel 2006).

Articulated corallines produce significant alterations in the benthic environment through the creation of a three-dimensional biogenic surface and the retention of sediment (Airoldi 2003, Schiel et al. 2006, Hurley 2009).

Opportunistic algae (Fig. 1.7) are primarily represented by brown algae of the genus *Colpomenia* and green algae of the genus *Ulva*, along with other less abundant green and brown algae with filamentous, foliose or tubular thalli (e.g., *Adenocystis utricularis*, *Chaetomorpha coliformis*, *Ectocarpus* sp., *Mesogloia intestinalis*, *Scytosiphon* sp., *Tinocladia novae-zelandiae*). In this system, opportunistic algae exhibit an ephemeral habit, as they are usually present in low abundance underneath furoid canopies, but rapidly increase their cover when the canopy is fragmented or removed. These blooms, however, are generally of short duration (Lilley & Schiel 2006). In eutrophic areas elsewhere, the rapid proliferations of ephemeral opportunistic algae have been shown to severely affect other benthic organisms, in particular perennial, habitat-forming macroalgae (Eriksson et al. 2002, Worm & Lotze 2006, Moy & Christie 2012).

CHAPTER 2

**Patterns of resistance and resilience in complex
macroalgal assemblages across gradients of
emersion and disturbance intensity**

2.1. ABSTRACT

In intertidal habitats, the impact of mechanical perturbations on macroalgal stands is increasing because of increased frequency and intensity of storms under altered global climate conditions and intensified human trampling at local scales. I tested the impacts of mechanical disturbance on macroalgal assemblages with a complex multi-layered structure (i.e., canopy, mid-canopy and basal layer) across a gradient of tidal elevation at two locations along the east coast of the South Island of New Zealand. Increasing disturbance intensities were simulated through the selective removal of different combinations of algal layers, starting from the simple thinning of the canopy to the destruction of the entire assemblage. The recovery of the canopy-forming fucoids *Hormosira banksii* and *Cystophora torulosa* was affected by disturbance intensity. For both species, even the lightest disturbance had an impact lasting for at least eighteen months. Following more intense disturbances, the regeneration of the canopies of *H. banksii* and *C. torulosa* was quicker when the mid-canopy was not removed, because of the development of conspecific juvenile plants into adult individuals. Canopy recovery was still incomplete in some of the treatments after thirty months and there were differences between sites and shore heights. The dominant fucoids and ephemeral algae were the only taxa to increase their abundance in response to disturbance, independently of the diversity and composition of understory assemblages at different sites and shore heights, confirming that functional redundancy is limited in this system. Understory assemblages, however, were resistant to the loss of the canopy, and they recovered more rapidly compared to the overlying canopy when directly impacted by disturbance. These results expand the findings of numerous studies investigating the loss of algal canopies in intertidal habitats, by showing the influence of both the dominant habitat-formers and of other less abundant understory components on assemblage trajectories of recovery following perturbations of different intensities.

2.2. INTRODUCTION

Natural and anthropogenic disturbance events are an integral part of the dynamics of all ecosystems. Disturbance plays a critical role in shaping the structure and diversity of natural communities by affecting the physical environment, the availability of resources, the distribution of species and their interactions (Connell 1978, Sousa 1984, Pickett & White 1985). Disturbances are inherently diverse and so are the responses of the impacted systems. Ecologists have long recognized the importance of understanding the mechanisms enabling natural communities to withstand or recover from perturbations of different extension, intensity, duration and frequency (McCabe & Gotelli 2000, White & Jentsch 2001, Bertocci et al. 2005, Hughes et al. 2007). This is now becoming an even more pressing priority, as anthropogenic influences pose new, unprecedented threats to all ecosystems and affect the patterns of intensity and temporal variation of natural disturbances, potentially exacerbating their impacts (Paine et al. 1998, IPCC 2013).

In rocky intertidal habitats, for example, canopy-forming macroalgae of the Order Fucales (furoids) are affected by increasing mechanical disturbances caused by more frequent and severe storms under altered global climate conditions (Underwood 1998, Hawkins et al. 2009, Schiel 2011) and by the the intensification of human trampling at local scales (Schiel & Taylor 1999, Araújo et al. 2009). Altered wave regimes and increasing trampling compound the impacts of other natural (e.g., ice, boulders, drifting materials; Sousa 2001) and anthropogenic disturbance agents (e.g., acute pollution, human harvesting; Thompson 2002) which can rapidly remove furoid canopies from intertidal reefs.

Given their key role as biogenic habitat-formers in intertidal systems worldwide (Chapman 1995, Schiel 2006), the recovery capacity of furoid macroalgae and the responses of the associated communities following their loss have been widely investigated. Numerous studies have tested the recovery capacity of canopy-forming furoids through their selective

removal (Underwood 1998, Jenkins et al. 1999a,b, 2004, Speidel 2001, Cervin et al. 2005, Lilley & Schiel 2006, Schiel 2006, Schiel & Lilley 2007, 2011). Other studies followed the recovery trajectories of furoid-dominated assemblages after all organisms were removed from the reef surface, either as part of the experimental manipulations or as a result of natural disturbance events (McCook & Chapman 1991, 1992, Dudgeon & Petraitis 2001, Bertness et al. 2002, Viejo 2009). The consequences of disturbance, however, can be far more complex than the extinction of a single organism or the destruction of the entire assemblage. Mosaics of patches with different species combinations are common in intertidal habitats following disturbance, as a result of differences in the intensity of disturbances and in the vulnerability of organisms to them (Dethier 1984, Sousa 1984, 2001).

Here I tested the responses of macroalgal assemblages to disturbance events of increasing intensity, simulated through the selective removal of different combinations of assemblage components. Disturbance was defined as any process causing the loss of biomass (Grime 1977) and disturbance intensity simply as a measure of the fraction of biomass removed. Algal assemblages dominated by furoid canopies in intertidal areas along the east coast of the South Island of New Zealand were used as a model system. These assemblages present a complex, multi-layered structure. The understory of furoid canopies is generally composed of two distinct layers of algae: a basal layer of encrusting and turf-forming coralline algae, above which is a mid-canopy layer of juvenile furoids and fleshy red, brown and green algae. The furoid canopy and basal layer are composed of a restricted number of taxa, but they account for the greatest portion of assemblage biomass. The mid-canopy has far more taxa, but these constitute only a small fraction of the total biomass (Lilley & Schiel 2006, Schiel 2006, Tait 2010, Tait & Schiel 2011b; see Chapter 1).

To investigate patterns of resilience (i.e., the ability to recover from perturbations; Pimm 1994) and resistance (i.e., the magnitude of change caused by perturbations; Pimm

1994) within this system, four levels of disturbance intensity were chosen to simulate a realistic pattern of species loss. The levels reflected the susceptibility of different algal forms to the impacts of natural and anthropogenic mechanical disturbances. The two lightest disturbance levels consisted in the partial and total loss of the canopy, as large canopy-forming fucoids are often the first species removed from intertidal reefs by waves (Denny 1995, Blanchette et al. 2000) and human trampling (Schiel & Taylor 1999, Araújo et al. 2009). Algae with small foliose and branched thalli (similar to those forming the mid-canopy in my experimental assemblages) are also known to be affected by elevated hydrodynamic forces, but with a lower probability of dislodgment (Denny 1995), and can become more prone to the impact of trampling and other mechanical perturbations in the absence of an overlaying canopy (Araújo et al. 2009, Bertocci et al. 2010). Therefore, to recreate the impact of a more intense disturbance, the loss of the fucoid canopy was combined with the elimination of the mid-canopy layer. Finally, the consequences of extreme, rare events clearing all organisms from the substrate (Ebeling et al. 1985, Denny 1995) were reproduced through the removal of all algal layers. The experiment was set up at two different tidal elevations to assess the responses of assemblages dominated by different canopy-forming fucoids and with different pools of species. Responses to disturbance may be affected by variations in the sign and strength of species interaction along a gradient of emersion, with facilitation dominating under harsh physical conditions and competition prevailing in more benign environments at lower elevations (Bertness & Callaway 1994, Bulleri 2009).

This design allowed the response of different assemblage layers to increasing disturbance to be tested. In particular, I tested whether the recovery of the canopy was affected by the intensity of disturbance. Fucoid canopies may regenerate faster when disturbance does not affect the other algal layers, as a result of the development of the juvenile mid-canopy plants into adults. Space pre-emption by the mid-canopy and the basal

layer, however, may affect the re-colonization of the disturbed patches by the recruits of the dominant fucoids (Britton-Simmons 2006, Viejo et al. 2008, Bellgrove et al. 2010). As a consequence, faster canopy recovery may take place when a larger fraction of assemblage biomass is removed by more intense disturbances. In addition, I tested the impacts of the experimental manipulations on the taxa in the mid-canopy and in the basal layer. These taxa are known to provide a relevant contribution to the dynamics of primary productivity of these assemblages (Tait 2010, Tait & Schiel 2011b; see Chapter 3), but their roles in successional sequences are not clear. Understanding how these taxa respond to the loss of other assemblage components, or recover when removed, is therefore essential to clarify their functional roles and the underlying drivers of assemblage structure and diversity.

2.3. MATERIAL AND METHODS

2.3.1. Study sites and assemblage composition

The experiment was done at two locations separated by about 400 km along the east coast of the South Island of New Zealand: Wairepo Flats, Kaikoura (42°25'S, 173°42'E) and Moeraki Point, Moeraki (45°21'S, 170°51'E). Both sites have large intertidal platforms which host diverse algal assemblages dominated by canopies of the fucoids *Hormosira banksii* and *Cystophora torulosa* (see Chapter 1). At both sites the experiment was set up in the mid-shore (0.5 to 1 m above the lowest astronomical tide level), which is covered by canopies of *H. banksii*, and in the low-shore (0.1 to 0.3 m above the lowest astronomical tide level), which is dominated by canopies of *C. torulosa*. Turf-forming articulate corallines (mainly *Corallina officinalis*) are the primary benthic space occupiers, while the remaining substrate is either bare or covered by encrusting corallines. The main components of the mid-canopy layer are juveniles of the perennial fucoids *Carpophyllum maschalocarpum*, *Cystophora retroflexa*, *Cystophora scalaris*, *Cystophora torulosa*, *Hormosira banksii*, and small fleshy brown

(*Adenocystis utricularis*, *Colpomenia* spp., *Dictyota* spp., *Ectocarpus* sp., *Halopteris* spp., *Mesogloia intestinalis*, *Scytosiphon* sp., *Tinocladia novae-zelandiae*, *Xiphophora gladiata*, *zonaria* sp.), green (*Chaetomorpha coliformis*, *Enteromorpha intesinalis*, *Ulva* sp.) and red algae (*Ballia* sp., *Bryocladia eriocoides*, *Ceramium* sp., *Champia* sp., *Echinothamnion* spp., *Gelidium* spp., *Gigartina chapmanii*, *Heterosiphonia* sp., *Hymenena* spp., *Laurencia* sp., *Lophothamnium* sp., *Lophurella* spp., *Polysiphonia* spp.).

2.3.2. Experimental design and data collection

At each site and within each tidal zone, fifteen 50 x 50 cm plots were selected. Before the experimental treatments were applied, the plots were visually sampled using a grid divided into 100 sub-quadrats and the percentage cover of all algae was recorded (Table 2.1A and B). At each location, three replicate plots were randomly chosen in each tidal zone and assigned to one of five experimental conditions to test the impacts of different disturbance intensities (Table 2.1C). Control plots (C) were left untouched, while in the plots assigned to light and medium disturbance intensities (LD and MD, respectively) 50% and 100% of the dominant furoid was removed. The high disturbance treatment (HD) consisted in the complete removal of both the canopy and all mid-canopy algae, leaving only the basal layer, while extreme disturbance (ED) was created by removing all assemblage components, so that the plots were reduced to denuded bare patches. The experimental manipulations were performed on a single occasion, at the start of the experiment, and were extended to the area surrounding the immediate edges of the plots to limit the influence of the organisms surrounding the boundaries. Algal removal was done using a knife, ensuring that non-target species were not affected. Partial canopy removal was achieved by haphazardly removing half of the plants throughout the plot. The basal layer was removed with a chisel.

The experiment was started in April 2010, at the beginning of the austral autumn. This allowed me to assess the trajectories of recovery of the experimental assemblages from the coolest months of the year, when disturbance events associated with severe weather are more likely to occur (Underwood 1998, Schiel 2011). The plots were sampled three, six, nine, twelve, eighteen, twenty-four and thirty months after the start of the experiment. On each occasion, all algae were identified to the greatest possible taxonomic resolution and their percentage cover was recorded. The percentage cover of all sessile invertebrates and the number of all mobile invertebrates were also recorded.

Following page

Table 2.1. A) Mean percentage cover (\pm SE) of canopy, mid-canopy and basal layer recorded at the two study sites in the mid- and in the low-shore before the start of the experiment (n = 15). B) List of all understory taxa and of their abundances at all sites and shore heights before the start of the experiment (n = 15). C) Overview of the experimental manipulations, involving the selective removal of different combinations of assemblage components to simulate the impact of increasing disturbance intensities. Canopy manipulation: 100% = intact canopy; 50% = half canopy removal; 0% = total canopy removal. Mid-canopy and basal layer manipulation: + = unmanipulated; - = removed.

A) Assemblage components	Mid-shore Kaikoura	Mid-shore Moeraki	Low-shore Kaikoura	Low-shore Moeraki
Canopy	95.6 ± 0.9	98.7 ± 0.3	91.9 ± 1.8	79.5 ± 2.3
Understory:				
• Mid-canopy	8.2 ± 0.8	6.8 ± 0.7	16.8 ± 2.2	10.4 ± 1.1
• Basal layer	63.1 ± 2.3	52.4 ± 6.4	57.8 ± 7.2	66.2 ± 4.3
B) Understory taxa	Mid-shore Kaikoura	Mid-shore Moeraki	Low-shore Kaikoura	Low-shore Moeraki
<i>Adenocystis utricularis</i>	0	0	0.1 ± 0.1	0
<i>Bryocladia eriocoides</i>	0	0	0	0.2 ± 0.1
<i>Carpophyllum maschalocarpum</i>	0.1 ± 0.1	0	1.0 ± 0.3	0
<i>Ceramium</i> spp.	0	0	0.1 ± 0.1	0
<i>Chaetomorpha coliformis</i>	0.2 ± 0.1	0	0.2 ± 0.1	0.2 ± 0.1
<i>Champia</i> sp.	0.2 ± 0.1	0	4.8 ± 0.9	0
<i>Colpomenia</i> spp.	0.4 ± 0.1	0	0.5 ± 0.1	0.1 ± 0.1
<i>Cystophora retroflexa</i>	0	0.8 ± 0.4	0	0.9 ± 0.2
<i>Corallina offinalis</i>	67.1 ± 3.0	52.3 ± 6.3	49.2 ± 7.1	43.9 ± 4.3
<i>Cystophora scalaris</i>	0.2 ± 0.1	0.4 ± 0.3	3.9 ± 0.8	0.5 ± 0.2
<i>Cystophora torulosa</i>	1.1 ± 0.3	3.1 ± 0.7	1.0	3.9 ± 0.7
<i>Dictyota</i> spp.	0	0	0.4 ± 0.1	0.4 ± 0.1
<i>Echinothamnion</i> spp.	1.9 ± 0.7	0	0.6 ± 0.3	0
<i>Enteromorpha intesinalis</i>	0.1 ± 0.1	0	0	0
<i>Gelidium</i> spp.	0	0	1.0 ± 0.2	0
<i>Halopteris</i> spp.	0	0	0	1.2 ± 1.0
<i>Heterosiphonia</i> sp.	0	0	0	0.7 ± 0.3
<i>Hormosira banksii</i>	3.3 ± 0.4	2.3 ± 0.2	1.6 ± 0.4	1.0 ± 0.3
<i>Hymenemia</i> spp.	0.1 ± 0.1	0	0.4 ± 0.1	0.1 ± 0.1
<i>Laurencia</i> sp.	0.3 ± 0.1	0.1	0.9 ± 0.4	0
<i>Jania</i> spp.	0	0	7.9 ± 4.9	20.0 ± 0.9
<i>Lophurella</i> spp.	0	0	0	0.3 ± 0.1
<i>Lophothamnion</i> sp.	0.1 ± 0.1	0.1	0	0.3 ± 0.1
<i>Polysiphonia</i> spp.	0	0	0.2 ± 0.1	0.3 ± 0.2
<i>Porphyra</i> sp.	0	0	0.1 ± 0.1	0
<i>Ulva</i> sp.	0.1	0	0	0
<i>Zonaria</i> sp.	0	0	0	0.3 ± 0.1
C) Disturbance intensity	Canopy	Mid-canopy	Basal layer	
Control (C)	100%	+	+	
Light disturbance (LD)	50%	+	+	
Medium disturbance (MD)	0%	+	+	
High disturbance (HD)	0%	–	+	
Extreme disturbance (ED)	0%	–	–	

2.3.3. Statistical analyses

For all response variables, either the response to the experimental manipulations at specific sampling times, or the mean response over time was analysed. This avoided repeated measures analyses, which present complex assumptions and provide a less straightforward interpretation of the results (Murtaugh 2007).

The percentage cover of *H. banksii* and *C. torulosa* adults (i.e., with thalli > 10 cm long) was analysed both after twelve months (to assess the short-term responses of the dominant fucoids following disturbances of different intensities), and at the conclusion of the experiment (to test the long term resilience of furoid canopies). Separate analyses were done for each species, both after twelve and thirty months, using a two-way ANOVA with the factors Site (random, with two levels) and Disturbance (fixed, with five levels: control, light disturbance, medium disturbance, high disturbance, extreme disturbance). α was Bonferroni-corrected to 0.025.

The total number of understory algal taxa, averaged across the period 3-30 months, was analysed with a three-way ANOVA with the factors Site (random, with two levels), Zone (fixed, with two levels: mid- and low-shore) and Disturbance (fixed, with five levels: control, light disturbance, medium disturbance, high disturbance, extreme disturbance). The starting sampling date was excluded as it was not informative about the responses to the experimental manipulations. Using the same three-way ANOVA, I also analysed the average percentage cover of a number of individual understory taxa across the period 3-30 months. Among the components of the basal layer, I analysed the mean abundance of turf-forming coralline algae, while mid-canopy taxa were divided into fucoids, ephemeral and non-ephemeral algae. The mean abundances of the main mid-canopy fucoids (i.e., *H. banksii*, *C. torulosa*, and *Cystophora* spp., representing the combined abundance of *C. retroflexa* and *C. scalaris*) were separately analysed. Furoid plants were considered as part of the mid-canopy, and not as

adult, canopy-forming individuals, when the length of their thalli was < 10 cm. Individuals with thalli < 2 cm long were classified as recruits. All furoid species showed similar temporal patterns of recruitment, with a maximum peak in the abundance of newly recruited plants in October 2011, eighteen months after the start of the experiment. Therefore, for each furoid, the abundance of the recruits at eighteen months was also analysed to assess how the recruitment of new plants affected the responses to the experimental manipulations, independently from the growth of the individuals already settled. The ANOVA design was appropriately reduced when mid-canopy furoids were only present at one shore height.

All the remaining mid-canopy taxa were divided in two broad categories, ephemeral and non-ephemeral algae, whose mean covers were analysed. Ephemeral algae were mainly fast-growing, opportunistic brown and green algae (e.g., *Colpomenia* spp., *Ulva* sp.), while non-ephemeral algae included red and brown algae with erect-habit producing branched or bush-like thalli (e.g., *Dictyota* spp., *Champia* sp., *Echinothamnion* spp., *Gelidium* spp., *Laurencia* sp.).

Temporal variations in the structure of the entire understory (i.e., mid-canopy + basal layer) in response to disturbance were described by calculating the total Euclidean distance covered by each experimental plot throughout the experiment. Observations were placed into Euclidean space by calculating principal coordinates (Gower 1966) from a Bray-Curtis dissimilarity matrix including the full set of data (fourth root transformed). For each plot I then calculated and added together the seven Euclidean distances between consecutive sampling dates (start-3 months, 3-6 months, 6-9 months, 9-12 months, 12-18 months, 18-24 months, 24-30 months) to quantify the temporal changes in algal assemblage structure. Finally, total Euclidean distances were analysed with a three-way ANOVA with the factors Site (random, with two levels), Zone (fixed, with two levels: mid- and low-shore) and Disturbance (fixed, with five levels: control, light disturbance, medium disturbance, high

disturbance, extreme disturbance). Non-metric multidimensional scaling (nMDS) plots were used to display the temporal trajectories of understory algal assemblages exposed to different disturbance intensities, separately for mid- and low-shore at each location. Furthermore, differences in the composition of understory assemblages at the end of the experiment, expressed by Bray-Curtis dissimilarities calculated on fourth root transformed data, were analysed using a permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) including the same combination of Site, Zone and Disturbance. When significant effects were detected, pair-wise t-tests between controls and each disturbance treatment were carried out. SIMPER analysis (Clarke 1993) was used to assess the contribution of individual taxa to multivariate dissimilarities.

Invertebrates were scarcely abundant in all treatments throughout the experiment and their abundance was not analysed. Before all univariate analyses, variance heterogeneity was tested with the Cochran's *C*-tests and removed with log transformation when required. When homogeneity of variances could not be achieved by transformation, data were analysed nonetheless by judging significance more conservatively ($\alpha = 0.01$). Student-Newman-Keuls (SNK) tests were performed for *a posteriori* comparisons of the means (Underwood 1997).

2.4. RESULTS

2.4.1. Canopy recovery

Patterns of canopy recovery varied depending on the intensity of disturbance and differed between species and study sites. In the mid-shore at both sites, the cover of *H. banksii* did not increase greatly until two years after treatment initiation (Fig. 2.1A and B). After twelve months, LD plots still had less canopy than the controls, while MD, HD and ED plots had the lowest cover of *H. banksii* and did not differ among each other (Table 2.2, Fig. 2.1A and B). After thirty months, the cover of *H. banksii* did not differ among treatments at Kaikoura

(Table 2.2, Fig. 2.1A), while ED plots were still separated from the other treatments at Moeraki (Table 2.2, Fig. 2.1B). At both sites, *H. banksii* canopy only reappeared during the final six months in the plots affected by extreme disturbance intensity, and at the conclusion of the experiment the ED plots had about 27% and 85% less canopy than the controls, at Kaikoura and Moeraki respectively (Fig. 2.1A and B).

In the low-shore, *C. torulosa* recovered much faster at Kaikoura than at Moeraki (Fig. 2.1C and D). After twelve months, however, the controls still had higher canopy cover compared to all other treatments at both sites. LD plots had more canopy than MD, HD and ED plots. Among these, the canopy had started to recover only in the MD plots, which had a cover of *C. torulosa* around 25% at both locations, significantly higher compared to HD and ED plots (Table 2.2, Fig. 2.1C and D). After thirty months the cover of *C. torulosa* did not differ among treatments at Kaikoura (Table 2.2, Fig. 2.1C). At Moeraki, no treatment converged with the controls by the end of the experiment. *C. torulosa* cover in the MD plots recovered to levels analogous to the LD plots and both treatments had less canopy than the controls, but more compared to HD and ED plots (Table 2.2, Fig. 2.1D).

Disturbance did not facilitate the colonization of other canopy formers. Canopy-forming individuals of the furoids *C. retroflexa*, *C. scalaris* and *H. banksii* coexisted with the dominant *C. torulosa* only in the low-shore at Kaikoura, but their cover was always below 5%.

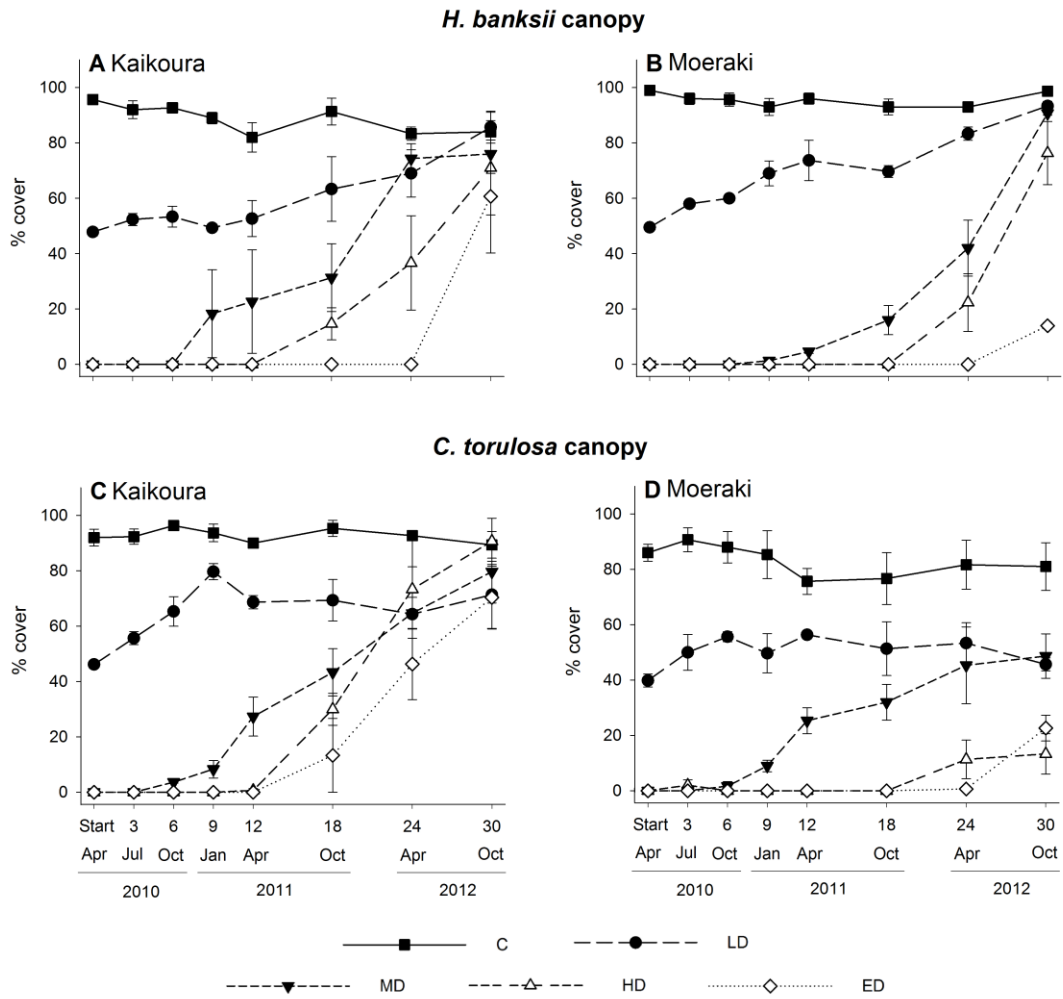


Fig. 2.1. Temporal variation in the mean percentage cover (\pm SE) of *H. banksii* (A and B) and *C. torulosa* canopies (C and D) following disturbance events of increasing intensity (C = control, LD = light disturbance, MD = medium disturbance, HD = high disturbance, ED = extreme disturbance) at the two study sites ($n = 3$).

Table 2.2. ANOVA testing the differences between sites (Kaikoura and Moeraki) and disturbance intensities (C = control, LD = light disturbance, MD = medium disturbance, HD = high disturbance, ED = extreme disturbance) in the percentage cover of *H. banksii* and *C. torulosa* canopies, both after twelve and thirty months from the start of the experiment. α was reduced to 0.025 to correct for repeated tests across sampling dates. *P < 0.025; **P < 0.01; ***P < 0.001.

Source of variation	<i>H. banksii</i>					<i>C. torulosa</i>			
	DF	12 months		30 months		12 months		30 months	
		MS	F	MS	F	MS	F	MS	F
Site (S)	1	86.70	0.61	5.63	0.02	258.13	8.35**	108.30	50.47***
Disturbance (D)	4	9896.50	29.22**	2950.53	2.92	8316.55	116.78***	1336.80	1.31
S x D	1	338.70	2.37	1009.30	3.45*	71.22	2.30	1020.67	4.76**
Residual	20	142.73		292.40		30.90		214.60	

2.4.2. Responses of understory taxa

Juvenile (i.e., < 10 cm long) and newly recruited (i.e., < 2 cm long) conspecific individuals of the dominant fucoids responded positively to the removal of the canopy. The abundance of *H. banksii* mid-canopy plants in the mid-shore, both at Kaikoura and Moeraki, increased following the loss of the entire canopy in MD, HD and ED plots, and across the period 3-30 months was higher in these treatments than in control and LD plots (Table 2.3A, Fig. 2.2A and C). At Kaikoura, the mean percentage cover of mid-canopy *H. banksii* was around 15% in MD, HD and ED treatments, and between 4-8% in control and LD plots (Table 2.3A, Fig. 2.2A). HD and ED plots had the highest abundance of recruits at eighteen months (Table 2.3B, Fig. 2.2B). At Moeraki, ED plots had the greatest mean cover of mid-canopy *H. banksii* (around 18%), significantly higher than MD and HD plots (between 10-13%) and LD and control plots, which had the lowest levels of mean abundance (around 2%; Table 2.3A, Fig. 2.2C). The highest abundance of recruits occurred in ED plots, and the lowest in controls and LD plots (Table 2.3B, Fig. 2.2D). In the low-shore at both locations, the average cover of *H. banksii* mid-canopy plants was below 5% (Fig. 2.2E and G) and the abundance of the recruits at eighteen months around 1% (Fig. 2.2F and H). ED plots at Kaikoura were the only treatment differing from the others, as they had a higher average cover of *H. banksii* mid-canopy plants (around 10%) and a larger abundance of newly recruited individuals compared to all low-shore plots at both locations (Table 2.3A and B, Fig. 2.2E and F).

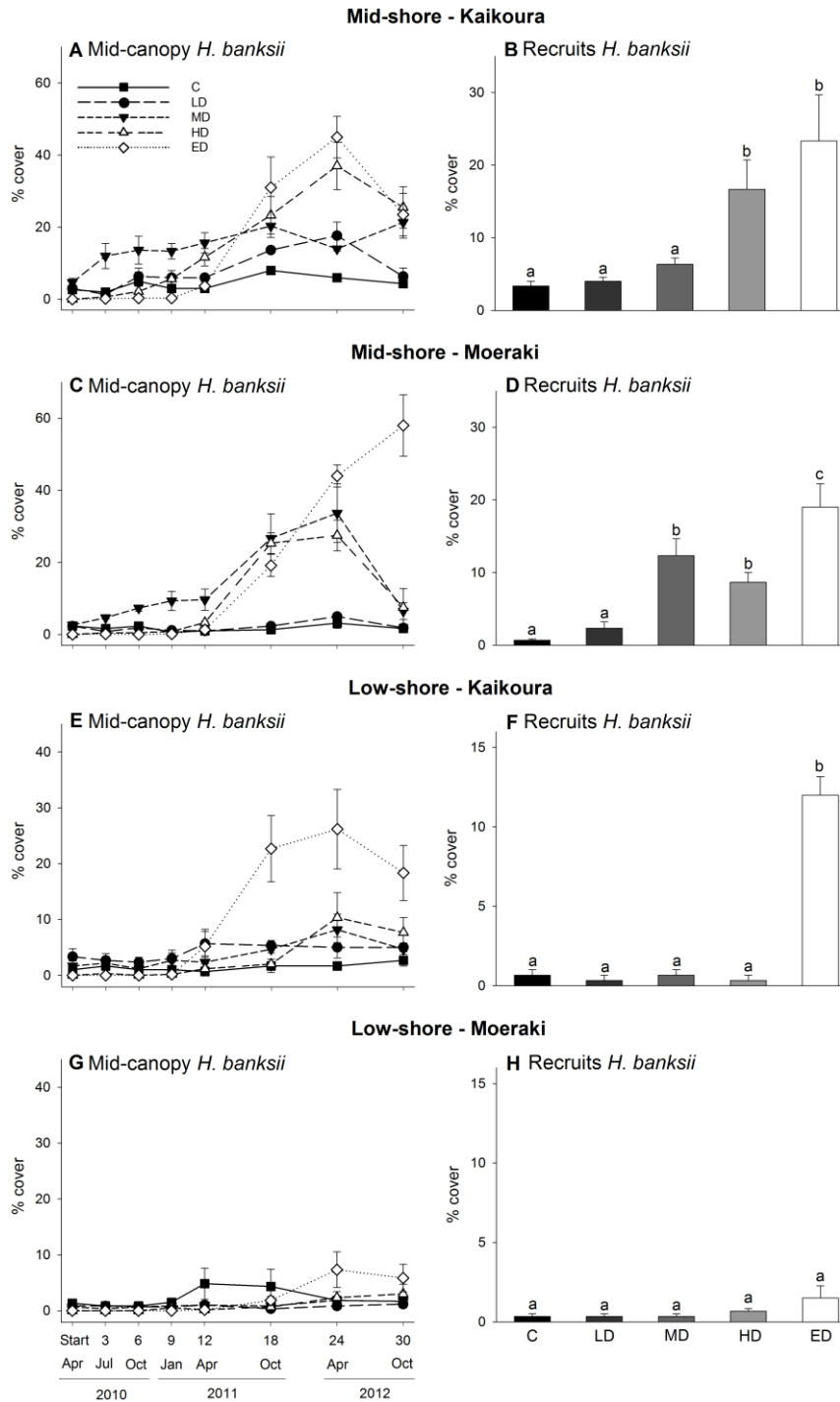


Fig. 2.2. Temporal variation in the mean percentage cover (\pm SE) of *H. banksii* mid-canopy plants (A, C, E and G) and mean percentage cover (\pm SE) of *H. banksii* recruits after eighteen months (B, D, F and H), following disturbance events of increasing intensity (C = control, LD = light disturbance, MD = medium disturbance, HD = high disturbance, ED = extreme disturbance) both in the mid- and in the low-shore at the two study sites (n = 3). The letters indicate the ranking of the means according to the SNK tests, separately for each zone and location.

The mean abundance of mid-canopy *C. torulosa* in the low-shore at Kaikoura was between 7-9% in MD, HD and ED plots, significantly higher compared to control and LD plots (between 3-5%; Table 2.3C, Fig. 2.3A). HD and ED plots had the highest abundance of recruits compared to the other treatments (Table 2.3D, Fig. 2.3B). At Moeraki, the mean abundance of mid-canopy *C. torulosa* was between 11-13% in MD and ED plots and 5-8% in the other treatments (Fig. 2.3C), but SNK tests did not highlight any difference among disturbance intensities. ED plots had the highest abundance of recruits at eighteen months (Table 2.3D, Fig. 2.3D). In the mid-shore, the mean abundance of *C. torulosa* mid-canopy plants was below 2% at both locations (Fig. 2.3E and G). Control plots (both at Kaikoura and Moeraki) and LD plots (at Kaikoura only) had an average cover of mid-canopy *C. torulosa* around 1%, significantly higher compared to the other treatments, where it was close to zero (Table 2.3C, Fig. 2.3E and G). Recruitment rates were always below 1% at both sites and were not influenced by the experimental manipulations (Table 2.3D, Fig. 2.3F and H).

Other species of *Cystophora* (i.e., *C. retroflexa* and *C. scalaris*) were only present in the low-shore. *Cystophora* spp. were more abundant at Kaikoura than at Moeraki (Table 2.3E, Fig. 2.4A and C) and their mean cover in the controls was around 13% at Kaikoura and 3% at Moeraki, in both cases significantly higher compared to all other treatments (Table 2.3E, Fig. 2.4A and C). Recruitment rates were also higher in the controls at both sites (Table 2.3F, Fig. 2.4B and D).

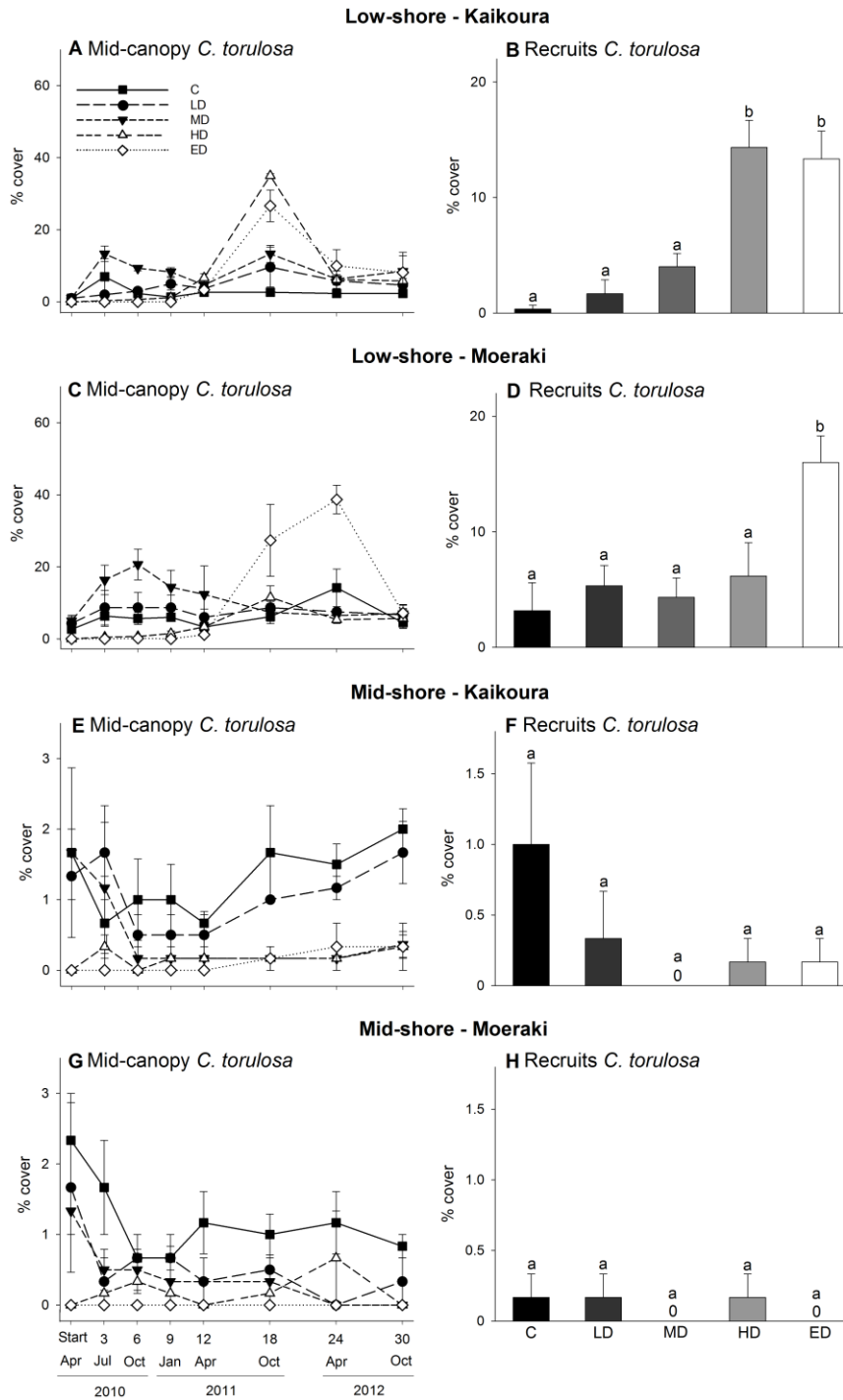


Fig. 2.3. Temporal variation in the mean percentage cover (\pm SE) of *C. torulosa* mid-canopy plants (A, C, E and G) and mean percentage cover (\pm SE) of *C. torulosa* recruits after eighteen months (B, D, F and H), following disturbance events of increasing intensity (C = control, LD = light disturbance, MD = medium disturbance, HD = high disturbance, ED = extreme disturbance) both in the low- and in the mid-shore at the two study sites (n = 3). The letters indicate the ranking of the means according to the SNK tests, separately for each zone and location.

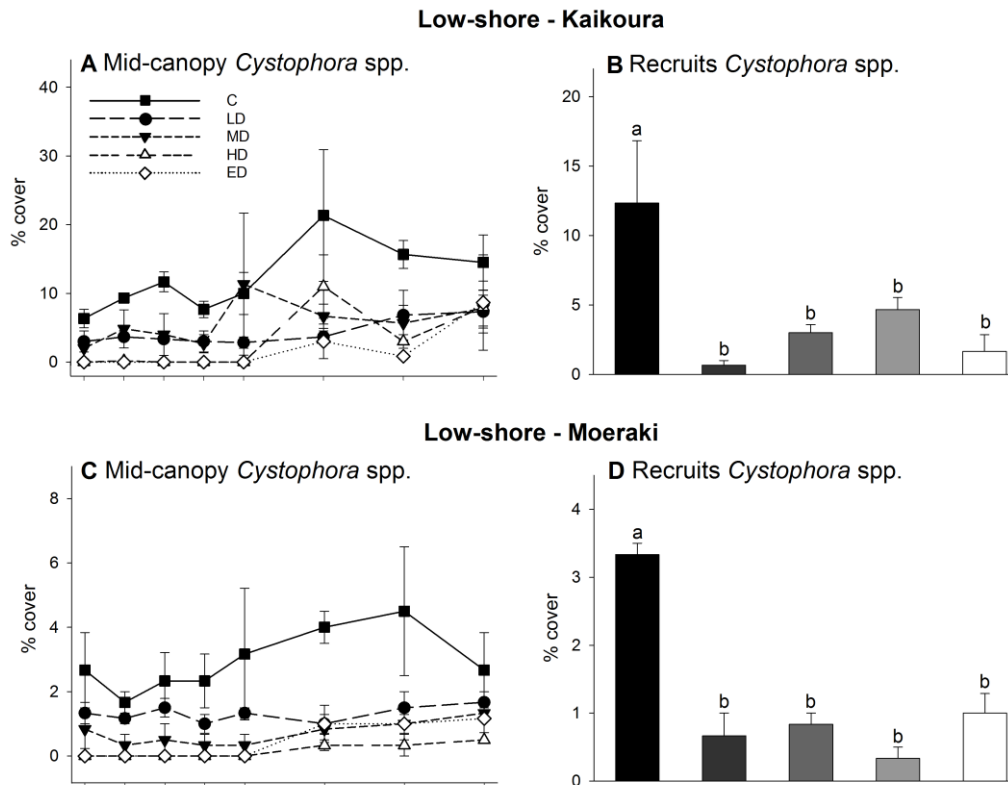


Fig. 2.4. Temporal variation in the mean percentage cover (\pm SE) of *Cystophora* spp. mid-canopy plants (A and C) and mean percentage cover (\pm SE) of *Cystophora* spp. recruits after eighteen months (B and D), following disturbance events of increasing intensity (C = control, LD = light disturbance, MD = medium disturbance, HD = high disturbance, ED = extreme disturbance) in the low-shore at the two study sites ($n = 3$). The letters indicate the ranking of the means according to the SNK tests, separately for each taxon and location.

The abundance of mid-canopy ephemeral algae was generally low, with short-lived peaks in the plots assigned to high and extreme disturbance intensities between October 2010 and April 2011 (i.e., spring-summer; Fig. 2.5A-D). In the mid-shore at Kaikoura, the average abundance of ephemeral algae over the period 3-30 months was higher in the plots initially affected by disturbance of extreme intensity (around 9%) than under the other experimental conditions (between 1-3%; Table 2.3G, Fig. 2.5A). This was the result of a single peak in their percentage cover after six months (Fig. 2.5A). Similarly, at Moeraki, the abundance of ephemeral algae peaked in the ED plots between October 2010 and April 2011, with a mean

cover around 4% compared to 1% in the other treatments (Table 2.3G, Fig. 2.5B). In the low-shore, ED plots had the highest average cover of ephemeral algae (between 18-20%) both at Kaikoura and Moeraki (Table 2.3G, Fig. 2.5C and D). Ephemerals also proliferated in the HD plots at both locations (mean cover around 18% at Kaikoura and 7% at Moeraki) and in the MD plots at Kaikoura (mean cover around 7%). Controls and LD plots had the lowest levels of ephemeral cover (around 1%) at both locations (Table 2.3G, Fig. 2.5C and D).

The average percentage cover of non-ephemeral mid-canopy algae was below 1% in the mid-shore at both locations and was not affected by the intensity of disturbance (Table 2.3H, Fig. 2.5E and F). In the low-shore, at Kaikoura, the average cover of non-ephemeral algae was higher in controls, LD and MD plots (between 10-19%) than in the plots affected by high and extreme disturbance intensities (around 3%; Table 2.3H, Fig. 2.5G). At Moeraki, the mean cover of non-ephemeral algae was between 5-12%, with no differences due to the experimental manipulations (Table 2.3H, Fig. 2.5H).

Articulated turf-forming coralline algae showed variable patterns of recovery in the plots reduced to denuded bare patches at the start of the experiment (Fig. 2.6A-D), but across the period 3-30 months their average abundance at all sites and shore heights was always lower in the ED plots (around 15%) compared to the other treatments (Table 2.3I, Fig. 2.6A-D). The average cover of coralline turfs, across all shore heights and disturbance levels, was higher at Moeraki (around 50%; Fig. 2.6B and D) than at Kaikoura (around 35%, Table 2.3I, Fig. 2.6A and C).

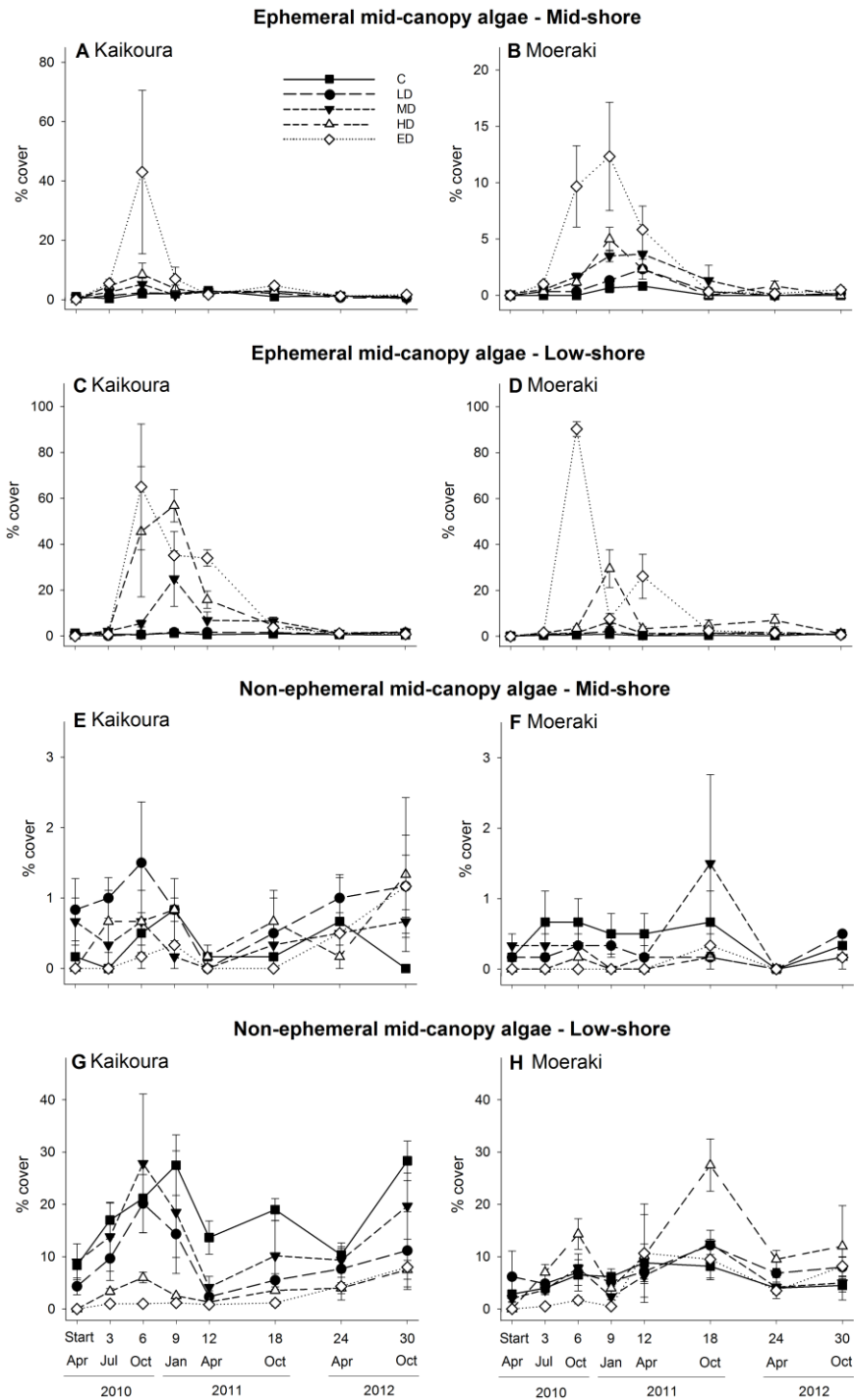


Fig. 2.5. Temporal variation in the mean percentage cover (\pm SE) of ephemeral (A-D) and non-ephemeral mid-canopy algae (E-H), following disturbance events of increasing intensity (C = control, LD = light disturbance, MD = medium disturbance, HD = high disturbance, ED = extreme disturbance) both in the mid- and in the low-shore at the two study sites ($n = 3$).

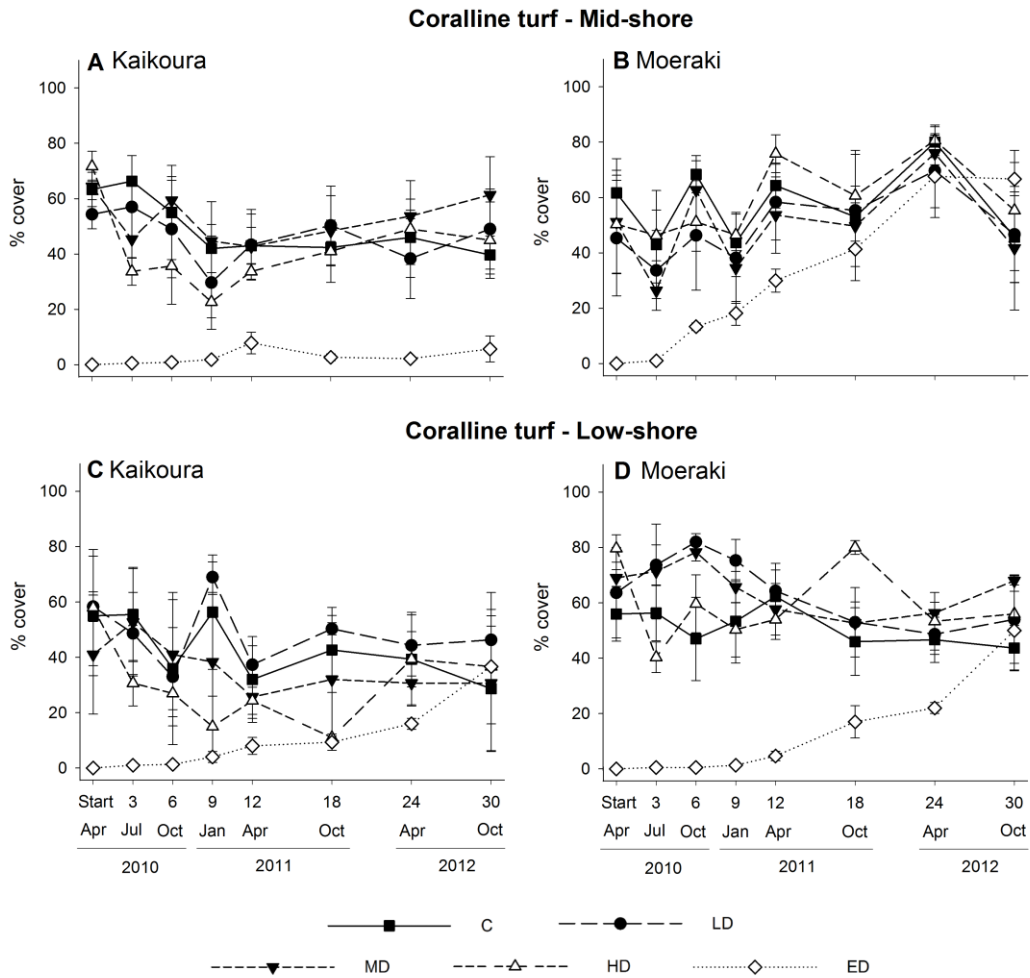


Fig. 2.6. Temporal variation in the mean percentage cover (\pm SE) of articulated turf-forming coralline algae following disturbance events of increasing intensity (C = control, LD = light disturbance, MD = medium disturbance, HD = high disturbance, ED = extreme disturbance) both in the mid- (A and B) and in the low-shore (C and D) at the two study sites ($n = 3$).

Table 2.3. ANOVA testing the differences between sites (Kaikoura and Moeraki), tidal zones (mid- and low-shore) and disturbance intensities (C = control, LD = light disturbance, MD = medium disturbance, HD = high disturbance, ED = extreme disturbance) in the average percentage cover, across the period 3-30 months, of selected understory algal taxa and on the percentage cover of newly recruited plants (< 2 cm long) of the most abundant mid-canopy fucoids at 18 months. Zone was omitted from the analysis for the taxa present only at one shore height. α was reduced to 0.01 when variance heterogeneity could not be removed through transformation. *P < 0.05; **P < 0.01; ***P < 0.001.

Source of variation	DF	A) Mid-canopy <i>H. banksii</i> (3-30m)		B) Recruits <i>H. banksii</i> (18m)	
		MS	F	MS	F
Site (S)	1	129.65	36.17***	1.67	15.36***
Zone (Z)	1	797.89	1770.47*	30.56	2709.19***
Disturbance (D)	4	152.46	23.17**	5.40	9.66*
S x Z	1	0.45	0.13	0.01	0.10
S x D	4	6.58	1.84	0.56	5.16**
Z x D	4	75.75	2.65	1.17	1.35
S x Z x D	4	28.56	7.97***	0.87	7.99***
Residual	40	3.59		0.11	

Source of variation	DF	C) Mid-canopy <i>C. torulosa</i> (3-30m)		D) Recruits <i>C. torulosa</i> (18m)	
		MS	F	MS	F
Site (S)	1	0.01	0.25	0.42	0.07
Zone (Z)	1	40.59	120.67	633.75	4225.00**
Disturbance (D)	4	0.11	0.93	79.61	4.44
S x Z	1	0.34	8.41**	0.15	0.02
S x D	4	0.12	2.93*	17.92	2.95*
Z x D	4	0.97	3.99	96.88	5.45
S x Z x D	4	0.24	6.10***	17.78	2.92*
Residual	40	0.04		6.08	

Table 2.3. continued

		E) Mid-canopy <i>Cystophora</i> spp. (3-30m)		F) Recruits <i>Cystophora</i> spp. (18m)	
Source of variation	DF	MS	F	MS	F
Site (S)	1	7.13	37.53***	3.30	20.52***
Disturbance (D)	4	1.85	10.31*	1.96	3.50
S x D	4	0.18	0.94	0.56	3.49*
Residual	20	0.19		0.16	

		G) Ephemeral mid-canopy algae (3-30m)		H) Non-ephemeral mid-canopy algae (3-30m)	
Source of variation	DF	MS	F	MS	F
Site (S)	1	3.17	44.50***	38.40	3.32
Zone (Z)	1	5.12	132.03	1046.67	39.25
Disturbance (D)	4	7.40	58.40***	35.46	0.68
S x Z	1	0.04	0.54	26.67	2.30
S x D	4	0.13	1.78	52.53	4.54**
Z x D	4	1.10	4.25	32.05	0.54
S x Z x D	4	0.26	3.63*	59.00	5.09**
Residual	40	0.07		11.58	

		I) Turf-forming coralline algae (3-30m)	
Source of variation	DF	MS	F
Site (S)	1	3515.94	14.19***
Zone (Z)	1	74.59	0.97
Disturbance (D)	4	2765.74	20.68***
S x Z	1	76.84	0.31
S x D	4	133.76	0.54
Z x D	4	126.61	0.37
S x Z x D	4	340.05	1.37
Residual	40	247.73	

2.4.3. Understory assemblage structure and temporal trajectories

A total of 22 and 21 understory algal taxa were recorded throughout the experiment in the mid-shore at Kaikoura and Moeraki respectively. Understory assemblages in the low-shore were more diverse, with a cumulative number of 36 taxa at Kaikoura and 34 at Moeraki. The average abundance of understory taxa across the period 3-30 months differed among locations, shore heights and disturbance intensities (Site x Zone x Disturbance: $F_{4,40} = 3.15$, $P < 0.05$). In the mid-shore at both sites, the number of taxa increased rapidly following the two highest disturbance intensities and, on average, there were no significant differences among treatments (Fig. 2.7A and B). In the low-shore, both at Kaikoura and at Moeraki, diversity remained low for about 12-18 months following extreme disturbance and ED plots had a lower average number of taxa (~ 11) compared to all other treatments (~ 15; Fig. 2.7C and D). This was because several non-ephemeral algae (e.g., *Dictyota* spp., *Champia* sp., *Gelidium* spp., *Hymenena* spp., *Laurencia* sp.) were rare, while ED plots were dominated by ephemeral algae during the first 9-12 months of the experiment.

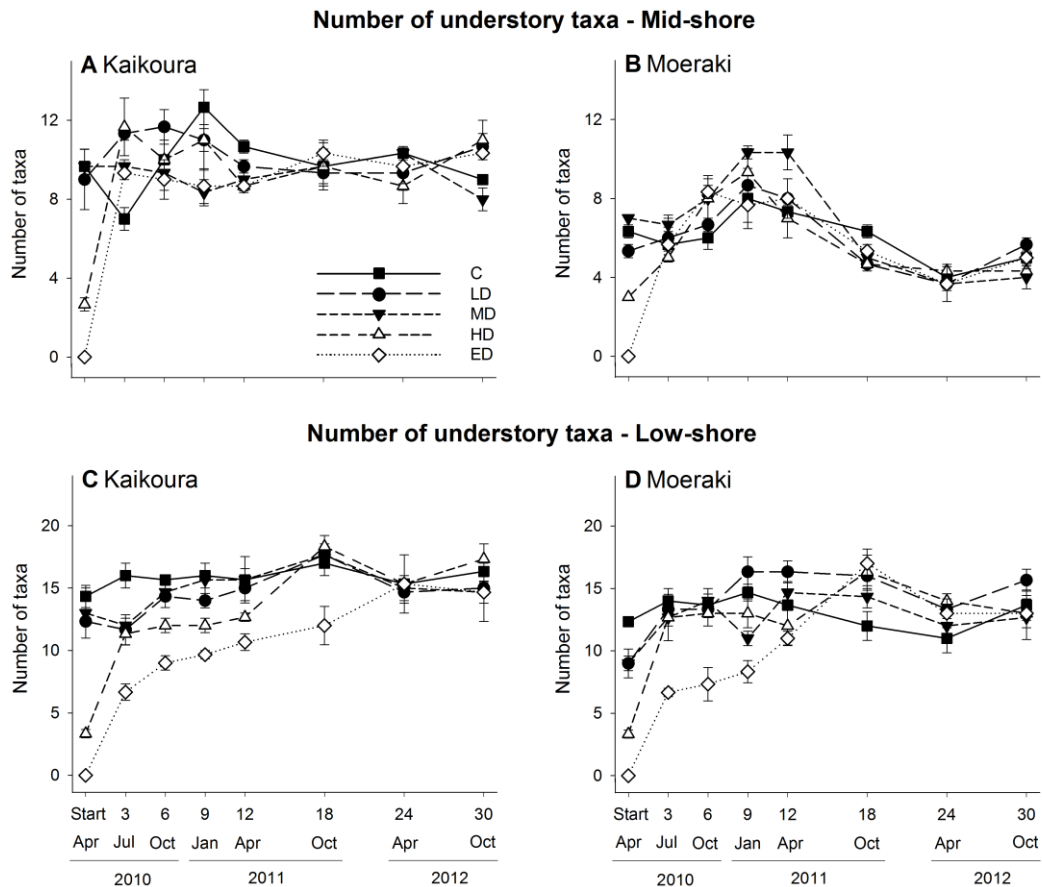


Fig. 2.7. Temporal variation in the mean number of taxa (\pm SE) following disturbance events of increasing intensity (C = control, LD = light disturbance, MD = medium disturbance, HD = high disturbance, ED = extreme disturbance) both in the mid- (A and B) and in low-shore (C and D) at the two study sites ($n = 3$).

The analysis of Euclidean distances showed that temporal changes in the structure of understory assemblages were dependent on the intensity of disturbance and differed between sites and shore heights. In the mid-shore, the temporal variability of understory assemblages did not differ in the plots affected by light, medium or high disturbance, which covered similar distances at both locations (Table 2.4A, Fig. 2.8A-D). Understory temporal variability was lower in the controls compared to MD, LD and HD plots at Moeraki, but not at Kaikoura (Table 2.4A, Fig. 2.8A-D). At both sites, HD and ED plots reduced their dissimilarity to the controls. This happened rapidly in the HD plots, which did not cover a longer distance

compared to the plots affected by lower disturbance intensities, while the temporal trajectories of ED plots were longer compared to all other treatments (Table 2.4A, Fig. 2.8A-D). The results of multivariate analyses showed that at both sites the structure of understory assemblages in the ED plots was still different from the controls after thirty months (Table 2.4B). SIMPER analysis indicated that at both sites mid-canopy plants of *H. banksii* and ephemeral algae (i.e., *Adenocystis utricularis* and *Colpomenia* spp.) were more abundant in the ED plots, while control plots had a greater cover of mid-canopy *C. torulosa* and of the red alga *Lophothamnium* sp. Articulated corallines were more abundant in the controls at Kaikoura and in the ED plots at Moeraki.

In the low-shore, both at Kaikoura and Moeraki, temporal changes in the structure of understory assemblages were larger when the entire canopy was removed compared to control and partial canopy removal plots (Table 2.4A, Fig. 2.8E-H). At both sites, HD and ED plots covered a longer distance compared to the other treatments as they moved closer to the controls (Table 2.4A, Fig. 2.8E-H). According to multivariate analyses, the structure of understory assemblages differed between ED plots and controls after 30 months at both sites (Table 2.4B). At Kaikoura, ED plots had a larger cover of mid-canopy plants of *H. banksii* and *Colpomenia* spp., while control plots had a greater abundance of the mid-canopy fucoids *C. scalaris* and *C. maschalocarpum* and of non-ephemeral red and brown algae such as *Dictyota* spp., *Champia* sp., *Gelidium* spp., *Hymenena* spp. and *Laurencia* sp. At Moeraki, the controls had a greater abundance of the mid-canopy furoid *C. retroflexa* and of *Dictyota* spp. and *Lophothamnium* sp., while in the ED plots, mid-canopy *C. scalaris* and *H. banksii*, the ephemerals *Colpomenia* spp., and various non-ephemeral algae (*Bryocladia eriocoides*, *Heterosiphonia* sp., *Halopteris* sp., *Hymenena* spp. and *zonaria* sp.) were more abundant.

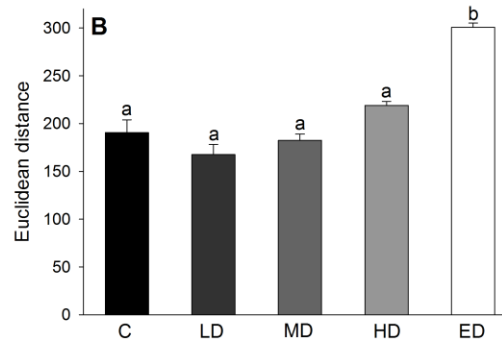
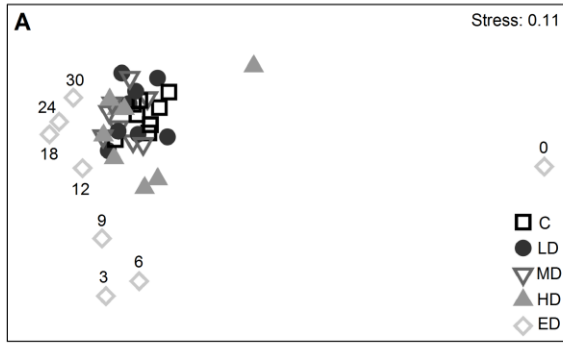
Table 2.4. A) ANOVA testing the differences between sites (Kaikoura and Moeraki), tidal zones (mid- and low-shore), and disturbance intensities (C = control, LD = light disturbance, MD = medium disturbance, HD = high disturbance, ED = extreme disturbance) in the total Euclidean distance covered by understory algal assemblages, expressing temporal variations in their composition. B) PERMANOVA testing the differences between sites, tidal zones and disturbance intensities (same as above) in the composition of understory algal assemblages at the conclusion of the experiment (30 months). *P < 0.05; **P < 0.01; ***P < 0.001.

Source of variation	A) Total Euclidean distance			B) Assemblage composition (30 m)	
	DF	MS	F	MS	Pseudo-F
Site (S)	1	193.30	0.60	10319.00	33.73***
Zone (Z)	1	1919.59	0.36	19064.00	5.84
Disturbance (D)	4	32233.47	54.37**	845.24	2.59*
S x Z	1	5328.50	16.62***	3264.60	10.67***
S x D	4	592.84	1.85	326.28	1.07
Z x D	4	1221.31	0.63	279.29	0.60
S x Z x D	4	1925.35	6.01***	464.00	1.52
Residual	40	320.51		305.93	

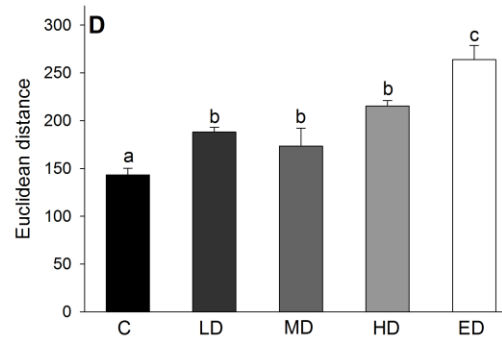
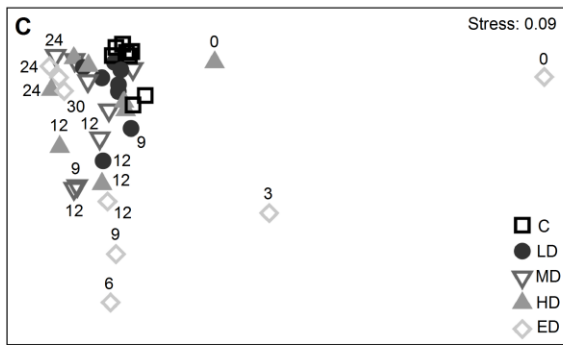
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Fig. 2.8. Left column panels: non-metric multidimensional scaling (nMDS) plots displaying the temporal trajectories of understory algal assemblages following disturbance events of increasing intensity (C = control, LD = light disturbance, MD = medium disturbance, HD = high disturbance, ED = extreme disturbance) both in the mid- (A and C) and in the low-shore (E and G) at the two study sites. The symbols represent assemblages' centroids under each disturbance intensity at each sampling date (n = 3). The numbers alongside the symbols indicate the time (months) from the start of the experiment. For the sake of simplicity, time was only indicated for the treatments which showed different temporal trajectories compared to the controls (Table 2.4B) and only when their centroids were clearly separated from the controls. Right column panels: total Euclidean distances (+SE) expressing understory assemblage temporal variability across all sampling dates following disturbance events of increasing intensities (same as above) both in the mid- (B and D) and in the low-shore (F and H) at the two study sites (n = 3). The letters above the bars indicate the ranking of the means according to the SNK tests, separately for each zone and location.

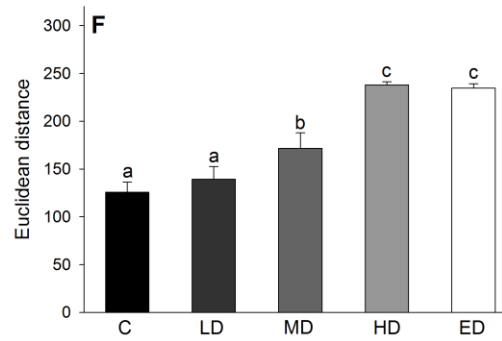
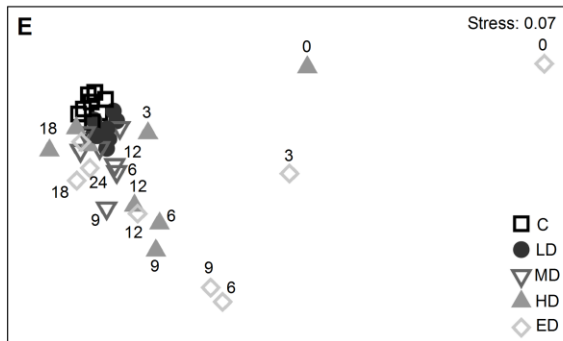
Mid-shore - Kaikoura



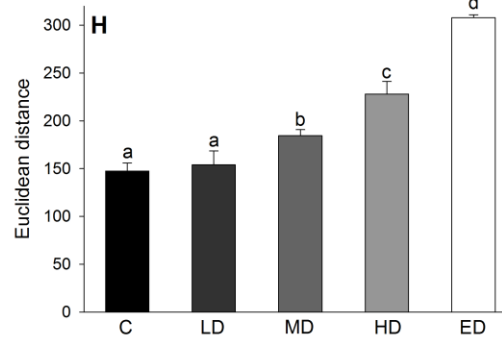
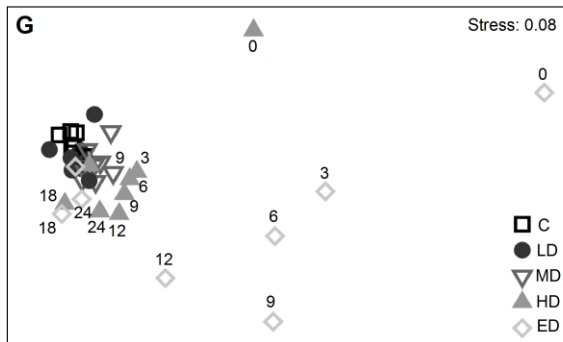
Mid-shore - Moeraki



Low-shore - Kaikoura



Low-shore - Moeraki



2.5. DISCUSSION

2.5.1. Canopy recovery

The dynamics of canopy recovery were affected by the intensity of the initial disturbance. Both for *H. banksii* and *C. torulosa*, even the lightest disturbance intensity had a long-lasting impact. The plots affected by the partial removal of the canopy were still separated from the controls after one year and did not always converge with the controls by the end of the experiment. Adult canopies are known to affect recruitment and growth of juvenile conspecific individuals (Vadas et al. 1992, Schiel & Foster 2006; see Chapter 3) and my results show that such strong suppressive effects may remain predominant also in the presence of thinned canopies. The impacts of light disturbance events were still evident at the conclusion of the experiment in the low-shore at Moeraki, where the cover of *C. torulosa* canopy increased by only 6% in thirty months. Low rates of gamete release and a narrow reproductive window (Taylor 2002, Dunmore 2006; see Chapter 6), combined with a more stressful wave climate at this southern site (Schiel 2011, Schiel & Lilley 2011) may explain the inability of *C. torulosa* to recover from the thinning of the canopy. Canopies of the fucoid *Fucus gardneri* have been shown to quickly regenerate following a range of reductions of their original cover between 20% and 80% (Speidel et al. 2001). Other fucoids, however, may not be as resilient to the reduction of their cover and different patterns of recovery may be observed as a result of the interplay between species-specific traits and local environmental conditions.

When the mid-canopy was not removed, the regeneration of the *H. banksii* and *C. torulosa* canopies which had been completely removed began within twelve months. This was because of the development of conspecific mid-canopy plants into adult individuals. In these plots the recruitment of new individuals was generally lower compared to the treatments where a higher portion of biomass was removed by disturbance. This was

probably due to a combination of suppressive effects of the newly regenerated canopy and of the algae occupying the underlying substrate. Previous studies have shown that the resilience of furoid canopies is enhanced when a few individuals survive the impact of disturbance (Speidel et al. 2001, Allison 2004), or if at least a portion of their thalli is preserved (McCook & Chapman 1992, Underwood 1998, Malm et al. 1999). Similarly, my results suggest that juvenile understory plants, which normally constitute only a small portion of the biomass of these multi-layered assemblages, may accelerate the rates of recovery when adult furoid canopies are lost and recruitment is impeded because of space pre-emption by other algae.

Following the two highest disturbance intensities, the rates of recruitment were generally higher for both species, particularly on bare, unoccupied substrates, but it took between eighteen and thirty months before the canopy started to reappear. The presence of the basal layer had a negative impact only on the formation of *C. torulosa* canopies at Moeraki, as suggested by its reduced recruitment rates. This was probably due to the characteristic of the local physical environment and of the life-history of *C. torulosa*, combined with the abundance and composition of the turfs at Moeraki. At this southern location, low-lying mats of articulated corallines are more widespread than at Kaikoura and are mainly composed by species with long, frondose branches (e.g., *Jania* spp.), which are more likely to obstruct furoid recruitment (Schiel & Lilley 2011; see Chapters 3 and 4).

Following disturbances of extreme intensity, the canopies of both *H. banksii* and *C. torulosa* were still sparse after thirty months at Moeraki, and *H. banksii* canopy only reappeared at the final sampling date at Kaikoura. Contrary to my expectations, the regeneration of the canopy was slower when extreme disturbance removed all potential competitors, probably because it was entirely reliant on the recruitment and growth of new plants. The holdfasts of the dominant furoids were cleared from the substrate in the plots allocated to the extreme disturbance treatment, while following less extreme perturbations,

the fronds regenerating from the holdfasts left on the substrate possibly contributed to a faster recovery of *H. banksii* and *C. torulosa* (McCook & Chapman 1992, Underwood 1998, Malm et al. 1999).

This detailed assessment of the mechanisms driving the responses of *H. banksii* and *C. torulosa* to disturbance is particularly relevant since there is no functional equivalent for these two species in this system. Despite the presence of four other furoids, the loss of *H. banksii* and *C. torulosa* was not compensated by the formation of alternative canopies, as documented in other intertidal systems (e.g., replacement of *Ascophyllum nodosum* by *Fucus* spp.; Jenkins et al. 1999a, 2004, Bertness et al. 2002). These results confirm the absence of functional replacement for the dominant furoids at these locations (Schiel 2006) and shed light on the mechanisms underlying their ability to recover from perturbations.

2.5.2. Responses of understory assemblages

Responses to the experimental manipulations varied among different components of the understory. Conspecific individuals of the dominant furoids responded positively to disturbance, but other minor mid-canopy furoids were less abundant in disturbed plots. In understory assemblages in the mid-shore, *C. torulosa* was more abundant under intact or thinned canopies than in disturbed plots. Similarly, in the low-shore, control plots had a higher cover of *C. retroflexa* and *C. scalaris* compared to the other treatments. This suggests that only intact assemblages may guarantee the ideal conditions for the development of these late successional, perennial understory macroalgae. Although the cover of understory plants of *C. torulosa*, *C. retroflexa* and *C. scalaris* was generally low, declining abundances of these species may have severe implications for assemblage functioning. *C. torulosa*, for example, has extremely high rates of productivity per biomass and its loss can cause a fall in production in *H. banksii* dominated assemblages (Tait 2010, Tait & Schiel 2011b). Low-shore

assemblages, on the other hand, have been shown to be able to maintain elevated rates of productivity even when deprived of *C. torulosa* canopies, and the congeneric *C. retroflexa* and *C. scalaris* are likely to be the primary drivers of assemblage productivity in its absence (Tait 2010).

Unlike these minor understory fucoids, the abundance of ephemeral algae increased dramatically when the original multi-layered structure of the assemblages was affected by disturbance. However, these blooms were of short duration. Opportunistic, fast-growing species can affect the development of habitat-forming macroalgae (Eriksson et al. 2002, Worm and Lotze 2006) and also cause a significant rise in productivity (Tait 2010, Crowe et al. 2013). Given their fugacious nature, however, these taxa seem to have no impact on the patterns of recruitment of the dominant fucoids in this system (see Chapter 4) and their contribution to assemblage productivity is surely short-lived.

In the basal layer, articulated corallines were generally resistant to the loss of the overlying algal layers, but scarcely resilient when removed themselves. Reduced abundance of coralline turfs may facilitate the recruitment of the dominant fucoids. However, long-term impacts on articulated corallines may also have flow-on effects on assemblage functioning, as coralline turfs can provide an important contribution to assemblage productivity under certain sedimentation regimes and light conditions (see Chapter 3).

Multivariate analyses showed that variations in the cover of the canopy were not always associated with changes in the structure of understory assemblages. In the mid-shore, the temporal variability in the structure of understory assemblages did not differ in the plots affected by light, medium and high disturbance. This suggests that understory assemblages were generally resistant to the partial or total removal of the canopy and also quick to recover from the loss of the entire mid-canopy. Only the assemblages recovering after being completely destroyed had different patterns of temporal variability and were still separated

from the controls after thirty months. I expected assemblage temporal variability and dissimilarity to the controls to increase in linear fashion with the intensity of disturbance at high tidal elevations, under stressful physical conditions. However, as Viejo (2009) has shown for rocky intertidal assemblages along the European Atlantic shores, these results indicate that environmental stress may act as a filter in the mid-shore, selecting a restricted number of highly tolerant species able to recover quickly from disturbance, as long as its impact is not extreme.

In the low-shore, the composition of understory assemblages remained stable following the thinning of the canopy, but assemblage temporal variability increased progressively in response to higher disturbance intensities. This suggests that responses to disturbance may be more complex in more diverse assemblages under more benign conditions (Viejo 2009). Nonetheless, all low-shore plots, aside from those affected by extreme disturbance, converged with the controls by end of the experiment at both locations, despite the poor canopy recovery rates at Moeraki. This indicates that patterns of understory resistance and resilience may be to some extent unrelated to the abundance of the canopy.

2.5.3. Conclusions

The results of this study provide numerous insights into the responses of complex macroalgal assemblages to perturbations of increasing severity and highlight potential implications for the structure and functioning of these intertidal systems. Patterns of recovery of furoid canopies differed between the species investigated and varied between study sites. This shows that resilience is an inherently spatial and species-specific quality which can vary across taxa and spatial scales as a result of the influence of the life history traits of the disturbed organisms and of the local physical environment (Chapman & Underwood 1998, Dudgeon & Petraitis 2001, Conway-Cranos 2012).

Increased cover of understory species is often an important compensatory mechanism promoting community stability following the loss of large habitat-formers, especially in species-rich systems (Allison 2004, Bulleri et al. 2012a, Valdivia et al. 2012). In this study, however, the dominant fucoids and ephemeral algae were the only taxa to increase their abundance in response to disturbance, regardless of the diversity of species at different sites and shore heights. It is, therefore, evident that functional redundancy is limited in this system (Schiel 2006, Tait 2010, Tait & Schiel 2011a,b) and that compensatory dynamics following the loss of fucoid canopies are entirely reliant on the patterns of recruitment and growth of these dominant habitat formers.

Understory taxa were generally resistant to the loss of the canopy and there was no evidence of dramatic declines in the cover and diversity of understory taxa which were observed in previous studies (Lilley & Schiel 2006, Schiel & Lilley 2007). Such discrepancies may be explained by differences in the size and timing of the experimental manipulations. The study of Lilley & Schiel (2006), for example, involved the clearance of *H. banksii* canopies from 9 m² plots, areas much larger than the experimental units in my study. In a further study, Schiel & Lilley (2007) removed different proportions of *H. banksii* canopies from 0.25 m² plots, areas the same size as the experimental units in my study, and observed a decline in richness and cover of understory taxa. Schiel & Lilley's (2007) experiment, however, was started in summer, while my study was set up in autumn. Nonetheless, given the delayed canopy recovery, understory assemblages in my study were probably exposed to stress levels analogous to those in the experiment of Schiel & Lilley (2007) during the warmest months of the year. Such discrepancies serve as reminder that discerning generalities in the impacts of disturbance is a difficult task because of the multifaceted nature of disturbance processes and of the responses of the impacted systems (White & Jentsch 2001).

CHAPTER 3

Effects of algal turfs and sediment accumulation on replenishment and primary productivity of furoid assemblages

The material contained in this chapter has been accepted for publication in Marine Ecology Progress Series, and at the time of the submission of the thesis was in press as: Alestra T, Tait LW, Schiel DR. Effects of algal turfs and sediment accumulation on replenishment and primary productivity of furoid assemblages. doi: 10.3354/meps10932 (see Appendix B).

3.1. ABSTRACT

As a result of anthropogenic habitat degradation worldwide, rocky intertidal and shallow subtidal systems are increasingly dominated by low-lying, turf-forming species, which proliferate at the expense of complex biogenic habitats such as kelp and furoid canopies. This results in dramatic alterations to the structure of the associated communities and large reductions in primary productivity. The persistence of turf-dominated systems has been attributed to the impacts of the turfs on the recovery of algal canopies and also to the different susceptibility of canopy- and turf-forming algae to altered physical conditions, in particular increased sedimentation. Here I tested the impacts of turfing geniculate coralline algae and sediment on furoid recovery dynamics and their influence on assemblage net primary productivity (NPP). The recruitment of the habitat-forming furoid *Hormosira banksii* on bare substrates was significantly higher than in treatments in which sediments, coralline turfs or turf mimics covered the substrate, indicating that sediment deposition and space pre-emption by algal turfs can synergistically affect the development of furoid beds. NPP of coralline turfs was much less than that of furoid-coralline assemblages, which included a *H. banksii* canopy, and was reduced further by sediment accumulation. When devoid of sediment, however, coralline algae contributed to the enhancement of furoid-coralline assemblage NPP, because of synergistic interactions among the components of the multi-layered assemblage in optimizing light use. These findings amplify extensive research addressing the global loss of macroalgal canopies and highlight key processes involving sediment accumulation in the benthic environment and effects on the replenishment and productivity of furoid stands.

3.2. INTRODUCTION

Nearshore ecosystems are increasingly under pressure from anthropogenic activities, many of which have the potential to cause widespread changes to ecosystem structure and functioning (Halpern et al. 2008, Crain et al. 2009, Schiel 2009). The fragmentation and loss of structurally complex habitats, shaped by canopy-forming macroalgae (kelps and fucoids), for example, have been reported worldwide (Steneck et al. 2002, Airoidi et al. 2008, Connell et al. 2008, Raybaud et al. 2013). In degraded environments, the recovery of algal canopies is usually inhibited by the rapid proliferation of low-lying, turf-forming algae, resulting in dramatic shifts to simplified systems with long-term impacts on community structure (Kennelly 1987, Connell et al. 2008, Bellgrove et al. 2010) and functioning (Tait & Schiel 2011a).

Turf-forming algae are a widespread and taxonomically diverse group of species with variable morphologies, ranging from filamentous to calcareous-articulated forms (Airoidi 2001, Connell et al. 2014). Independent of their composition, algal turfs are abundant in disturbed areas because of their ability to tolerate stressful conditions such as elevated nutrient and sediment loads (Airoidi & Virgilio 1998, Gorgula & Connell 2004). Sediment, in particular, is considered a structural component of algal turfs because it is often trapped in great abundance within their densely packed, mat-like structure (Airoidi & Virgilio 1998, Airoidi 2003). Differences among taxa in their ability to tolerate sediment may explain the concomitant increase in spatial dominance of algal turfs and regression of canopy stands (Airoidi et al. 2008, Connell et al. 2008). Increased sediment loads can have strong impacts on the early life stages of kelps and fucoids (Vadas et al. 1992, Schiel & Foster 2006, Schiel et al. 2006, Irving et al. 2009) and many studies have suggested that turfs and sediments may provide positive feedbacks to each other, thereby contributing to preventing the recovery of algal canopies (Airoidi & Virgilio 1998, Connell 2005, Bellwood & Fulton 2008).

Such processes may be particularly relevant to New Zealand's coastlines, which are affected by exceptionally high sediment loads originating from geological and climatic processes as well as human land-uses (Griffiths & Glasby 1985, Goff 1997). Algal assemblages in mid-intertidal regions in New Zealand are occupied by canopies of the fucoid macroalga *Hormosira banksii*, while algal turfs composed of geniculate coralline algae are usually the main benthic space occupiers (Schiel 2004, 2006). *H. banksii* is a key foundation species and research in New Zealand and Australia has described dramatic structural changes following its loss, with a rapid monopolization of the substrate by extensive mats of articulated coralline algae (Lilley & Schiel 2006, Bellgrove et al. 2010, Schiel & Lilley 2011). These studies highlighted negative impacts of coralline turfs on the recruitment of *H. banksii*, showing how increasing abundance and thickness of the turfs can contribute to the decline of this fucoid. None of them, however, tested the influence of sediment accumulation within the turfs on *H. banksii*. Furthermore, little is known about the consequences of sediment build-up within coralline turfs on assemblage productivity. The primary productivity of coralline algae is generally considered negligible compared to canopy-forming species (Littler & Arnold 1982, Tait & Schiel 2011b). As a consequence, the loss of structural complexity associated with the advent of coralline turfs is likely to result in a substantial and long-lasting loss of ecosystem function (Tait & Schiel 2011a,b), especially under elevated sediment loads.

Here I examined the influence of sediment on the interactions between *H. banksii* and turf-forming coralline algae and their implications for the functioning of intertidal autotrophic assemblages. I first tested how coralline turfs can affect the recruitment of *H. banksii* by altering the physical properties of the benthic environment and the dynamics of sediment accumulation. Algal turfs are known to competitively exclude other algal species through the monopolization of primary substrate and the creation of a complex biogenic surface

unsuitable for colonization (Britton-Simmons 2006, Daleo et al. 2006). I expected sediments to compound the impact of coralline turfs on the recruitment of *H. banksii*, both by accumulating within the turfs and through the deposition on unoccupied substrates. In addition, using *in situ* and laboratory photorespirometry techniques (Tait & Schiel 2010), I evaluated the contribution of coralline algae to assemblage net primary productivity (NPP) and the impacts of sediment accumulation within coralline turfs. I expected coralline turf NPP to be significantly lower than that of experimental assemblages including *H. banksii* canopy, especially in the presence of sediment.

3.3. MATERIALS AND METHODS

Field experiments were done at Wairepo Reef, Kaikoura (42°25'S, 173°42'E), a large intertidal platform where fucoid species and turfs of geniculate coralline algae (predominantly *Corallina officinalis*) coexist in high abundance (see Lilley & Schiel 2006 for full site description), providing the opportunity to investigate the nature and strength of their interactions. Because of coastal erosion and riverine inputs, the waters surrounding Kaikoura are characterized by elevated sediment loads, with large quantities of sediment (mainly fine sand; grain size: 100-250 µm) accumulating in the benthic environment in many places, especially within the turfs (Schiel et al. 2006, Hurley 2009). Previous studies in Kaikoura highlighted a negative relationship between the recruitment of fucoid macroalgae, including *H. banksii*, and the abundance of turf-forming species and deposited sediment in the benthic environment (Schiel et al. 2006, Hurley 2009).

3.3.1. Impacts of coralline turfs and sediment on *H. banksii* recruitment

To examine the mechanisms regulating the impacts of algal turfs on canopy recovery, I tested the influence of three distinctive traits of coralline turfs on the recruitment of *H. banksii*: 1)

the rapid pre-emption of primary substrates; 2) the creation of morphologically complex habitats; and 3) the retention of sediment. To tease out the impact of each of these factors on *H. banksii*, I monitored its recruitment over a period of twelve months in five experimental habitat types: 1) coralline turf; 2) bare rock; 3) artificial turf; 4) artificial turf control; 5) fucoid-coralline assemblage. Along a one kilometre stretch of shore twelve 25 x 25 cm replicate plots of each habitat were set up in the mid-intertidal zone (0.5 to 1 m above the lowest astronomical tide level). Coralline turf plots were occupied by articulated corallines only (with a mean percentage cover ~ 90 %), while all other algal species (which were in low abundances) were removed. Bare rock plots were obtained through the complete clearing of all algal species. The artificial turf plots were patches of synthetic grass glued to fibrolite plates and were fitted flush with the substrate using a hammer and chisel to create a depression. This material is considered to be a reasonably good mimic for coralline turfs, as it is characterised by an analogous dense mat-like structure (Kelaher 2002). The artificial fronds were 10 mm long, similar to the branches of coralline algae at my study site, and produced a three-dimensional matrix that was capable of trapping sediment. I compared *H. banksii* recruitment rates between coralline turf and bare rock plots to assess the impact of space pre-emption by the turfs, and between coralline turfs and artificial mimics to evaluate the importance of the physical complexity of the corallines, separating it from the influence of alternative mechanisms such as the release of allelopathic compounds (Jeong et al. 2000, Kim MJ et al. 2004), or the breakage of the fronds. In addition, artificial turf control plates with the fronds removed were used to ensure that the effects produced by such artificial habitats were related to their morphological complexity. Finally, I also included fucoid-coralline assemblage plots consisting of a basal layer of coralline turf (mean percentage cover ~ 90 %) and a canopy of *H. banksii* (mean percentage cover ~ 85 %), because at this location areas covered exclusively by corallines are alternated with zones where *H. banksii* canopies

and turfs coexist. These fucoid-coralline assemblages were used to tease out the influence of coralline turfs from that of the overlying canopy.

Before the start of the experiment, newly recruited plants of *H. banksii* were absent from all habitats and all experimental units were cleared of sediment using a hose connected to a bilge pump, so that the initial conditions were the same for all treatments. To evaluate the impact of sediment accumulation in the benthic environment, half of the replicates of each habitat were assigned to periodic sediment removal throughout the duration of the experiment (twelve months). Every two weeks the sediment was gently washed from the plots, ensuring that coralline algae and *H. banksii* recruiting plants were not affected. Similar sediment manipulation procedures were previously used at this location without any impact on small fucoid recruits (Hurley 2009).

Rates of sediment deposition were estimated before the start of the experiment by measuring the dry weight of sediment accumulating within twelve additional 25 x 25 cm coralline turf plots. These plots were first simultaneously cleared of sediment, and sediment samples were collected from three of them to establish a baseline level. Successively, all plots were again cleared of sediment, four at a time at intervals of five days (fifteen days in total) and sediment was collected to estimate its rate of accumulation. The rate of sediment accumulation per plot was around 9 g d⁻¹ (equivalent to 144 g m⁻² d⁻¹) and after fifteen days the amount of sediment trapped within the turfs was back to the original levels of around 150 g per plot (equivalent to 2400 g m⁻² d⁻¹). These estimates are in line with the rates of sediment deposition previously recorded in Kaikoura (Schiel et al. 2006, Hurley 2009).

The percentage cover of *H. banksii* recruits colonizing the five experimental habitats under ambient and reduced sedimentation was measured after three, six, nine and twelve months from the start of the experiment. In the coralline turf and fucoid-coralline assemblage plots there were small patches of unoccupied substrate. I recorded only the percentage cover

of the recruits growing within the turfs in these plots. Because of their slow growth rates, the recruits were always clearly distinguishable from the adults. In contrast to the frondose, canopy-forming structure of the adults (with thalli 15-20 cm long), the recruits presented short, erect, tubular thalli (< 2 cm long) and their percentage cover accurately reflected their density. At the end of the experiment, however, I also counted the number of the recruits within each plot and I measured the lengths of ten of them randomly selected in each plot.

3.3.2. Net primary productivity

To test the impact of coralline algae and sediment on assemblage primary productivity, I measured changes in dissolved oxygen as a proxy for net primary productivity (NPP) for two habitat types: fucoid-coralline assemblages (i.e., coralline turf + *H. banksii* canopy) and coralline turf alone, each with two levels of sediment in the turf (present/removed). NPP of both fucoid-coralline assemblages and coralline turfs was determined by incubating algae in sealed photorespirometry incubation chambers filled with seawater. The chambers are composed by a clear Perspex cylinder closed on top by a lid and can be fitted around macroalgal assemblages attached to the reef surface, or used in the laboratory to incubate algae removed from the shore (Tait & Schiel 2010 for details). For both habitat types coralline algae occupied ~ 90% of the substrate enclosed within the chambers (276 cm²), while *H. banksii* canopy, when present, had a percentage cover around 85%. To evaluate the interactions between coralline turf and the *H. banksii* canopy, other sub-canopy species, which can add substantially to the NPP of intact assemblages (Tait & Schiel 2011b), were removed from the experimental plots by carefully picking them off by hand. These included the fucoids *Cystophora torulosa* and *Carpophyllum maschalocarpum* and several ephemeral species.

NPP of both habitat types was estimated through *in situ* and laboratory incubations. In the field, the chambers were fixed around existing macroalgal assemblages, randomly assigned to one of the four combinations of experimental treatments (fucoid-coralline assemblage +sediment; fucoid-coralline assemblage –sediment; coralline turf +sediment; coralline turf –sediment), each replicated four times. The incubations were completed under full sunlight ($1500\text{-}2000 \mu\text{mol m}^{-2} \text{s}^{-1}$) during the summer months (from December 2010 to February 2011). Irradiance was measured with a LiCor meter (LI-192 quantum sensor). Each replicate in the field was incubated on two different days at approximately the same time (between 10:00 and 13:00) for no longer than 40 minutes. This ensured that super-saturation of oxygen did not occur and that essential nutrients were not depleted (Tait & Schiel 2010). In the replicates allocated to sediment removal coralline algae were cleared of sediment immediately before the incubations using the procedures outlined previously.

Field incubations were performed during periods of partial emersion between consecutive high tides to assess the influence of the experimental factors on NPP during periods of similar light conditions. However, to account for potential variability in the light conditions, the effects of different light levels on the experimental habitats were tested under controlled laboratory conditions. Representative assemblages containing adult individuals of *H. banksii* and patches of coralline algae were removed from the reef surface and used to recreate coralline and fucoid-coralline assemblages for laboratory incubations. The two habitat types were incubated at five light intensities (0, 150, 800, 1500, $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$), both in the presence and absence of sediment within the corallines ($n = 6$ for each combination of habitat and sediment manipulation), in order to generate their light response curves (*P-E* curves) and determine key photosynthetic parameters (Tait & Schiel 2011b). Dark respiration was measured by covering the chambers to omit light.

Both in the field and in the laboratory water samples were extracted from the chambers using a syringe and oxygen concentration was measured using a Hach LDO meter (Model HQ40d). NPP was estimated as the increase in oxygen concentration after 20 and 40 minutes of incubation (Tait & Schiel 2010). Changes in dissolved oxygen over time were converted to changes in carbon uptake using a P:Q (photosynthetic quotient) ratio of 1:1 (Kirk 1994) and standardized to carbon uptake per m² of reef surface (g C m⁻² h⁻¹). Before each incubation, all visible invertebrates were removed from the corallines to limit the influence of heterotrophic respiration. Following laboratory incubations, the dry weight of algae was recorded and used to standardize NPP also by dry biomass of algal material (mg C gDW⁻¹ h⁻¹), thereby accounting for any differences in the amount of biomass between fucoid-coralline assemblages and coralline algae alone. In the laboratory I also recorded the dry weight of the sediment contained within coralline turfs and fucoid-coralline assemblages assigned to the + sediment treatment and, from six of these sediment samples, the dry biomass of the invertebrates that could not be removed before the incubations.

3.3.3. Statistical analyses

The effects of coralline turfs and sediment deposition on percentage cover, number and length of *H. banksii* recruits recorded after twelve months were analysed with a two-way ANOVA with the fixed factors: Habitat (5 levels: coralline turf, artificial turf, artificial turf control, bare rock, fucoid-coralline assemblage) and Sediment (2 levels: present and removed). Only the final percentage cover data, recorded after twelve months, were formally analysed as they were representative of the temporal trends observed under each combination of treatments throughout the experiment. This avoided statistical analyses including repeated measures, which present complex assumptions and provide a less straightforward interpretation of the results (Murtaugh 2007).

Data of NPP recorded in the field were analysed with a two-way ANOVA with the fixed factors: Habitat (2 levels: furoid-coralline assemblage and coralline turf) and Sediment (2 levels: present and removed). Data from laboratory incubations, standardized both per-area and per-biomass, were used to generate photosynthesis-irradiance ($P-E$) curves, separately for each replicate incubation. Several photosynthetic parameters were calculated from the $P-E$ curves (Walsby 1997), including P_m , the maximum photosynthetic rate at light saturating irradiances; R , the rate of respiratory oxygen production, α , the gradient observed at light-limiting irradiances and β , the negative gradient due to photoinhibition. When saturation in photosynthesis did not occur, the value of P_m was designated as the highest level of irradiance tested (i.e., $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$). For each replicate incubation, the light-use efficiency at light-limiting irradiances (α) was calculated as the slope of a linear regression between 0 and $150 \mu\text{mol m}^{-2} \text{s}^{-1}$. Similarly, β (photoinhibition) was calculated as the slope of a linear regression between the two irradiances where photoinhibition occurred. When photoinhibition did not occur, the direction of change between 1500 and $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$ was calculated to give an indication of non-saturation at high light levels. A further parameter, E_c , the irradiance at compensation (i.e., where net photosynthesis = 0) was also calculated using the linear regression of light-use efficiency (α) to determine the irradiance at which $y = 0$. The influence of habitat type and sediment manipulation on these photosynthetic parameters was examined with a two-way ANOVA analogous to the one used to analyse *in situ* NPP data.

Before all the analyses, variance heterogeneity was tested with the Cochran's C -tests and removed with log transformation when required. Student-Newman-Keuls (SNK) tests were performed for *a posteriori* comparisons of the means (Underwood 1997).

3.4. RESULTS

3.4.1. Impacts of coralline turfs and sediment on *H. banksii* recruitment

The one-year field experiment showed a separation of treatments through time, beginning at around three months, and by the end of the experiment there was a clear interaction between habitat type and sediment ($F_{4,50} = 6.34$, $P < 0.001$; Fig. 3.1A and C). SNK tests showed that, at the end of the experiment, the influence of sediment removal on the abundance of the recruits varied among the experimental habitats. In the fucoid-coralline assemblages the combination of a fucoid canopy and coralline algae suppressed the cover of *H. banksii* recruits to near-zero, both in the presence (Fig. 3.1A) and absence of sediment (Fig. 3.1C). Under ambient sedimentation, the percentage cover of *H. banksii* recruits was similar in all other habitats, ranging between 28-33% at the end of the experiment (Fig. 3.1A). When sediment was removed, the recruitment of *H. banksii* increased significantly only in bare rock and artificial turf control plots compared to the cover levels observed under ambient sedimentation (Fig. 3.1C). With reduced sediment loads the final cover of the recruits in bare rock and artificial turf control plots was around 40-50% and was significantly higher compared to all other habitats (Fig. 3.1C). The percentage cover of the recruits, on the contrary, was reduced to 20% and 24% in coralline turf and artificial turf plots allocated to sediment removal, respectively, but SNK tests did not highlight these differences as significant (Fig. 3.1C).

The number of recruits per plot at the end of the experiment was also a product of an interaction between habitat and sediment ($F_{4,50} = 6.53$, $P < 0.001$, Fig. 3.1B and D). The few *H. banksii* recruits present under the canopy in both sediment treatments reflected their poor cover (Fig. 3.1B and D). In all other habitats, the erect growth habit of the recruits allowed them to reach extremely high densities (between 225 and 550 individuals per plot). Under ambient sedimentation, the density of the recruits did not differ between coralline turf,

artificial turf, bare rock and artificial turf control plots. With reduced sedimentation, recruit number increased in bare rock and artificial turf control plots compared to the densities recorded under ambient sediment loads, and these two habitats had significantly more recruits compared to all others (Fig. 3.1D). Following sediment removal there was also a reduction in the number of recruits in coralline turf and artificial turf plots, which was not statistically significant according to SNK tests (Fig. 3.1D). Differences in recruit cover did not result from variable growth rates among treatments, as the length of the plants after twelve months (mean \pm SE: 13.48 \pm 0.14 mm) did not differ among habitats ($F_{4,50} = 1.49$, $P = 0.22$) or sediment levels ($F_{1,50} = 0.22$, $P = 0.64$).

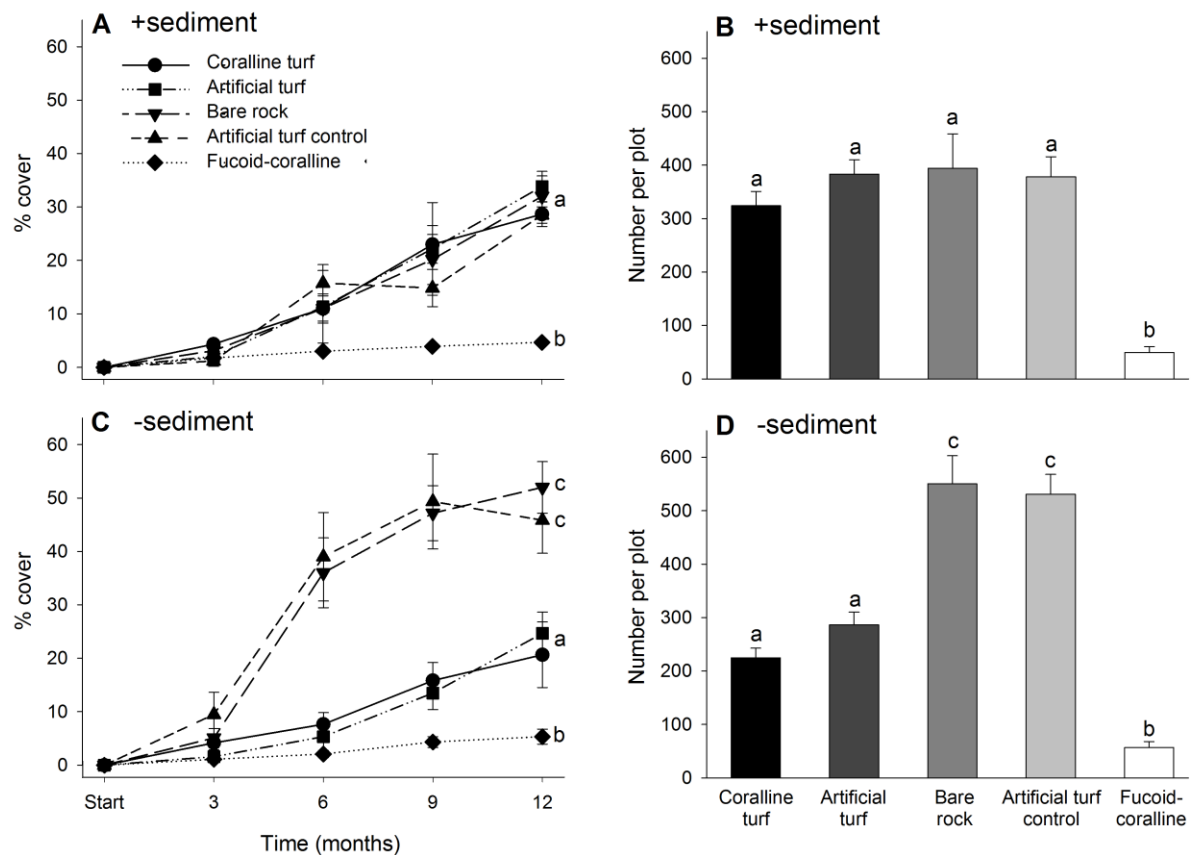


Fig. 3.1. Temporal variation in the mean percentage cover (\pm SE) of *H. banksii* recruits in coralline turf, artificial turf, artificial turf control, bare rock and fucoid-coralline assemblage plots, under ambient (A) and reduced (C) levels of sediment accumulation ($n = 6$), and mean number of *H. banksii* recruits per plot recorded after twelve months under the same combinations of habitat and sediment manipulation (B and D, $n = 6$). The letters indicate the ranking of the means according to the SNK tests.

3.4.2. Net primary productivity

There was a significant interaction between habitat and sediment in NPP dynamics *in situ* ($F_{1,12} = 5.14$, $P < 0.05$; Fig. 3.2). Furoid-coralline assemblages, both in the presence and absence of sediment, had the greatest NPP at around $1.3 \text{ g C m}^{-2} \text{ h}^{-1}$. Coralline turfs showed reduced NPP compared to furoid-coralline assemblages, with plots containing sediment having less than half the productivity (at around $0.4 \text{ g C m}^{-2} \text{ h}^{-1}$) of coralline plots without sediment (Fig. 3.2).

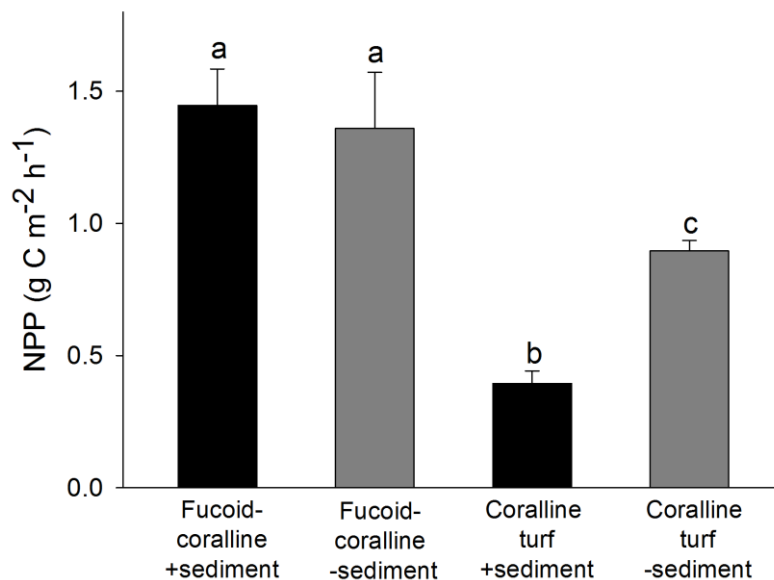


Fig. 3.2. Net primary productivity (NPP) standardized by area of reef (+SE), of furoid-coralline assemblages and coralline turfs incubated in the field under full sunlight ($1500\text{-}2000 \mu\text{mol m}^{-2} \text{ s}^{-1}$) in the presence and absence of sediment ($n = 4$). The letters above the bars indicate the ranking of the means according to the SNK tests.

Consistent with *in situ* results, data from laboratory incubations, standardized on a per-area basis, showed that furoid-coralline assemblages had higher maximum photosynthetic rates (P_m) than coralline turfs. P_m of both habitats (i.e., with and without a *H. banksii* canopy) was reduced by sediment load within the corallines (Table 3.1, Fig. 3.3A and B). In the presence of sediment, photoinhibition (β) was more severe and started at lower irradiance

(about $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$) in the coralline turfs compared to furoid-coralline assemblages ($> 1500 \mu\text{mol m}^{-2} \text{s}^{-1}$; Table 3.1, Fig. 3.3A and B). Furoid-coralline assemblages also required higher light intensities to reach a net carbon gain (i.e., compensating irradiance E_c) and were characterized by higher levels of respiration (R) compared to coralline turfs (Table 3.1, Fig. 3.3A and B). For both coralline and furoid-coralline assemblages, respiration rates did not differ in the presence and absence of sediment, suggesting that the influence of the heterotrophic organisms associated with the sediment was negligible. The dry biomass of invertebrates isolated from the sediment samples ($4.75 \pm 0.34 \text{ g}$, $n = 6$) was, in fact, very low compared to the amount of sediment contained within the turfs ($142.49 \pm 4.10 \text{ g}$, $n = 12$) and the biomass of algal material used in the incubations ($91.05 \pm 2.82 \text{ g}$ and $145.12 \pm 7.67 \text{ g}$ for coralline and furoid-coralline assemblages, respectively, $n = 12$).

Laboratory experiments also allowed comparisons between treatment effects assessed on a per-area and per-biomass basis. The response curves under the two standardisations were virtually identical both for furoid-coralline assemblages (Fig. 3.3A vs. 3.3C) and coralline turfs (Fig. 3.3B vs. 3.3D). The analyses confirmed that differences in NPP between habitats were not driven by variations in biomass alone. Even on a per-biomass basis, furoid-coralline assemblages had higher maximum photosynthetic rates (P_m) than coralline turfs ($F_{1,20} = 6.59$, $P < 0.05$; Fig. 3.3C and D). Photoinhibition (β) was stronger in the coralline turfs ($F_{1,20} = 6.66$, $P < 0.05$; Fig. 3.3C and D), but the corallines reached the compensation point (E_c) at lower irradiances ($F_{1,20} = 32.40$, $P < 0.001$; Fig. 3.3C and D). The only exceptions were respiration (R) and light-use efficiency (α). With the data standardized by dry weight of algae the respiration rates of the two habitats did not differ ($F_{1,20} = 0.09$, $P = 0.77$; Fig. 3.3C and D), indicating that the differences observed on a per-area basis were affected by the higher biomass of furoid-coralline assemblages compared to coralline turfs. Per-biomass results also

showed differences among habitats in the values of α ($F_{1,20} = 8.16$, $P < 0.01$; Fig. 3.3C and D), with coralline turfs showing higher light-use efficiency at low irradiance.

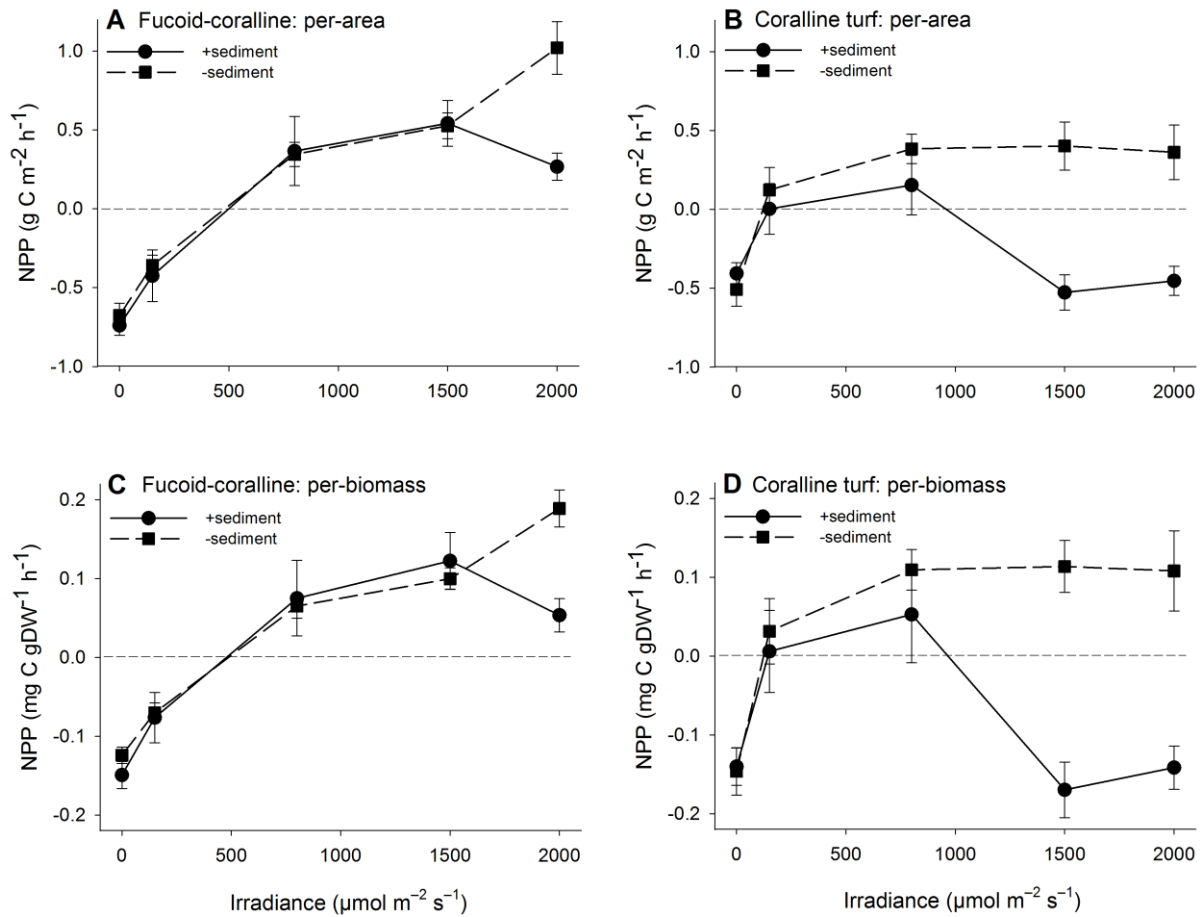


Fig. 3.3. Net primary productivity (NPP) variations ($\pm\text{SE}$), across irradiance levels in fucoid-coralline assemblages (A and C) and coralline turfs (B and D) incubated in the laboratory in the presence and absence of sediment ($n = 6$). Data in panels A and B are standardized by area of reef, while data in panels C and D are standardized by dry weight of algae.

Table 3.1. (A) Photosynthetic parameters (mean \pm SE) estimated during laboratory incubations from data standardized on a per-area basis, separately for each combination of the experimental factors. (B) ANOVA testing the influence of habitat type (fucoid-coralline assemblage and coralline turf) and sediment manipulation (sediment present and removed) on the photosynthetic parameters. P_m : maximum photosynthetic rate; R : respiration; α : slope at light-limiting irradiance; β : slope at saturating irradiance; E_c : irradiance at compensation. *P < 0.05; **P < 0.01; ***P < 0.001.

A) Photosynthetic parameters											
Experimental treatments	P_m (g C m ⁻² h ⁻¹)		R (g C m ⁻² h ⁻¹)		α (g C m ⁻² h ⁻¹)		β (g C m ⁻² h ⁻¹)		E_c (μ mol m ⁻² s ⁻¹)		
Fucoid-coralline +sediment	0.54 \pm 0.15		-0.74 \pm 0.06		0.0021 \pm 0.0007		-0.0005 \pm 0.0004		499.10 \pm 107.28		
Fucoid-coralline -sediment	1.02 \pm 0.17		-0.68 \pm 0.08		0.0021 \pm 0.0007		0.0010 \pm 0.0002		480.07 \pm 56.21		
Coralline turf +sediment	0.15 \pm 0.19		-0.41 \pm 0.07		0.0027 \pm 0.0006		-0.0010 \pm 0.0001		148.88 \pm 27.52		
Coralline turf -sediment	0.40 \pm 0.15		-0.51 \pm 0.11		0.0042 \pm 0.0013		-0.0001 \pm 0.0003		120.79 \pm 23.69		
B) ANOVA											
Source of variation	DF	MS	F	MS	F	MS	F	MS	F	MS	F
Habitat (H)	1	1.52	9.38**	0.38	9.67**	1.11E-05	2.41	3.33E-06	6.87*	9.71	31.57***
Sediment (S)	1	0.79	4.88*	0.01	0.06	3.33E-06	0.72	8.86E-06	18.28**	0.01	0.02
H x S	1	0.08	0.49	0.04	1.04	3.18E-06	0.69	6.24E-07	1.29	0.17	0.55
Residual	20	0.16		0.04		4.60E-06		4.85E-07		0.31	

3.5. DISCUSSION

This study showed an important interplay between coralline turfs and sediment in influencing replenishment and productivity of macroalgal stands. Sediment deposition on unoccupied substrates combined with space pre-emption by low-lying algal turfs to suppress the recruitment of the dominant furoid, and its accumulation within the turfs greatly altered primary production dynamics. These results contribute to a better mechanistic understanding of the implications of processes affecting rocky shores worldwide such as the spread of benthic turfs and increased sediment loads in the coastal zone.

The suppressive effects of algal canopies on intra- and interspecific recruitment of kelps and fucoids have been widely documented (Vadas et al. 1992, Schiel & Foster 2006), but those relating to the conditions in the benthic environment less so. In my study, sediment accumulation on bare substrates reduced the recruitment of the dominant furoid to the same levels as in the presence of the turfs (both coralline and artificial). Sediment is known to override the influence of habitat heterogeneity (Balata et al. 2007), eliminating biotic differences generated by the presence of distinct physical elements in the environment such as substrates with different inclination and topography. My results show a homogenizing effect of sediment deposition across substrates with different structural complexity. In addition, the absence of differences between coralline turfs and artificial mimics confirms the importance of the physical properties of such biogenic habitats in regulating furoid recruitment.

Contrary to my expectations, reduced sedimentation did not increase the recruitment of *H. banksii* in coralline and artificial turf plots. Turfs are known to stabilize sediment accumulation, by retaining elevated sediment loads independently of its fluctuations in the surrounding environment (Stewart 1983, Airoidi & Virgilio 1998). Despite the fortnightly removal treatment, therefore, sediment possibly re-accumulated quickly within the turfs

compared to the other habitats. Furthermore, percentage cover and number of the recruits decreased both in coralline and artificial turf plots when sediment was removed. Even if not statistically significant, these variations suggest that the recruits may have been loosely attached within the turfs, making them more prone to the impact of natural disturbances (e.g., wave force; Taylor & Schiel 2003) and potential artifact perturbations due to sediment removal.

My results amplify a growing body of research on the impacts of sediment on recruitment of furoids (Vadas et al. 1992, Schiel et al. 2006, Irving et al. 2009). In laboratory-based experiments, Schiel et al. (2006) showed that a light dusting of sediment reduced the settlement of *H. banksii* by 34% relative to controls, and complete sediment cover prevented attachment altogether. In the present study, however, *H. banksii* did recruit under ambient levels of sedimentation. This and other field investigations at this location (Hurley 2009) suggest that temporal fluctuations in the sediment environment may open windows of opportunity for furoid recruitment, allowing the persistence of abundant adult stands. Furthermore, *H. banksii* was able to recruit also within the turfs (both coralline and artificial), provided there was no furoid canopy, indicating that turfs of small thickness (~ 10 mm) may not represent an insurmountable barrier for this species. These results are in line with the findings of Bellgrove et al. (2010) who showed that thick mats of corallines (3-4 cm high) are virtually inaccessible for *H. banksii*, which can, however, be highly abundant in areas colonized by less developed turfs (around 10mm thick or less). Similarly, Schiel & Lilley (2011) observed that the long-term recovery of *H. banksii* canopies is influenced by the composition and morphological traits of the turfs, with slower recovery rates in the presence of articulated corallines with long, frondose branches (e.g., *Jania* spp.). My study shows that the effects of shorter turfs of *Corallina officinalis* may not be as strong. The length of the recruiting plants, in addition, was not affected by the properties of the habitats or

sedimentation levels, suggesting that once juvenile individuals overcome the critical bottleneck represented by settlement and early post-settlement phases, the nature of the substrate and the deposition of sediment may have limited influence on their development.

Net primary productivity was regulated by a combination of biotic (i.e., canopy-understory interactions; Tait & Schiel 2011b) and abiotic factors (i.e., sediment deposition). In the field, furoid-coralline assemblages were more productive than coralline turfs, both in the presence and absence of sediment. Analogously, in the laboratory coralline algae alone could not match the photosynthetic rates reached by furoid-coralline assemblages, despite showing higher light-use efficiency (α) at low irradiance, probably as a result of their adaptation to shaded sub-canopy conditions (Irving et al. 2004, Gattuso et al. 2006).

Both field and laboratory incubations highlighted a detrimental impact of sediment on NPP of coralline turfs and, under controlled laboratory conditions, this also compromised the functioning of furoid-coralline assemblages at elevated light intensities. In the presence of sediment, *P-E* curves of coralline algae and furoid-coralline assemblages showed photo-inhibition under increasing irradiance, with coralline turfs shifting into net respiration beyond $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$. This was most likely due to photo-inhibitive mechanisms within the turfs, induced by the accumulation of sediment. Sediment constitutes a clear physical obstruction for low-lying benthic taxa like coralline algae, as only small portions of their thalli are exposed to direct sunlight (Fig. 3.4A). The simplification of the three-dimensional structure of the latticed coralline algae likely reduces their ability to make use of the full irradiance gradient. Turfs with little sediment obstructing photosynthetic tissues (Fig. 3.4B), on the other hand, seem able to maintain their photosynthetic capacity at relatively high irradiance, possibly through increased self-shading and a higher leaf area index. Complex assemblages have a greater ability to convert incoming photons into carbon fixation at the higher end of the irradiance gradient, because although some components will be undergoing photo-

inhibition, others will be photosynthesizing efficiently (Binzer et al. 2006). In addition, the instantaneous response of coralline turfs to sediment removal suggests a remarkable recovery or persistence of photosynthetic activity. Analogously, various species of crustose corallines have been shown to restore their photosynthetic capacity quickly after sedimentation stress (Harrington et al. 2005).

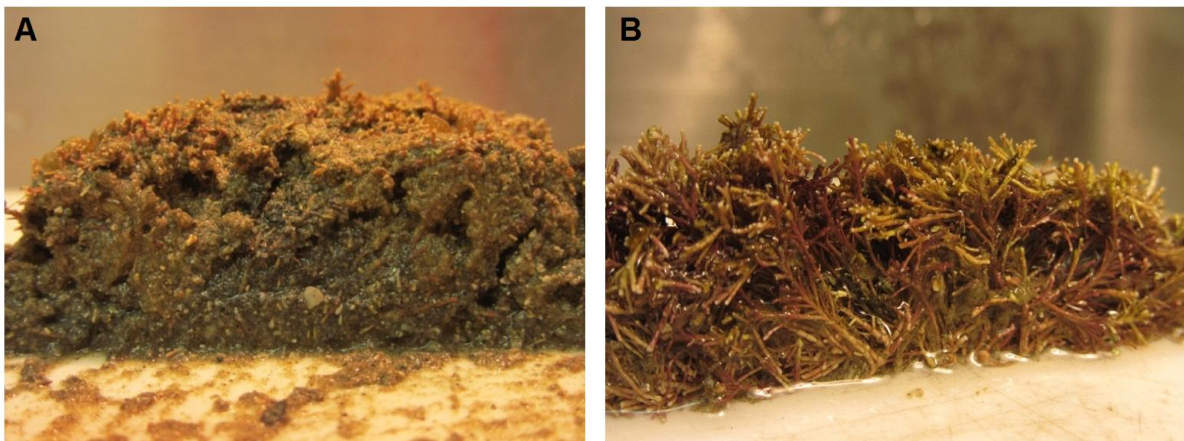


Fig. 3.4. Cross sections of a patch of coralline turf (around 10 mm thick) collected in the field and used for laboratory incubations. Note the high load of sediment in (A) obstructing the thalli of the corallines. The same patch following sediment removal (B) shows the potential for increased light penetration

Collectively the NPP dynamics described here indicate that even if the photosynthetic capacity of coralline algae is limited in comparison with *H. banksii* canopies, depending on the light environment these species have the potential to exert a strong influence over assemblage functioning. When devoid of sediment, coralline algae contributed to the enhancement of fucoid-coralline assemblage NPP, highlighting the importance of synergistic interactions among the components of multi-layered macroalgal assemblages in optimizing light use (Binzer et al. 2006, Tait & Schiel 2011b). Similarly, Chisholm (2003) has shown that crustose corallines make a larger contribution to organic production on coral reefs than previously thought. These results, however, also highlight the consequences of sediment

accumulation within the turfs and stronger impacts on assemblage photosynthetic processes are likely to occur when larger amounts of sediment are suspended in the water column, a scenario commonly observed in coastal areas in New Zealand and worldwide (Airoldi 2003, Thrush et al. 2004).

The overwhelming influence of anthropogenic perturbations is reshaping the structure of coastal systems worldwide and a better mechanistic understanding of the causes and the effects of these alterations is often advocated (Airoldi et al. 2008, Connell et al. 2008, Foster & Schiel 2010). This study sheds light on the influence of altered physical and biotic conditions on the persistence and functioning of benthic assemblages dominated by macroalgal canopies and highlights the potential implications of the impairment of key ecological processes within these complex biogenic habitats. The combined impacts of multiple perturbations, however, remain difficult to predict and synergies among stressors may be critical for the outcome of the interactions between canopy- and turf-forming algae (Connell & Russell 2010, Falkenberg et al. 2012, 2013a). Further studies will no doubt clarify the effects of altered sediment dynamics in combination with other anthropogenic influences acting across global to local scales.

CHAPTER 4

**Furoid recruitment under increased nutrient loading:
influence of ephemeral algae and coralline turfs**

4.1. ABSTRACT

Coastal eutrophication is known to promote the spread of fast-growing, ephemeral algae, often with severe consequences for benthic organisms, in particular perennial, habitat-forming macroalgae. In addition, the shift from canopy- to turf-dominated systems generally observed in areas affected by nutrient pollution is known to facilitate the occurrence of further ephemeral algae blooms. In contrast to this pattern, however, turfs of articulated coralline algae can suppress the growth of ephemeral green algae such as *Ulva*. Here I tested whether coralline turfs can facilitate the recruitment of intertidal furoids under increased nutrient loads by limiting the growth of ephemeral algae, and whether this indirect positive effect can offset the impact of the corallines on furoid settlement. A field experiment involving the manipulation of coralline turf abundance and nutrient availability was done for one year. As expected, nutrients fostered the growth of ephemeral species, but this did not affect the recruitment of the dominant furoids *Cystophora torulosa* and *Hormosira banksii*. The presence of the turfs, however, was a major barrier to furoid recruitment. Coralline turfs also limited the growth of some ephemerals such as *Ulva* spp., but facilitated the spread of others such as brown algae of the genus *Colpomenia*. These results highlight the tolerance of two important habitat-forming furoids to the competition with ephemeral algae and confirm the profound influence of algal turfs on assemblage structure and stability. A comparison with the findings of previous studies indicates that biotic responses to nutrient enrichment can be extremely complex and difficult to frame within pre-constructed models, as they are strictly related to local environmental conditions and species-specific functional traits of the species involved.

4.2. INTRODUCTION

Human activities are altering the chemistry of Earth's atmosphere, soil and water at unprecedented rates (Vitousek et al. 1997). As a result, disproportionate quantities of macronutrients, mainly compounds of nitrogen and phosphorous, are introduced into freshwater, estuarine and marine ecosystems because of agricultural practices, industrial runoffs and urban discharges (Carpenter et al. 1998, Cloern 2001). In New Zealand, for example, where the economy largely depends on agriculture and dairy farming, the increased accumulation of reactive nitrogen in the environment is altering biogeochemical cycles of terrestrial, freshwater, coastal and oceanic ecosystems with dramatic consequences to biodiversity and human health (Parfitt et al. 2008).

Large floristic changes commonly occur in estuarine and coastal areas affected by excessive nutrient enrichment, as uncontrolled blooms in the abundance of fast-growing, ephemeral species (predominantly foliose and filamentous green and brown algae) cause severe and long-lasting impacts on the structure of benthic communities (Duarte 1995, Valiela 1997, Herbert & Fourqurean 2008). Considerable research effort has been devoted to the identification of physical and biotic factors controlling the occurrence of macroalgal blooms (Grall & Chauvaud 2002, Krause-Jensen et al. 2008). Among these, the presence of canopy-forming species, like furoids and kelps, has been shown to exert a strong control on the spread of ephemeral algae, thereby buffering the propagation of nutrient-driven alterations (Russell & Connell 2005, Eriksson et al. 2006, 2007, Falkenberg et al. 2012).

Because of coastal habitat degradation, however, furoid and kelp canopies are in decline in many places worldwide (Benedetti-Cecchi et al. 2001, Airoidi et al. 2008, Connell et al. 2008). Fragmentation and loss of such canopies facilitate blooms of fast-growing algae and increased levels of interspecific competition from stress-tolerant, ephemeral species pose a further threat to the persistence of kelp and furoid populations (Worm et al. 2001, Steen

2004, Worm & Lotze 2006, Moy & Christie 2012; see Chapter 5). These alterations are compounded by the fact that low-lying, turf-forming algae usually become dominant following canopy loss, obstructing the recovery of perennial species (Kennelly 1987, Gorman & Connell 2009, Bellgrove et al. 2010), but not the spread of opportunistic algae (Russell & Connell 2005, Eriksson et al. 2006, 2007).

Shifts from canopy- to turf-domination and blooms of ephemeral algae are part of a positive feedback loop that is likely to escalate the impacts of nutrient enrichment on benthic communities. It is increasingly recognized, however, that turf-forming algae are extremely diverse (Airoldi 2001, Connell et al. 2014) and that species-specific functional traits are likely to dictate the outcome of their interactions with other species (Wieters 2005). For example, turfs of filamentous species can be outcompeted by ephemeral green algae such as *Ulva* and *Enteromorpha* (Bulleri et al. 2012b), but coralline turfs, composed of articulated coralline algae, have been shown to limit the development of *Ulva lactuca* (Daleo et al. 2006).

This study examined the influence of turf-forming articulated corallines and ephemeral, fast-growing algae on furoid recruitment under increased nutrient loads. Coralline turfs are a known obstacle to canopy recovery, but depending on the abundance and the morphology of the corallines, this does not necessarily result in the exclusion of perennial species (Benedetti-Cecchi & Cinelli 1992a, Bellgrove et al. 2010, Schiel & Lilley 2011; see Chapter 3). Here I tested whether coralline turfs can indirectly facilitate furoid recruitment under increased nutrient concentrations by reducing competition from ephemeral species, and whether this indirect positive effect can offset the impact of the corallines on the settlement of the fucoids. Besides facilitating furoid recruitment, I also expected the negative impact of coralline turfs on ephemeral algae to increase the temporal stability of the entire algal assemblage by

preventing significant changes in species composition and relative abundances under increased nutrient levels.

To test these hypotheses, I compared the structure of intertidal algal assemblages recruiting on unoccupied substrates and on surfaces dominated by coralline turfs, both under ambient and increased nutrient availability. Four different scenarios were hypothesized (Fig. 4.1), based on the literature testing the interactions among furoid, articulated coralline and ephemeral algae, as well as on prior knowledge of algal assemblage dynamics at the study area (Taylor & Schiel 2003, Lilley & Schiel 2006, Schiel & Lilley 2011). At this location, coralline turfs usually limit the abundance of both furoids and ephemeral species under ambient nutrient levels (Fig. 4.1A). In the absence of coralline algae, both ephemerals and furoids generally benefit from the increased availability of unoccupied primary substrate (indicated as bare rock), without significantly interfering with each other (Fig. 4.1B). Under enhanced nutrient concentrations, however, ephemeral algae may reach higher levels of abundance and persist for longer periods of time on unoccupied substrates. This may impede the recruitment of the furoids, or affect the plants already settled (Fig. 4.1C), and produce significant alterations to the structure of the entire assemblage. The presence of the corallines may prevent such nutrient-driven alterations and increase assemblage stability by suppressing the abundance of the ephemerals (Fig. 4.1D). Depending on its intensity, the negative effect of the turfs on the ephemerals may either indirectly facilitate the furoids, increasing their chances of recruitment (a), or be outweighed by the impact of the turfs on the settlement of the furoids (b). Although positive and negative effects of nutrient enrichment on the early life history of furoids have been observed in laboratory experiments (Kevekordes 2001, Steen 2004; see Chapters 5 and 6), such direct effects were considered to be negligible in the field in comparison to the indirect impact of nutrients associated with the bloom of ephemeral algae and are not shown in Fig. 4.1.

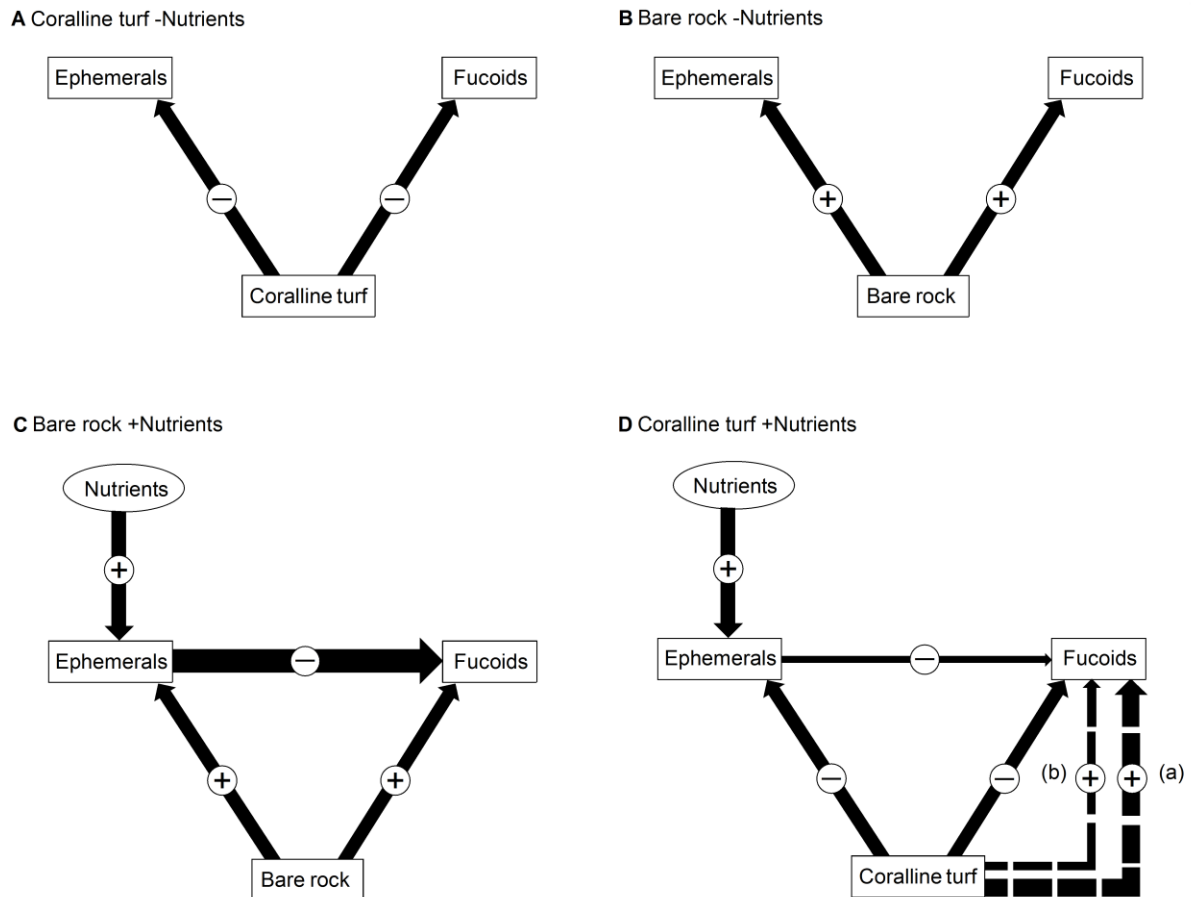


Fig. 4.1. Overview of the expected interactions among furoid recruits and ephemeral algae both in the presence (A and D) and absence of coralline algae (B and C) and under ambient (A and B) and increased nutrient regimes (C and D). Solid and dotted lines show direct and indirect interactions respectively, while the intensity of positive (+) and negative (-) effects is indicated by arrows of different thicknesses. Lowercase letters are used in paned D to distinguish between two alternative outcomes of indirect facilitation (see text for a detailed description of the four scenarios).

4.3. MATERIALS AND METHODS

4.3.1. Study site

The experiment was done at Wairepo Flats, in Kaikoura (42°25'S, 173°42'E), on the north-east coast of the South Island of New Zealand. This site presents a partially sheltered, large intertidal platform covered by canopies of various species of furoids. Coralline algae

(predominantly *Corallina officinalis* and *Jania* spp.) are the dominant primary space occupiers. Ephemeral green (*Ulva* spp.) and brown algae (*Adenocystis utricularis*, *Colpomenia* spp., *Ectocarpus* spp., *Scytosiphon lomentaria*, *Tinocladia novae-zelandiae*) tend to become abundant in spring and early summer, especially on unoccupied surfaces in the absence of algal canopies (Taylor & Schiel 2003, Lilley & Schiel 2006). Nutrients are likely to be a limiting factor for algal growth at this location, as the waters surrounding the east coast of New Zealand are known to be relatively nutrient-poor because of downwelling (Menge et al. 1999, 2003, Guerry et al. 2009).

4.3.2. Experimental design and data collection

Sixty 25 x 25 cm plots were marked in the low intertidal zone (ca. 0.1 to 0.3 m above the lowest astronomical tide level) along a stretch of shore of about half a kilometre. These plots were dominated by mixed canopies of the fucoids *Cystophora torulosa* and *Hormosira banksii*, with a basal layer of articulated coralline algae (mean cover ~ 90%; thickness ~ 10 mm). *C. torulosa* and *H. banksii* adult plants, along with all fleshy and foliose understory species, were removed by hand picking from thirty of the plots, and from the area surrounding their immediate edges, to create experimental units of coralline turf alone. The remaining thirty plots were cleared of all algae using hammer and chisel to create denuded patches of bare rock. These plots were not recolonized by the coralline turfs during the experiment. Half of the replicates of each habitat type were assigned to the nutrient enrichment treatment and equipped with two polyethylene mesh dispenser bags attached in proximity to two opposite corners. Each dispenser was filled with 150g of coated slow-release fertilizer pellets (Osmocote[®] Pro 3-4 months release: 17, 4.8, 8.3 N-P-K), so that each plot was enriched with 300g of fertilizer, a quantity shown to increase water nutrient concentration and stimulate macroalgal growth in a previous experiment done nearby

Kaikoura (Guerry et al. 2009). The selected amount of fertilizer and the distance among the plots (at least 2m from each other) reduced the chances of nutrient spillover, ensuring independent treatment effects (Worm et al. 2000). Osmocote pellets were replaced every six weeks.

Twelve additional plots (six coralline turf and six bare rock plots) were set up with dispenser bags filled with plastic beads of the same size and shape as the Osmocote pellets. These plots were compared with a randomly selected subset of no-enrichment plots (i.e., not surrounded by dispensers) from the main experiment to test for potential artifacts caused by the dispensers.

Before the start of the experiment all the plots were gently washed using a hose connected to a bilge pump to remove sediment and any algal spores and zygotes, so that all treatments were exposed to the same initial conditions. The experiment was then started at the beginning of the austral autumn (March 2012). At this location both furoid reproduction and ephemeral species' blooms mainly occur during spring and early summer (Taylor & Schiel 2003, Lilley & Schiel 2006). The autumn start allowed a test of whether nutrient enrichment can stimulate algal blooms in the coldest seasons of the year and an assessment of the responses of furoids and ephemerals in spring and summer after a prolonged exposure to increased nutrient loads.

The plots were sampled after four, eight and twelve months from the start of the experiment. In each occasion all algal species were identified to the greatest possible taxonomic resolution and their percentage cover was recorded using a grid divided into 100 sub-quadrats. Water samples were collected six weeks after the start of the experiment, immediately before the first fertilizer replacement, to test the efficacy of the enrichment treatment. This was done while the plots were covered by about 50 cm of water during a receding tide. A plastic syringe was used to withdraw 100 ml of seawater about 10 cm above

the centre of 24 plots randomly selected (six for each combination of habitat type and nutrient manipulation). Water samples were filtered in the field through 25 mm glass fiber filters, stored in acid-washed polyethylene vials, frozen, and successively analysed for nitrate, ammonium and phosphate using a spectrophotometer. Ammonium and phosphate were determined as described by Koroleff (1983a,b) and nitrate by Parsons et al. (1984).

4.3.3. Statistical analyses

Differences in ammonium, nitrate and phosphate concentrations among treatments were analysed with a two-way ANOVA with the fixed factors: Habitat (coralline turf vs. bare rock) and Nutrients (enrichment vs. no-enrichment).

The percentage cover of the most abundant species of furoid and ephemeral algae colonizing the experimental plots was analysed both after eight and twelve months using this same ANOVA design; α was Bonferroni corrected to 0.025. In addition, the Relative Interaction Index (RII; Armas et al. 2004) was calculated, separately for different species of furoids, and used to describe the intensity and direction of their interactions with coralline turfs under ambient and increased nutrient levels at each sampling date. The RII is expressed as $RII = (B_w - B_o) / (B_w + B_o)$, where B_w and B_o are the percentage cover of furoid recruits in the presence and absence of coralline algae, respectively. The RII ranges between 1 and -1, with negative values indicating competition and positive values showing facilitation. In this experiment, B_o represented the average furoid percentage cover in bare rock plots, estimated separately for each nutrient level. RII values relative to the final sampling date were analysed with a one-way ANOVA with the fixed factor Nutrients (enrichment vs. no-enrichment).

The influence of coralline turfs and nutrient manipulation on assemblage structure was assessed with a combination of univariate and multivariate techniques. Differences in assemblage composition at the end of the experiment, expressed by Bray-Curtis

dissimilarities calculated on untransformed data, were analysed with a permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) including the same combinations of Habitat and Nutrient levels used for univariate analyses. SIMPER analysis (Clarke 1993) was used to assess the contribution of individual taxa to multivariate dissimilarities. To describe the temporal changes in assemblage composition that occurred throughout the experiment in coralline turf and bare rock plots under the two different nutrient regimes, the average dissimilarity across all sampling dates was calculated for each experimental plot. I first placed the observations into Euclidean space by calculating principal coordinates (Gower 1966) from a Bray-Curtis dissimilarity matrix including the full set of data. Then, for each plot, I calculated and averaged the three Euclidean distances between consecutive sampling dates (start-4 months, 4-8 months, 8-12 months) to quantify the mean temporal change experienced by the algal assemblages. Finally, mean Euclidean distances were analysed with the two-way ANOVA design previously described and displayed using non-metric multidimensional scaling (nMDS) plots showing the centroids of each treatment-by-time combination.

To test for experimental artifacts, I analysed the abundance of furoid and ephemeral species and assemblage structure and temporal variability using a design with the fixed factors: Habitat (coralline turf vs. bare rock) and Artifact Control (dispensers present vs. absent) and employing the same univariate and multivariate techniques previously described.

Before all univariate analyses, variance heterogeneity was tested with the Cochran's *C*-tests and removed with log transformation when required. When homogeneity of variances could not be achieved by transformation, data were analysed nonetheless by judging significance more conservatively ($\alpha = 0.01$). Student-Newman-Keuls (SNK) tests were performed for *a posteriori* comparisons of the means (Underwood 1997).

4.4. RESULTS

4.4.1. Efficacy of nutrient enrichment

Six weeks after the first addition of fertilizers water samples collected from enrichment plots had higher levels of ammonium (mean \pm SE: 18.90 ± 2.70 vs. $2.81 \pm 0.03 \mu\text{mol l}^{-1}$; $F_{1,20}=33.29$, $P < 0.001$), nitrate (14.33 ± 2.03 vs. $1.29 \pm 0.33 \mu\text{mol l}^{-1}$; $F_{1,20}=36.75$, $P < 0.001$) and phosphate (6.19 ± 0.71 vs. $0.17 \pm 0.02 \mu\text{mol l}^{-1}$; $F_{1,20}=66.26$, $P < 0.001$) in comparison to no-enrichment plots. Both for the enrichment and the no-enrichment plots, no differences were detected between coralline turf and bare rock plots in the concentration of any of the macronutrients (ammonium: $F_{1,20}=0.32$, $P = 0.58$; nitrate: $F_{1,20}=0.06$, $P = 0.81$; phosphate: $F_{1,20}=1.30\text{E-}03$, $P = 0.97$). Nutrient levels in the enrichment plots align with the concentrations recorded in eutrophic coastal areas around New Zealand (Barr 2007), indicating that the enrichment treatment successfully increased nutrient concentrations.

4.4.2. Responses of furoid and ephemeral algae

C. torulosa and *H. banksii* were the most abundant furoids colonizing the experimental plots. The percentage cover of *C. torulosa* and *H. banksii* was low for the first eight months of the experiment, with no differences related to the experimental treatments (Table 4.1A, Fig. 4.2A and C). The abundance of both species increased significantly in the bare rock plots during the final four months (spring-summer) to around 13%, while it remained below 4% in the coralline turf plots. No effects of nutrient enrichment were detected (Table 4.1B, Fig. 4.2A and C). Because of their slow growth rates, recruits of both species were still less than 2 cm long after twelve months and presented short, erect thalli (see Chapter 3). This ensured that post-settlement growth was not a confounding factor, as the percentage cover of the recruits reflected their density, which was related to the rates of recruitment.

Negative RII values through time indicated that the recruitment of *C. torulosa* and *H. banksii* was limited by the competition with coralline algae after eight and twelve months (Fig. 4.2B and D). The direction of coralline-furoid interactions did not vary with increased nutrient concentrations and after twelve months RII values did not differ between nutrient levels both for *C. torulosa* ($F_{1,28} = 0.46$, $P = 0.50$; Fig. 4.2B) and *H. banksii* recruits ($F_{1,28} = 0.30$, $P = 0.59$; Fig. 4.2D). After twelve months the recruits of another furoid, *Cystophora retroflexa*, were also more abundant on bare rock compared to coralline turf, despite low percentage cover (3.33 ± 1.05 vs. 0.40 ± 0.20 ; $F_{1,56} = 7.53$, $P < 0.01$).

Brown algae of the genus *Colpomenia* and green algae of the genus *Ulva* were the most abundant ephemeral species colonizing the plots. Both *Colpomenia* spp. and *Ulva* spp. (hereafter referred to as species and labelled simply as *Colpomenia* and *Ulva*) produced extensive blooms after eight months (spring), but were scarcely abundant at the other sampling dates (Fig. 4.2E and F). After eight months the abundance of *Colpomenia* was independently enhanced by the presence of coralline algae and nutrient enrichment, with values of percentage cover over 40% in coralline turf plots subjected to fertilization, and between 10-23% in all the other habitat-nutrient combinations (Table 4.1A, Fig. 4.2E). After twelve months, however, the cover of *Colpomenia* was reduced to about 1% with no differences between habitats and nutrient levels (Table 4.1B, Fig. 4.2E). *Ulva* also strongly responded to nutrients after eight months, but it was more abundant in bare rock plots, where its cover was around 25%, compared to 1-5% under all other combination of treatments (Table 4.1A, Fig. 4.2F). After twelve months the cover of *Ulva* was reduced to less than 1% and although there were significant differences between +Nutrient and -Nutrient treatments (0.30 ± 0.05 vs. 0.02 ± 0.02 ; Table 4.1B, Fig. 4.2F), these were probably biologically irrelevant.

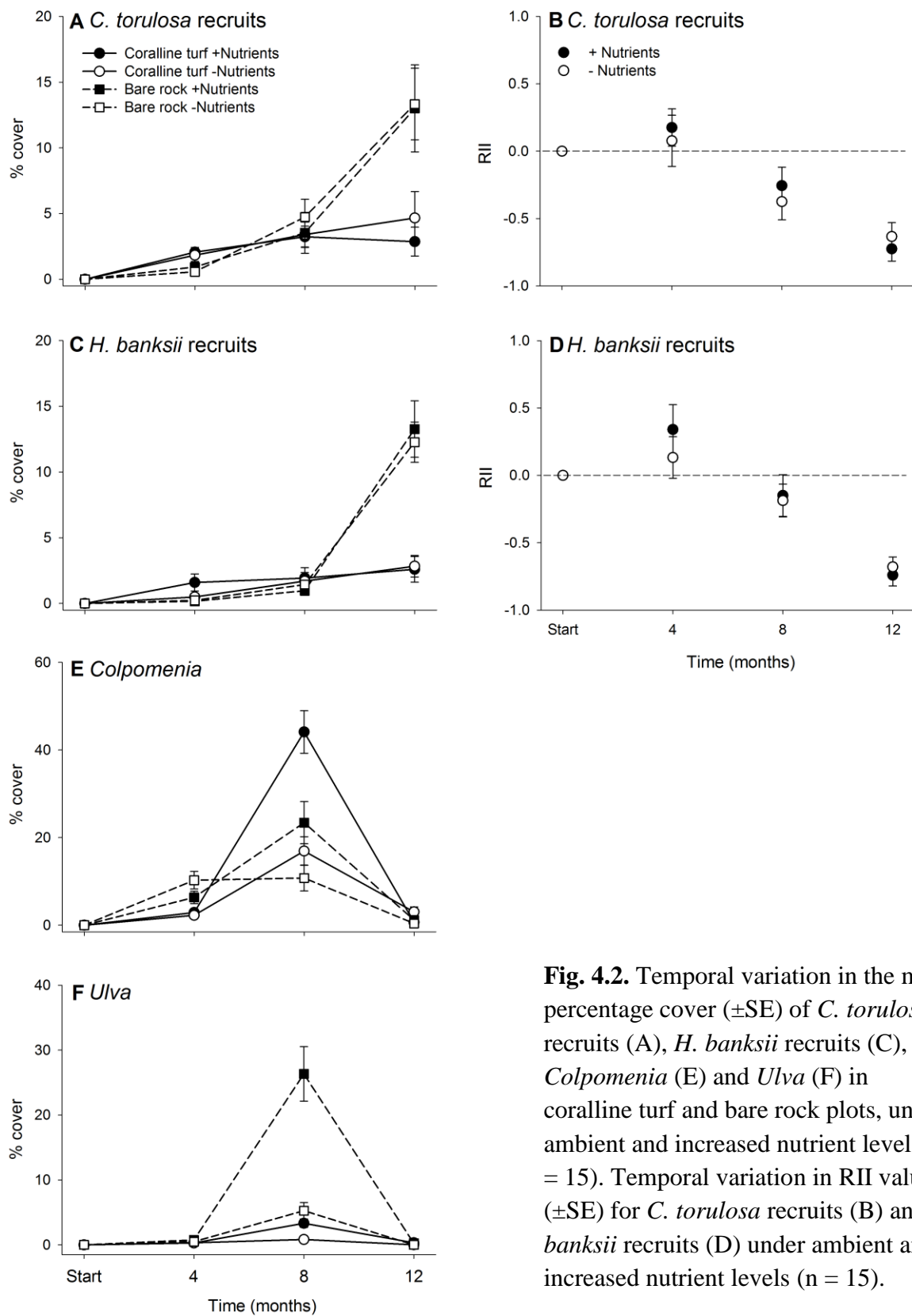


Fig. 4.2. Temporal variation in the mean percentage cover (\pm SE) of *C. torulosa* recruits (A), *H. banksii* recruits (C), *Colpomenia* (E) and *Ulva* (F) in coralline turf and bare rock plots, under ambient and increased nutrient levels ($n = 15$). Temporal variation in RII values (\pm SE) for *C. torulosa* recruits (B) and *H. banksii* recruits (D) under ambient and increased nutrient levels ($n = 15$).

Following page

Table 4.1. ANOVA on percentage cover of *C. torulosa* recruits, *H. banksii* recruits, *Colpomenia* and *Ulva* recorded in the main experiment (A and B) and in the artifact control tests (C). The abundances of the four species under different combinations of habitat type (coralline turf vs. bare rock) and nutrient manipulation (enrichment vs. no-enrichment) were separately analysed at eight (A) and twelve months (B) in the main experiment. Artifact control tests (C) included analyses of *C. torulosa* and *H. banksii* recruit abundances at twelve months and of *Colpomenia* and *Ulva* abundances at eight months in different habitat types (coralline turf vs. bare rock), both in the presence and absence of dispenser bags with no fertilizer. α was reduced to 0.025 to correct for repeated tests across sampling dates and to 0.01 when variance heterogeneity could not be removed through transformation. *P < 0.05; **P < 0.01; ***P < 0.001.

A) Main experiment (8 m)		<i>C. torulosa</i> recruits		<i>H. banksii</i> recruits		<i>Colpomenia</i>		<i>Ulva</i>	
Source of variation	DF	MS	F	MS	F	MS	F	MS	F
Habitat (H)	1	10.00	0.46	0.06	0.20	2706.82	10.94**	29.20	64.61***
Nutrients (N)	1	7.00	0.32	0.21	0.65	5940.15	24.01***	20.94	46.33***
H x N	1	4.00	0.18	0.10	0.32	792.07	3.20	2.00	4.42
Residual	56			0.32		247.36		0.45	

B) Main experiment (12 m)		<i>C. torulosa</i> recruits		<i>H. banksii</i> recruits		<i>Colpomenia</i>		<i>Ulva</i>	
Source of variation	DF	MS	F	MS	F	MS	F	MS	F
Habitat (H)	1	23.10	24.11***	31.05	51.97***	17.07	2.77	0.04	1.05
Nutrients (N)	1	0.54	0.56	0.22	0.37	9.60	1.56	1.20	33.72***
H x N	1	0.25	0.26	0.05	0.08	36.82	5.98	0.00	0.12
Residual	56	53.63		0.60		6.15		0.04	

C) Artifact control tests		<i>C. torulosa</i> recruits (12 m)		<i>H. banksii</i> recruits (12 m)		<i>Colpomenia</i> (8 m)		<i>Ulva</i> (8 m)	
Source of variation	DF	MS	F	MS	F	MS	F	MS	F
Habitat (H)	1	1283.34	82.12***	437.76	32.24***	882.09	8.64**	301.04	25.92***
Artifact control (AT)	1	3.76	0.63	41.34	3.05	78.84	0.39	6.00	0.52
H x AT	1	49.59	0.09	38.76	2.85	36.26	0.56	16.67	1.44
Residual	20	15.63				102.15		11.61	

4.4.3. Assemblage temporal variability and composition

In the absence of nutrients, there was little variability in assemblage structure through time in the coralline turf plots (Fig. 4.3A), while there were larger variations in the bare rock plots (Fig. 4.3B). This was due to the fact that where the corallines were present the abundance of the ephemerals remained low and there was limited recruitment of the dominant furoids and other algae. On unoccupied substrates, on the other hand, there was higher recruitment of the dominant furoids and of other algal species. The addition of nutrients increased assemblage structure temporal variability in both habitat types, because of the blooms in the abundance of ephemeral algae after eight months (Fig. 4.3A and B). These results were summarized through the analyses of mean Euclidean distances, which showed interactive effects of habitat type and nutrient addition on assemblage structure variability through time (Table 4.2A, Fig. 4.3C). Mean Euclidean distances were about 25% larger in the bare rock plots compared to the coralline turf plots in the absence of nutrients (Table 4.2A, Fig. 4.3C). Mean Euclidean distances increased in both habitats under increased nutrient levels and did not differ between bare rock and coralline turf plots, indicating that both habitats were prone to nutrient-driven structural changes (Table 4.2A, Fig. 4.3C). At the end of the experiment, however, assemblage composition differed only between habitats, while there were no effects associated with nutrient manipulation (Table 4.2A), suggesting that nutrient-driven alterations were transient. SIMPER analysis indicated that the differences between habitats at the conclusion of the experiment were mainly driven by furoid patterns of recruitments, with 86.62% of the dissimilarity explained by the preferential recruitment of *H. banksii* (37.74%), *C. torulosa* (35.94%) and *C. retroflexa* (12.94%) in bare rock plots. Other less abundant taxa (mean percentage cover < 3%) accounting for the remaining portion of variability among habitats at the conclusion of the experiment included: *Adenocystis utricularis*, *Carpophyllum maschalocarpum*, *Cystophora scalaris*, *Colpomenia* spp., *Ectocarpus* spp., *Gelidium*

caulacanthum, *Halopteris* spp., *Scytosiphon lomentaria*, *Tinocladia novae-zelandiae* and *Ulva* spp.

Table 4.2. ANOVA on mean Euclidean distances among centroids and PERMANOVA on multivariate data of assemblage composition (after twelve months) for the main experiment (A) and the artifact control tests (B). The analyses for the main experiment (A) tested the influence of habitat type (coralline turf vs. bare rock) and nutrient regime (enrichment vs. no-enrichment), while the artifact control tests (B) tested the differences between the two habitats (coralline turf vs. bare rock) in the presence and absence of dispenser bags. In the univariate analyses α was reduced to 0.01 when variance heterogeneity could not be removed through transformation. *P < 0.05; **P < 0.01; ***P < 0.001.

A) Main experiment		Mean Euclidean distance		Assemblage composition (12 m)	
Source of variation	DF	MS	F	MS	Pseudo-F
Habitat (H)	1	755.30	17.92***	17828.00	26.00***
Nutrients (N)	1	2219.64	52.66***	783.11	1.14
H x N	1	319.29	7.57**	858.40	1.25
Residual	56	42.15		38418.00	

B) Artifact control tests		Mean Euclidean distance		Assemblage composition (12 m)	
Source of variation	DF	MS	F	MS	Pseudo-F
Habitat (H)	1	267.65	6.22*	8573.50	37.08***
Artifact control (AT)	1	6.22	0.14	371.05	1.60
H x D	1	2.21	0.05	131.50	0.57
Residual	20	43.03		231.21	

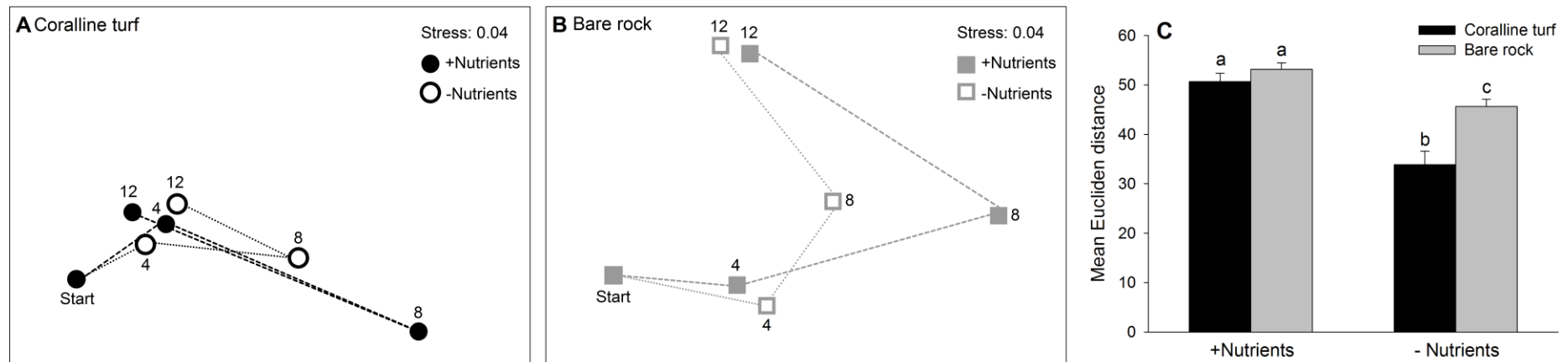


Fig. 4.3. Non-metric multidimensional scaling (nMDS) plots showing temporal changes in algal assemblages developing in coralline turf (A) and bare rock plots (B), under ambient and increased nutrient levels. Separate plots are presented for clarity, but they originated from the same nMDS. Symbols represent assemblage centroids under each combination of habitat and nutrient manipulation ($n = 15$) at each sampling date (the numbers besides the symbols indicate the months from the start of the experiment). Mean Euclidean distances (+SE) across all sampling dates (C) express assemblage temporal variability under each combination of the experimental treatments ($n = 15$). The letters above the bars show the results of SNK tests.

4.4.4. Artifact control

Artifact control tests indicated that the use of the dispensers did not affect the results of the main experiment. Analyses on the abundance of *C. torulosa* and *H. banksii* recruits (at twelve months) and of *Colpomenia* and *Ulva* (at eight months) did not show any difference between controls and plots surrounded by the dispensers (Table 4.1 C). Analogously, assemblage final composition and mean temporal variability did not differ between controls and plots surrounded by the dispensers (Table 4.2B).

4.5. DISCUSSION

Ephemeral species responded positively to nutrient enrichment, but did not have any impact on the recruitment of the furoids (Fig. 4.4A and B), or on final assemblage composition. *C. torulosa* and *H. banksii* recruited abundantly onto bare rock, despite the strong seasonal blooms of *Colpomenia* and *Ulva*, showing that furoid recruitment was not affected by elevated nutrient levels and increased abundance of ephemeral algae (Fig. 4.4A). These findings, however, show the very dominant effect of established coralline turfs on recruitment of furoids. The domination of primary space by corallines was, in fact, the main barrier to furoid recruitment and although coralline turfs limited the growth of some ephemeral species (i.e., *Ulva*), they also fostered the spread of others (i.e., *Colpomenia*; Fig. 4.4B).

Despite the ability of *H. banksii* to invade mats of articulated corallines of reduced thickness (10mm or less) observed at this location (Schiel & Lilley 2001; see Chapter 3) and elsewhere (Bellgrove et al. 2010), here the recruitment of both *H. banksii* and *C. torulosa* was extremely limited in the presence of the corallines. This was probably due to the fact that the experiment was set up in the low-intertidal zone in order to keep the plots underwater as long as possible and maximize the efficacy of the enrichment treatment. Articulated corallines with long, frondose branches, like *Jania* spp., which are a bigger obstacle to furoid

recruitment compared to shorter turfs (Schiel & Lilley 2011), are more abundant in the low-intertidal zone compared to higher elevations (see Chapter 3). As suggested by Schiel & Lilley (2011), therefore, differences in the composition and in the morphology of the turfs are likely to underlie the variability in the patterns of furoid recruitment at this location.

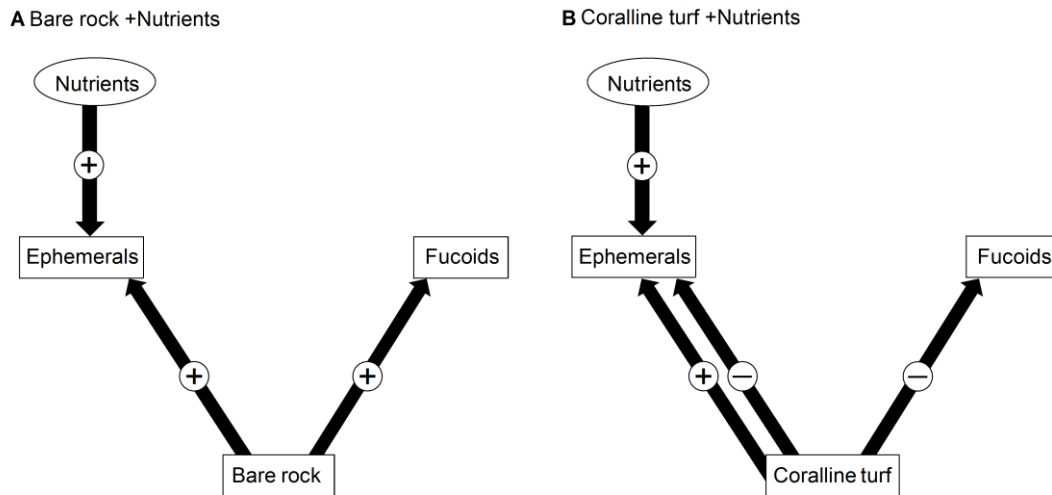


Fig. 4.4. Overview of the experimental results, showing the absence of any impact of ephemeral algae on furoid recruitment, both in bare rock (A) and coralline turf plots (B), despite their increased abundance in response to nutrient enrichment. The interactions between coralline turfs and furoids remained negative under increased nutrients loads, while both positive and negative effects of the turfs on the abundance of the ephemerals were observed (B).

Coralline turfs posed a barrier to canopy recovery, but were overgrown by *Colpomenia* when its abundance increased in response to nutrient enrichment. Independently of the presence or absence of the corallines on the substrate, there were large fluctuations in the structure of the assemblages recruiting under increased nutrient levels, due to the increase in the abundance of opportunistic species. These results add to a large body of evidence showing the limited ability of structurally simplified assemblages, dominated by turf-forming species, to withstand further perturbations (e.g., mechanical disturbances, Bertocci et al. 2010; thermal

stresses, Lilley & Schiel 2006; exotic invasions, Bulleri et al. 2010). Blooms of ephemeral macroalgae were dominated by different groups of species when occurring in the presence of coralline turfs or on unoccupied surfaces. Consistent with the findings of Daleo et al. (2006), *Ulva* had a limited ability to grow within the turfs, which were, however, the most favourable habitat for the spread of *Colpomenia*. The outcome of plant interactions is dictated by a complex interplay between the functional traits of the species involved and the physical environment (Bertness & Callaway 1994, Callaway & Walker 1997, Bulleri 2009). Species with globular thalli such as *Colpomenia* are very tolerant to desiccation (Oates 1985, 1988) and are known for their ability to grow as epiphytes on articulated corallines (Oates 1989). Foliose algae like *Ulva* have different morphological and physiological attributes, which, as suggested by Daleo et al. (2006), may result in a reduced ability to colonize the complex biogenic surfaces created by the turfs and to withstand the desiccation stress at the surface of the corallines.

The final abundance of *C. torulosa* and *H. banksii* and of the other algal species recruiting in the experimental plots was not affected by the ephemerals. This highlights the tolerance of these intertidal communities to short term (one year) nutrient stress and suggests that the effects of ephemeral algae on canopy-forming species may often be idiosyncratic (Viejo et al. 2008). Along the European Atlantic shores, for example, Viejo et al. (2008) found that green ephemeral algae had opposite impacts on two different fucoids, inhibiting the establishment of *Fucus vesiculosus* and facilitating the recruitment of *Himanthalia elongata*. In my study, on the other hand, ephemeral green and brown algae had no effect on the recruitment of *C. torulosa* and *H. banksii*.

It is important to keep in mind, however, that ephemeral blooms were limited to spring, while both *Colpomenia* and *Ulva* were scarcely abundant during the rest of the experiment. This indicates that growth and persistence of these opportunistic species are not limited by

nutrient availability only. Herbivory (Schiel & Lilley 2011) and wave action (Taylor & Schiel 2003) are known to have a minor impact at this location, but a variety of other environmental factors such as temperature, salinity, desiccation and excessive light exposure may be related to the die-back of *Colpomenia* and *Ulva* (Fong 1996, Kim KY et al. 2004). In addition, because of the limited duration of this study, it was not possible to assess the long-term consequences of eutrophication, while nutrient-driven alterations often become evident across extended temporal scales. The abundance of ephemeral green algae, for example, has been shown to build up with prolonged periods of nutrient enrichment, which after several years may lead to the collapse of furoid assemblages (Kraufvelin et al. 2006). Furthermore, over long periods of time, the establishment of propagule banks is also likely to provide a major contribution to the spread of ephemeral algae (Lotze et al. 2000, Worm et al. 2001).

Collectively, the results of this study suggest that the interactions between coralline turfs and fucoids are unlikely to switch from negative to positive in response to elevated nutrients. The trade-off between positive and negative interactions involving coralline turfs and ephemeral species, on the other hand, may either mitigate or exacerbate the biotic consequences of organic enrichment. Facilitative interactions have the potential to exert a destabilizing influence on community dynamics (Bulleri 2009, Butterfield 2009). Articulated corallines, in particular, are known to facilitate the settlement of the invasive kelp *Undaria pinnatifida* in the intertidal zone in New Zealand (Thompson & Schiel 2012) and here I showed that they also are a favourable substrate for the growth of disturbance-oriented brown algae. Although, to the best of my knowledge, no impact of any species of *Colpomenia* on other seaweeds has been reported, the influence of these species on other benthic organisms deserves further investigation. *Colpomenia* spp. can, in fact, easily overgrow algae (Oates 1989) and corals (Coles 1988) and their extensive blooms can make large portions of the substrate inaccessible for other species.

As shown by this study, biotic responses to nutrient enrichment can be extremely complex and do not necessarily result in a simple and immediate switch to ephemeral-dominated assemblages. Different responses may well be expected in the presence of a different pool of species (e.g., turfs of filamentous algae in place of articulated corallines) and under different physical conditions (Krause-Jensen et al. 2008). Furthermore, synergisms between organic enrichment and other anthropogenic perturbations are likely to add further to this complexity (Gorgula & Connell 2004, Russell et al. 2009, Falkenberg et al. 2013b), making short- and long-term consequences of eutrophication difficult to predict.

CHAPTER 5

Effects of opportunistic algae on the early life history of a habitat-forming furoid: influence of temperature, nutrient enrichment and grazing pressure

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5.1. ABSTRACT

Fragmentation and loss of extensive populations of habitat-forming macroalgae have occurred worldwide as a result of human-driven coastal habitat degradation. Contributing to such declines may be the influence of opportunistic algae which quickly respond to stresses such as nutrient loading and warmer sea temperatures. The early life stages of furoids are particularly likely to be affected by the combined impacts of altered physical conditions and increased competition with stress-tolerant species. In this study I examined the interactions between the early life stages of the intertidal furoid *Hormosira banksii* and fast-growing, opportunistic green algae, *Ulva* spp. Through a series of laboratory experiments, I tested: 1) the impact of *Ulva* spp. on the settlement of *H. banksii* zygotes; 2) the impact of *Ulva* spp. on the rates of post-settlement survival and growth of *H. banksii* germlings, under ambient and increased levels of temperature and nutrient concentration; 3) the interactions between the two taxa under grazing pressure of the abundant intertidal trochid *Lunella smaragdus*. *Ulva* spp. impaired the settlement of *H. banksii* zygotes, through both physical and chemical mechanisms, and the growth of the germlings, but was also preferentially consumed by the grazers, thereby indirectly facilitating *H. banksii*. In addition, *Ulva* spp. responded positively to increased temperature and nutrients, while there was an indication that post-settlement survival of *H. banksii* may decline with warmer waters. These findings augment extensive field-based research addressing the loss of algal beds and shed light on biotic and physical mechanisms affecting the most critical phases of the life cycle of a key habitat-forming species.

5.2. INTRODUCTION

The structure and functioning of many marine ecosystems are shaped by the presence of either a single or a few habitat-forming species (Bruno & Bertness 2001). Well documented examples include canopy-forming macroalgae of the Order Fucales (fucoids), which support high levels of diversity and productivity on temperate intertidal rocky reefs worldwide, despite the extreme physical challenges of these habitats (Chapman 1995, Schiel 2006). It is not surprising, therefore, that the decline of large populations of fucoid algae reported worldwide, especially around urbanised areas, has caused great concern and stimulated extensive ecological research (Benedetti-Cecchi et al. 2001, Berger et al. 2004, Irving et al. 2009, Bellgrove et al. 2010).

In degraded environments, slow-growing perennial algae such as fucoids can be directly harmed by modified physical conditions (e.g., sedimentation, eutrophication, chemical pollution), and also by competition with stress-tolerant opportunistic species (Berger et al. 2004, Kraufvelin et al. 2006, Worm & Lotze 2006). Impacts on their early life stages are particularly likely to provide explanations for the regression of fucoid populations. These microscopic phases are known to suffer from high levels of mortality and represent a critical bottleneck in the development and persistence of adult stands (Vadas et al. 1992, Schiel & Foster 2006). Ephemeral algae can negatively affect the early demography of fucoids either by blocking the settlement of zygotes or by reducing the post-settlement survival rates of germlings (Worm et al. 1999, 2001, Berger et al. 2003, Isæus et al. 2004). Herbivory, however, may release fucoids from competition with opportunistic algae. In eutrophic environments intense grazing pressure has been shown to facilitate weak competitors (i.e., perennial, slow-growing macroalgae) by preferentially consuming ephemeral species (Lubchenco 1983, Kim 1997, Worm et al. 1999, 2001).

Here I examined the impacts of fast-growing, opportunistic algae, *Ulva* spp. (hereafter referred to as a single species, i.e., *Ulva*), on the early life-history of the intertidal furoid *Hormosira banksii*, which is a key structural component of intertidal algal assemblages in New Zealand and south-eastern Australia. No other furoid species in New Zealand is able to provide the same ecosystem services in mid-shore habitats (Schiel 2006; see Chapter 2), and there are long-lasting impacts on community diversity and productivity following *H. banksii* removal (Schiel & Lilley 2011, Tait & Schiel 2011a). *Ulva* is a cosmopolitan genus comprising several species of fast-growing green algae commonly found in intertidal and estuarine habitats (Guiry & Guiry 2013). In eutrophic conditions ulvoids can produce nuisance blooms, with detrimental ecological effects and serious economic consequences (Anderson et al. 1996, Valiela et al. 1997).

Building on earlier field-based work, I used a series of laboratory experiments to test the impact of *Ulva* on the early life history of *H. banksii*. These included tests of different levels of temperature, nutrients and grazing pressure on the interactions between the two species. *Ulva* is known to have allelopathic properties that inhibit zygote development (Nelson et al. 2003), so I began by testing whether such effects were evident on *H. banksii*.

I then tested the effects of the presence of *Ulva* on the rates of survival and growth of *H. banksii* in the first six weeks of the post-settlement period. During this critical phase, the minute *H. banksii* germlings may easily be overgrown and outcompeted by *Ulva*. Furthermore, increased nutrient concentration and rising seawater temperatures may differentially affect the two species and their interactions. The abundance of fast-growing ephemeral species can be rapidly boosted by nutrient enrichment and warmer temperatures (Lotze et al. 1999, Lotze & Worm 2002, Steen 2004). The geographic range of numerous furoids, on the other hand, has shifted or retracted in response to water warming (Southward et al. 1995, Smale & Wernberg 2013) and there is experimental evidence linking these

patterns to the thermal sensitivity of their early life stages (Andrews et al. 2014). In addition, the development of the early life stages of various fucoids, including *H. banksii*, has been shown to be impaired by elevated nutrient levels (Kevekordes 2001, Bergström et al. 2003). In combination with the presence or absence of *Ulva*, therefore, temperature and nutrient levels were also manipulated. I expected increased temperature and eutrophication to have a direct detrimental effect on the fitness of the germlings and also to stimulate the growth of *Ulva*, thereby exacerbating its impact on *H. banksii*.

Finally, I assessed how the interactions between the two species can be modulated by the presence of the abundant intertidal trochid gastropod *Lunella smaragdus* (formerly *Turbo smaragdus*). This is one of the most abundant grazers in the intertidal zone of New Zealand, reaching densities of over 100 individuals per m² and it is known to graze preferentially on ephemeral algal species (Walker 1998, Schiel 2006). In combination with presence or absence of *L. smaragdus*, I manipulated the density of *Ulva* to simulate the biotic consequences of eutrophication scenarios of increasing intensity. I expected to observe a negative impact of *Ulva*, proportional to its abundance, on the survival and growth of *H. banksii* germlings in the absence of grazing; a negative effect of *L. smaragdus* on both algal species, with a preference for *Ulva*; and, potentially, an indirect facilitative effect of *L. smaragdus* on *H. banksii* through the relaxation of competition with *Ulva*.

5.3. MATERIALS AND METHODS

The experiments were carried out in the facilities of the Edward Percival Field Station in Kaikoura, New Zealand. Settlers of the two algal species were obtained from adult plants collected in the field were grown on 50 x 50 x 7 mm fibrolite plates. *H. banksii* settlement density was not manipulated, but was kept at around 300 cm⁻² in all the experiments. These values are in line with the settlement rates observed in the field in Kaikoura (Dunmore 2006).

The plates were housed in plastic tanks (37 x 25 x 7 cm) filled with filtered (1 μm) and UV sterilized seawater. Air pumps were used to aerate the tanks and light racks provided illumination at an intensity of $\sim 100 \mu\text{mol m}^{-2} \text{s}^{-1}$ under a 12:12 hour light:dark cycle. The plates were submerged throughout the duration of experiments to exclude additional stress sources related to aerial exposure. A previous field-based study in Kaikoura showed a negative relationship between *H. banksii* germling survival and shore height, with 100% mortality in the high shore and increasing rates of survival at lower elevations (Dunmore 2006). By culturing *H. banksii* early life stages in benign and stable conditions, it was possible to test the effects of the experimental factors more accurately.

5.3.1. Experiment 1: impact of *Ulva* on *H. banksii* zygote settlement

I compared the attachment of *H. banksii* zygotes experimentally settled on: 1) unoccupied plates (control); 2) unoccupied plates housed in tanks previously occupied by *Ulva* (to test the impact of chemical alterations in the growth medium) and 3) plates 50% colonized by *Ulva* (to test the impact of substrate pre-emption). Each settlement condition was replicated in two tanks, each containing four plates.

Before the start of the experiment, 32 plates were distributed among eight tanks (four plates per tank) each filled with 4 L of seawater. The plates were soaked for two days and successively four of the tanks received 1 L of *Ulva* zooid solution, while 1 L of seawater was added to the remaining four to equalize the volume. All the plates were kept submerged at 17 °C for 30 days and the water was changed twice weekly. After 30 days, the plates seeded with *Ulva* were examined and the percentage cover of *Ulva* was visually estimated using a 5 x 5 cm fine plastic grid divided into 25 sub-quadrats. Eight plates with 53.55 ± 5.55 (mean \pm SE) percentage cover of *Ulva* were selected to represent the treatment with 50% colonized substrates. These were reintroduced into two of the tanks originally seeded with *Ulva*. The

remaining plates containing *Ulva* were removed from their tanks and replaced by eight unoccupied plates. These constituted the treatment with unoccupied substrates housed in tanks previously occupied by *Ulva*. The remaining unoccupied plates (control) were not moved from their original tanks. After rearranging the substrates, 1 L of *H. banksii* zygote solution, obtained from ~ 20 adult plants, was added to each tank. After 24 hours all the plates were examined under a binocular microscope and the number of settled zygotes was estimated in three haphazardly chosen 1 cm² areas.

5.3.2. Experiment 2: influence of temperature and nutrients on species interactions

I tested whether particular combinations of temperature and nutrient levels would favour *H. banksii* or *Ulva*. These factors were manipulated in crossed combination: 1) Temperature (17 °C vs. 20 °C); 2) Nutrients (ambient vs. increased concentration) and 3) Culture type (*H. banksii* monocultures vs. mixed cultures).

The experiment was run for six weeks to assess the experimental responses over a longer period of time compared to similar studies reported in the literature (Lotze & Worm 2002, Steen 2004). After six weeks, however, it was no longer possible to culture *H. banksii* and *Ulva* in isolation, as other unwanted species (mainly microalgae) began to appear on the plates. The ambient sea water temperature, 17 °C, was the maximum observed at Kaikoura during summer (Chiswell & Schiel 2001), the period of peak reproduction of *H. banksii*. The higher temperature, 20 °C, was chosen in line with predictions by the IPCC (2007) for the end of the 21st century for New Zealand and Southern Australia. Increased nutrient concentrations were obtained through the addition of 20 µM N (nitrate and ammonia added at a ratio of 1:1) and 2 µM P (phosphate) per L of seawater in order to match the values observed in eutrophic coastal areas around New Zealand (Barr 2007). Two temperature-controlled rooms equipped with independent thermostats were used to maintain the selected

temperature levels throughout the experiment. It was not possible to allocate multiple rooms to the two temperature levels. The two rooms, however, were identical in all respects and the experimental set up (i.e., the positions of tanks, lights and air pumps) did not differ between them. Within each room, two tanks were assigned to each possible combination of nutrient concentration and presence/absence of *Ulva*, with four plates in each tank.

Before the start of the experiment, each tank (16 in total) was filled with 4 L of seawater and the plates were soaked for two days. One litre of *H. banksii* zygote solution, obtained from ~ 50 adult plants, was then gently poured over the plates in each tank. After four days the water in each tank was replaced and the initial abundance of *H. banksii* germlings was recorded. The manipulation of temperature and nutrient levels was then initiated and the tanks allocated to mixed cultures of *H. banksii* and *Ulva* received 1 L of *Ulva* zooid solution. The total volume of water was brought up to 5 L in each tank. The water was replaced twice weekly throughout the experiment and nutrients were re-added to the + Nutrients tanks after each water change.

The plates were sampled after two, four and six weeks from the initial monitoring (four days). At each sampling date, every plate was examined under a binocular microscope and the number of *H. banksii* germlings was estimated as previously described. Percentage survival of *H. banksii* germlings was expressed as the proportional difference in the number of germlings in relation to the abundance recorded in the initial sampling. At the end of the experiment, the mean size of the germlings was calculated from ten individuals randomly selected from each plate. These were detached from the plates and measured lengthwise using an eyepiece graticule. The growth of *Ulva* was also monitored throughout the experiment, with values of percentage cover recorded at each sampling date. In addition, the Relative Interaction Index (RII; Armas et al. 2004) was calculated based on *H. banksii* germling percentage survival data recorded at each sampling date and used to describe the intensity

and direction of the interactions between the two species under different combinations of temperature and nutrient levels. The RII is expressed as $RII = (B_w - B_o) / (B_w + B_o)$, where B_w and B_o represent the performance (percentage survival in this study) of the target species (*H. banksii*), with or without neighbours (*Ulva*) respectively. The RII ranges between 1 and -1, with negative values indicating competition and positive values showing facilitation. In this experiment, *H. banksii* survival rates in the presence of *Ulva* (B_w), recorded from the plates assigned to mixed cultures of the two species, were contrasted with mean values of B_o , calculated by averaging the survival rates of *H. banksii* germlings in the monocultures, separately for each combination of temperature and nutrient levels.

5.3.3. Experiment 3: influence of grazing on species interactions

I tested the impact of grazing by *L. smaragdus* on *H. banksii* germlings grown in isolation and in mixed cultures with various densities of *Ulva*. The experiment involved two factors: Grazing (present vs. absent) and Culture type (*H. banksii* monocultures vs. mixed cultures with low and high density of *Ulva*). Each experimental condition was replicated in two tanks, each containing four plates.

Six medium-sized *L. smaragdus* (average shell length: 22.17 ± 0.41 mm), were collected and allowed to acclimatise to laboratory conditions for two weeks before being introduced into the experimental tanks. Before the start of the experiment, the plates were soaked for 48 hours in 4 L of seawater. One litre of *H. banksii* zygote solution, obtained from ~ 40 adult plants, was then added to each tank. The zygotes were allowed to settle and develop for four days before the first water change, which was followed by the inoculation of *Ulva*. Differing densities of *Ulva* were achieved by seeding the experimental tanks with different volumes of *Ulva* zooid solution. One litre of *Ulva* zooid solution was added to four tanks to obtain mixed cultures with a high density of *Ulva*, and four tanks were seeded with

0.5 L of the solution to create mixed cultures with a low density of *Ulva*. The total volume of water was then brought up to 5 L in each tank. The cultures were grown at 17 °C for 30 days to allow the development of *Ulva*. The water was replaced twice weekly. After 30 days, the number of *H. banksii* germlings and percentage cover of *Ulva* were recorded. After this initial period, I started the experiment by adding one specimen of *L. smaragdus* to half of the experimental tanks assigned to each culture type.

The abundance of *H. banksii* germlings was monitored two, four and six weeks after the introduction of the grazers and their percentage survival was estimated relative to the values recorded in the initial sampling. Ten *H. banksii* individuals from each plate were measured at the end of the experiment. Variations in the percentage cover of *Ulva* in relation to the initial values were also calculated at each sampling date. *H. banksii* germling percentage survival data were used to calculate the Relative Interaction Index (RII), describing species interactions relative to *Ulva* density and grazing pressure. Here, B_0 represented the average percentage survival of *H. banksii* germlings in the absence of *Ulva*, calculated separately for the two levels of grazing pressure.

5.3.4. Statistical analyses

Zygote abundance data from Experiment 1 were analysed using a two-way analysis of variance (ANOVA) with the fixed factor Settlement Conditions (control vs. growth medium alteration vs. substrate pre-emption) and the random factor Tank (nested within Settlement Conditions).

Data of percentage survival and size of *H. banksii* germlings, and percentage cover of *Ulva* recorded at the conclusion of Experiment 2 were analysed using a four-way ANOVA with the fixed factors: 1) Temperature (17 °C vs. 20 °C); 2) Nutrients (ambient vs. increased concentration); 3) Culture type (*H. banksii* monocultures vs. mixed cultures) and 4) the

random factor Tank (nested within Temperature, Nutrients and Culture type). RII values relative to the final sampling date were analysed with a three-way ANOVA including the same crossed combinations of the factors Temperature and Nutrients and the random factor Tank.

Data of percentage survival and size of *H. banksii* germlings and percentage cover variation of *Ulva* recorded at the conclusion of Experiment 3 were analysed using a three-way ANOVA with the fixed factors: 1) Grazing (present vs. absent); 2) Culture type (*H. banksii* monocultures vs. mixed cultures with low density of *Ulva* vs. mixed cultures with high density of *Ulva*) and 3) the random factor Tank (nested within Grazing and Culture type). RII values relative to the final sampling date were analysed with a three-way ANOVA, including the fixed factors: 1) Grazing (present vs. absent); 2) Culture type (mixed cultures with low density of *Ulva* vs. mixed cultures with high density of *Ulva*) and 3) the random factor Tank.

When the variability among tanks was negligible ($P > 0.25$) pooling procedures were applied according to Underwood (1997). Cochran's *C*-tests were used to test for homogeneity of variances before each analysis. No transformation was required for any of the response variables. Student-Newman-Keuls (SNK) tests were performed for *a posteriori* comparisons of the means (Underwood 1997).

5.4. RESULTS

5.4.1. Experiment 1: impact of *Ulva* on *H. banksii* zygote settlement

There were significant differences among treatments in the initial attachment of *H. banksii* zygotes ($F_{2,21} = 58.75$, $P < 0.001$, tested against the pooled term Tank + Residual; Fig. 5.1), resulting from allelopathy and space pre-emption. The average number of successfully settled *H. banksii* zygotes was around 300 per cm^2 in the control tanks, whereas just over half that

number attached where the medium had been previously occupied by *Ulva*, and about one-third that number when there was a 50% cover of *Ulva*.

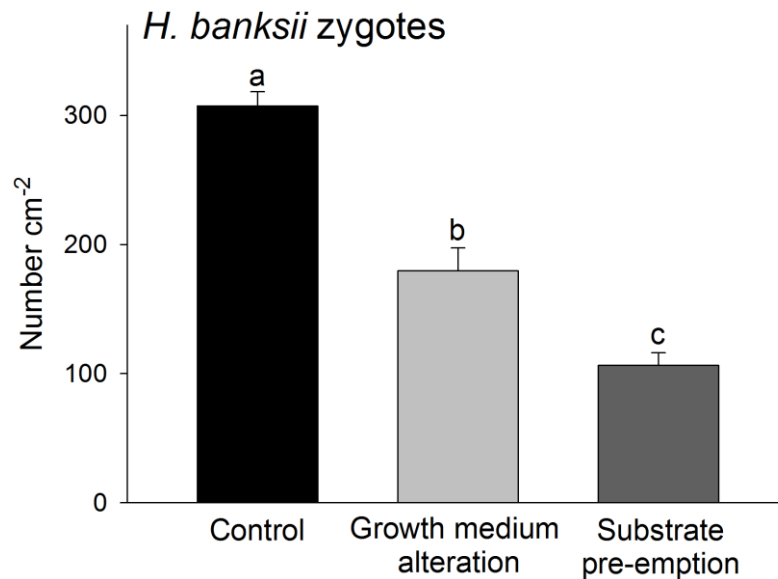


Fig. 5.1. Mean abundance (+SE) of attached *H. banksii* zygotes recorded after 24 hours on: unoccupied plates (Control), unoccupied plates housed in tanks previously occupied by *Ulva* (Growth medium alteration) and plates 50% colonized by *Ulva* (Substrate pre-emption), $n = 8$. The letters above the bars indicate the ranking of the means according to the SNK tests.

5.4.2. Experiment 2: influence of temperature and nutrients on species interactions

At the start of the experiment, the average number of the germlings was 306.07 ± 12.35 per cm^2 ($n = 60$). After six weeks the survival of *H. banksii* germlings was not significantly affected by temperature, nutrient levels or the presence of *Ulva* (Table 5.1A). Although 88.16% (± 3.05) of germlings survived at 17 °C and 76.92% (± 3.04) at 20 °C, these apparent differences were not significant ($F_{1,8} = 5.19$, $P = 0.052$). *H. banksii* germling sizes, however, were affected by *Ulva* (Table 5.1B, Fig. 5.2A). The germlings grown alone were significantly larger than those grown with *Ulva*, indicating an inhibitive interaction.

The growth of *Ulva* was stimulated by nutrient enrichment in the mixed cultures, with a clear separation of treatments becoming evident after four weeks (Fig. 5.3B). Unexpectedly, *Ulva* also appeared in the *H. banksii* monocultures at around four weeks and maintained percentage covers between 40-47% in the 17 °C + Nutrients treatment, but near zero in all others (Fig. 5.3A). This contamination was of unknown origin, but it may have occurred during the water changes. At the end of the experiment, however, *Ulva* was more abundant in the mixed cultures for all the combinations of temperature and nutrient levels. In the mixed cultures its percentage cover was greater in the + Nutrients treatments and highest at 20 °C, after six weeks (Table 5.1C, Fig. 5.3A and B).

Throughout the experiment the RII values were always close to zero indicating the absence of either positive or negative impacts of *Ulva* on *H. banksii* germling survival. After six weeks the RII ranged from -0.06 ± 0.04 to 0.05 ± 0.06 and did not vary significantly with temperature ($F_{1,4} = 0.26$, $P = 0.63$) or nutrients ($F_{1,4} = 1.17$, $P = 0.34$).

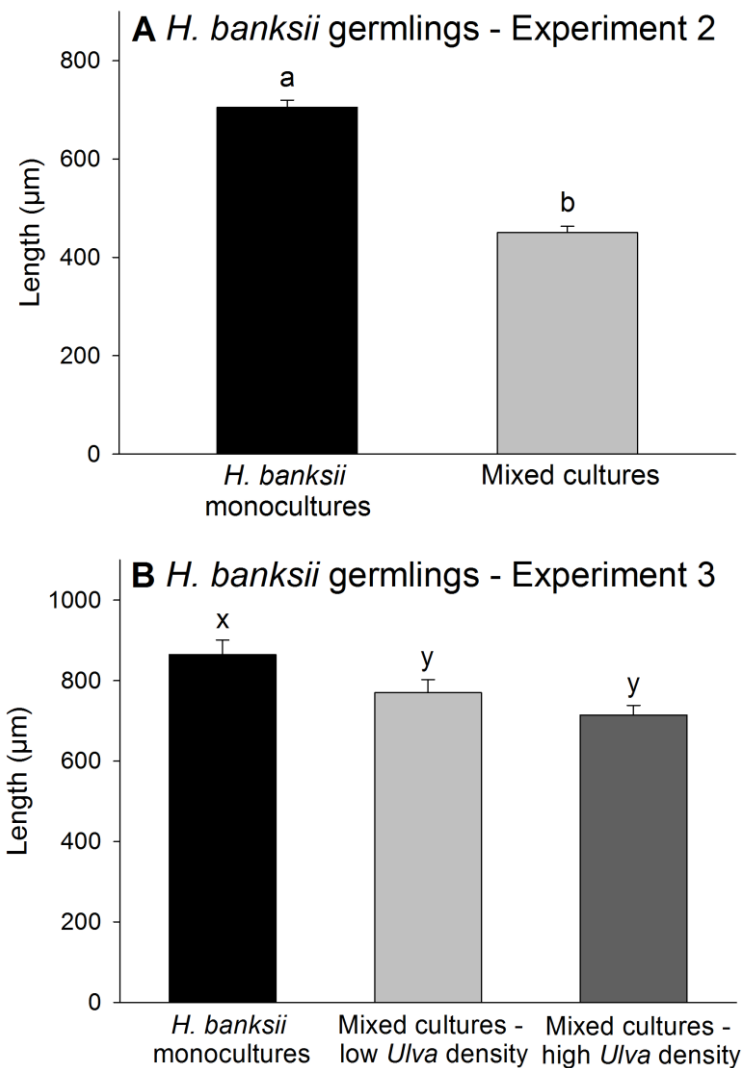


Fig. 5.2. Mean length (+SE) of *H. banksii* germlings in: (A) *H. banksii* monocultures and mixed cultures with *Ulva* combined across all levels of temperature and nutrient concentration (n = 32), recorded at the end of Experiment 2 (after 6 weeks); (B) *H. banksii* monocultures and mixed cultures with low and high density of *Ulva* combined across all levels of grazing (n = 16), recorded at the end of Experiment 3 (after 6 weeks). The letters above the bars indicate the ranking of the means according to the SNK tests.

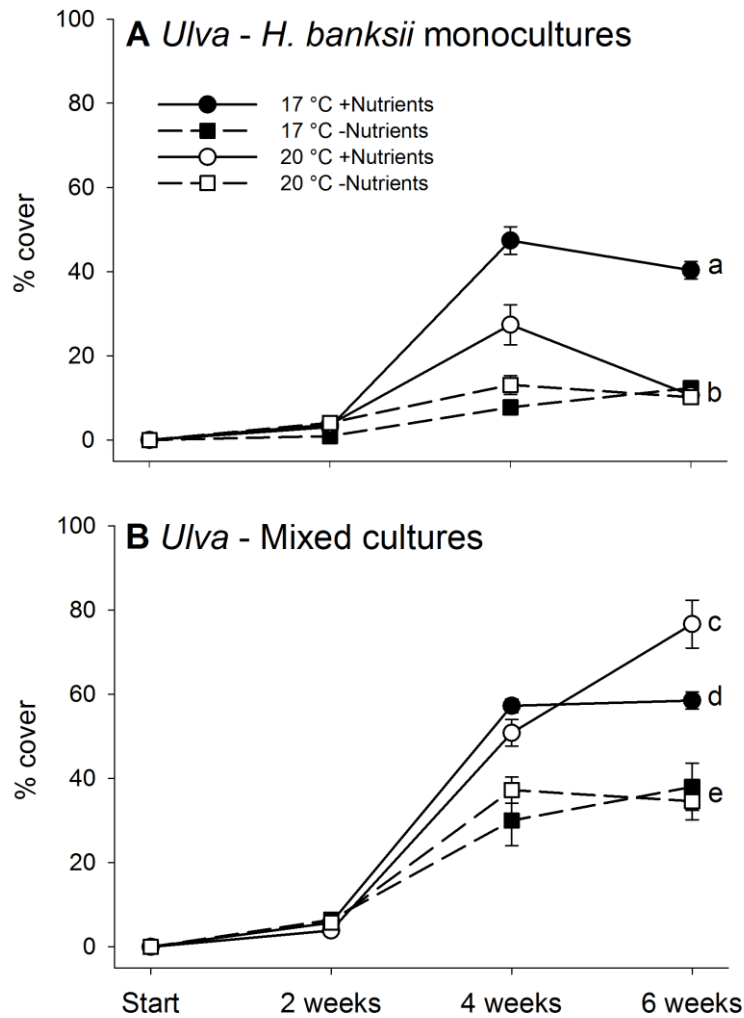


Fig. 5.3. Temporal variation in the mean percentage cover (\pm SE) of *Ulva* in *H. banksii* monocultures (A) and mixed cultures (B) under both ambient and increased levels of temperature and nutrient concentration (n = 8). The letters beside symbols show the ranking of the means according to the SNK tests for the final sampling date and allow comparisons of percentage cover values across graphs.

Table 5.1. ANOVA on data of percentage survival and size of *H. banksii* germlings and percentage cover of *Ulva* recorded at the final sampling date (six weeks) of Experiment 2 in different cultures types (*H. banksii* monocultures vs. mixed cultures) and under various temperature (17 °C vs. 20 °C) and nutrient (ambient vs. increased concentration) levels. *P < 0.05; **P < 0.01; ***P < 0.001.

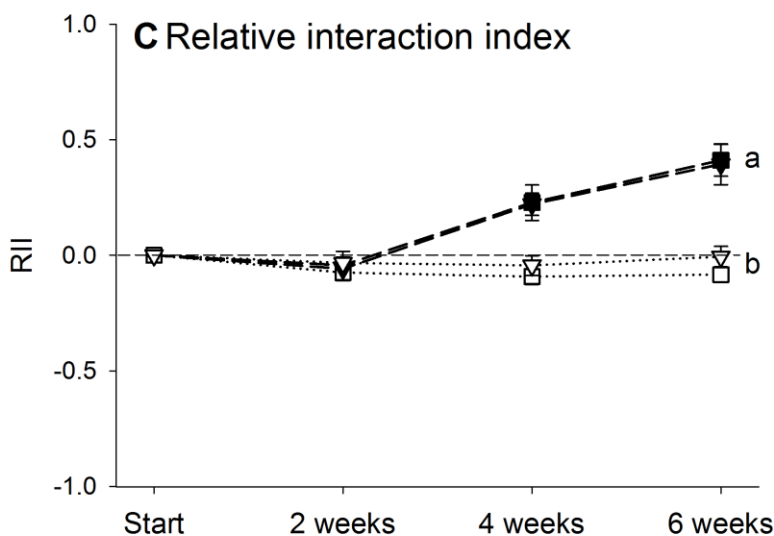
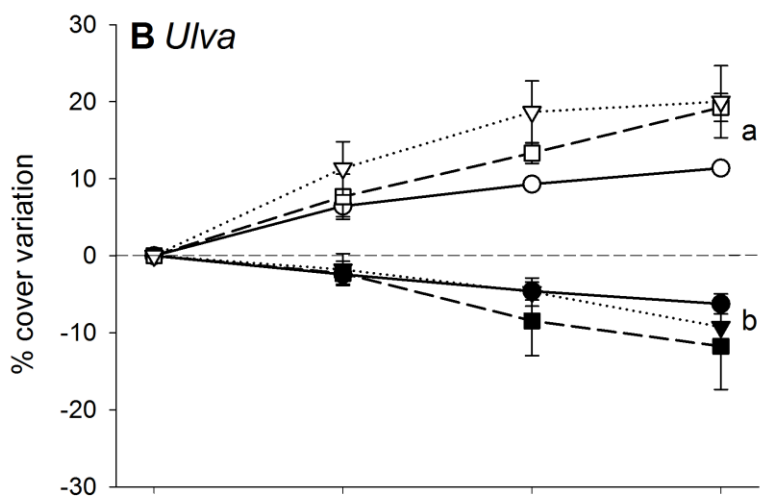
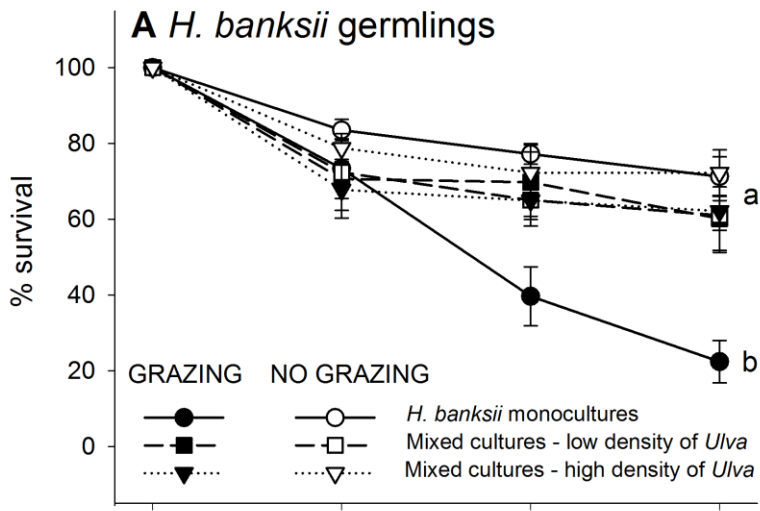
Source of variation	DF	A. <i>H. banksii</i> germling % survival		B. <i>H. banksii</i> germling size (µm)		C. <i>Ulva</i> % cover	
		MS	F	MS	F	MS	F
Temperature (T)	1	2013.77	5.19	156.25	0.01	284.77	1.20
Nutrients (N)	1	656.64	1.69	61256.25	4.56	8212.89	34.70***
Culture type (CT)	1	213.89	0.55	1035306.25	77.14***	17989.52	76.01***
T x N	1	172.27	0.44	56.25	0.00	37.52	0.16
T x CT	1	87.89	0.23	17117.80	1.28	2150.64	9.09*
N x CT	1	337.64	0.87	10850.35	0.81	1147.52	4.85
T x N x CT	1	337.64	0.87	42368.05	3.16	2413.27	10.20*
Tank (T x N x CT)	8	388.33	1.39	13421.22	4.41***	236.67	3.28**
Residual	48	279.48		3105.81		72.22	

5.4.3. Experiment 3: influence of grazing on species interactions

At the start of the experiment the average number of the germlings was 297.22 ± 12.58 per cm^2 ($n = 48$). In the absence of *Ulva*, *L. smaragdus* rapidly compromised the survival of *H. banksii* to around 20% after six weeks (Grazing x Culture Type: $F_{1,42} = 6.52$, $P < 0.01$, tested against the pooled term Tank + Residual; Fig. 5.4A). All other treatments showed similar survival of *H. banksii* between 60-72%, indicating that *H. banksii* had protection from herbivory through the association with *Ulva*. As in Experiment 2, the size of the germlings was significantly larger when *H. banksii* was grown in isolation compared to the tanks with high and low densities of *Ulva*, across both levels of grazing pressure (Culture Type: $F_{2,42} = 5.77$, $P < 0.01$, tested against the pooled term Tank + Residual; Fig. 5.2B).

At the start of the experiment, the percentage cover of *Ulva* was 39.37 ± 3.80 and 65.84 ± 4.94 for the cultures with low and high density of *Ulva*, respectively. As happened in Experiment 2, *Ulva* was also present in *H. banksii* monocultures, even if with low coverage (9.24 ± 0.71). Throughout the experiment, variations in the cover of *Ulva* were strongly influenced by grazers, regardless of its initial abundance, with negative values recorded in the presence of *L. smaragdus*, and positive values in its absence (Grazing: $F_{1,42} = 87.17$, $P < 0.001$, tested against the pooled term Tank + Residual; Fig. 5.4B). At the end of the experiment the percentage cover of *Ulva* in the monocultures was reduced to very low values (2.92 ± 0.75) when exposed to the action of the grazers, while it reached $20.52 \pm 0.37\%$ in the absence of *L. smaragdus*. Without grazing *Ulva* percentage cover increased to 65.73 ± 2.01 and 83.37 ± 3.90 in the mixed cultures with low and high density of *Ulva*, respectively. These same culture types had values of *Ulva* percentage cover equal to 20.54 ± 5.47 and 57.13 ± 10.61 , respectively, when *L. smaragdus* was present.

Throughout the experiment RII values were always close to zero in the absence of the grazers (Fig. 5.4C). When *L. smaragdus* was present, however, the RII assumed positive



values in both culture types (around 0.45 after six weeks; Grazing: $F_{1,28} = 51.80$, $P < 0.001$, tested against the pooled term Tank + Residual; Fig. 5.4C), which indicates a facilitative action of *Ulva* towards *H. banksii* germlings.

Fig. 5.4. Temporal variation in the mean values of: A) percentage survival (\pm SE) of *H. banksii* germlings grown in mono- and mixed cultures with low and high density of *Ulva*, both in the presence and absence of *L. smaragdus* ($n = 8$); B) percentage cover variation (\pm SE) of *Ulva* in the three different culture types both in the presence and absence of *L. smaragdus* ($n = 8$); C) RII (\pm SE) in mixed cultures with low and high density of *Ulva*, both in the presence and absence of *L. smaragdus* ($n = 8$). The letters beside symbols show the ranking of the means according to the SNK tests for the final sampling date.

5.5. DISCUSSION

The results of this study provide a mechanistic understanding of initial conditions for attachment, settlement and growth which are likely to set the trajectory for the development of furoid populations. I showed that common, opportunistic algae may benefit from high nutrients and temperature increase and have suppressive effects of on settlement and growth of a dominant furoid. However, I also observed indirect facilitation of the perennial furoid by the ephemeral algae moderated through preferential grazing.

Ulva may affect *H. banksii* from the earliest stages of its life cycle, with chemical inhibition compounding the impact of pre-emption of space. Zygote settlement was reduced by 42% compared to controls when there had been a prior presence of *Ulva*, while the lowest levels of settlement occurred when *Ulva* was present on the plates (-66% compared to the controls). This type of pre-emption of space by ephemeral algae interfering with the attachment of furoid zygotes has been described in other studies (Worm et al. 1999, 2001, Berger et al. 2003, Isæus et al. 2004). When unoccupied plates were translocated into tanks previously occupied by *Ulva*, on the other hand, the zygotes were probably affected by the legacy of chemical alteration left in the culturing medium by *Ulva* after its removal. The ability of ulvoids to produce and release allelochemicals is increasingly recognized (Nelson et al. 2003). These products often degrade rapidly (Jin & Dong 2003, Wang et al. 2007), but this study showed that they can potentially affect *H. banksii* in the first 24 hours of its life cycle even without a continuous secretion from fresh tissue. Similarly, Nelson et al. (2003) described the impact of the toxic properties of extracts from the green algae *Ulva fenestrata* and *Ulvaria obscura* on the development of *Fucus gardneri* zygotes.

In the six-week experiments, it was not survival but growth that was greatly compromised by the presence of *Ulva*. In one sense, this is surprising, given that there were allelopathic effects on attachment in Experiment 1. If allelopathy were a major influence, it

might be expected to compromise also the survival of settlers, but this was not evident in my study. Instead, there was suppressed growth of *H. banksii* in the presence of *Ulva*. This was probably due to nutrient depletion (Fong et al. 1993) and light attenuation (Brun et al. 2003), rather than chemical inhibition. The high tolerance shown by *H. banksii* germlings to interspecific competition with *Ulva* is remarkable, since other studies of similar or shorter duration have described strong impacts of ephemeral species on post-settlement survival of the early life stages of various species of furoids, both in field (Berger et al. 2003, Isæus et al. 2004) and laboratory contexts (Steen 2004). Reduced growth rates, however, may represent a serious handicap for a slow-growing species like *H. banksii*, with important implications for population persistence and replenishment. Living on the substrate, small germlings face challenging physical (e.g., sediment scouring and burial, canopy shading and sweeping) and biotic conditions (e.g., competition with low-lying algal mats and turfs, invertebrate grazing) which generally have only a minor influence on adults (Vadas et al. 1992, Schiel & Foster 2006). As a consequence, delayed development and prolonged exposure to the rigours of benthic life may well result in increased mortality through time in natural conditions.

This study also highlighted the importance of biotic and abiotic influences in regulating the outcome of the interaction between the two species. The herbivorous snail preferentially grazed on *Ulva* and, as a result, was diverted from *H. banksii*. Grazers are known to exert a strong top-down control on ephemeral species, which can indirectly facilitate the establishment of late successional, perennial macroalgae (Lubchenco 1983, Kim 1997, Worm et al. 1999, 2001). My results are consistent with this large body of evidence and also indicate that the interactions between perennial and ephemeral algae may not necessarily be always negative. When competition affects growth but not mortality, species can simultaneously compete with and facilitate each other (Bruno et al. 2003). Even if the association with *Ulva* led to a competitive cost for *H. banksii*, attested by reduced growth rates, the reduction of

consumption was an obvious advantage. Associational defence in marine and terrestrial habitats usually occurs when the focal species is surrounded by unpalatable neighbours (Hay 1986, Barbosa et al. 2009), but in this case *Ulva* acted as a sink for the herbivores and *H. banksii* benefitted from its elevated palatability. These results amplify the findings of field-based experiments in which *L. smaragdus* showed a marked preference for other ephemeral, disturbance-oriented species like the brown algae *Adenocystis utricularis* and *Colpomenia sinuosa*, but had only minor effects on *H. banksii* (Walker 1998, Schiel 2006).

Increased temperature and nutrient levels synergistically enhanced the growth of *Ulva*. Similar results were found in other laboratory studies (Lotze et al. 1999, Lotze & Worm 2002, Steen 2004) and are consistent with the literature describing the association between coastal eutrophication and the rapid spread of opportunistic species leading to dramatic floristic changes (Valiela et al. 1997, Worm et al. 1999, Worm & Lotze 2006). A negative trend in *H. banksii* survival rates in response to temperature increase was also observed, but it was not statistically significant. Nonetheless, such findings are consistent with the results of further laboratory experiments where I recorded reduced levels of survival for the germlings of *H. banksii* and two other fucoids (*Cystophora torulosa* and *Durvillaea antarctica*) when exposed to a temperature increase of 3 °C during the initial eight weeks of their life cycle (see Chapter 6). Similarly, recent field observations and laboratory experiments have shown that the juvenile stages of the fucoid *Scytothalia dorycarpa* have a narrow optimal temperature window and are severely affected by temperatures just 2 °C above this range (Andrews et al. 2014).

Collectively my experiments indicate that the strength and direction of fucoid-ephemeral interactions may vary temporally and spatially in response to environmental conditions and herbivore pressure. Altered physical conditions may potentially shift the balance of the interactions between the two species in favour of *Ulva*. Based on these results

an increased competitive impact of *Ulva* under high temperature and nutrient levels is likely to be associated with a reduced fitness of *H. banksii* germlings in warmer waters. Such a combination of long-term climatic changes and anthropogenic nutrient loading is particularly likely to affect sheltered coastal areas (Schiel 2013), which represent favourable habitats for many ephemeral species (Berger et al. 2003), as well as for *H. banksii* (Morton & Miller 1968) and for numerous other species of furoids (Blanchette et al. 2000). Herbivory may release *H. banksii* from the competition with *Ulva*, and this latter, in the presence of the grazers, may turn out to be an unexpected ally for the furoid. As *L. smargdus* is by far the dominant grazer in southern New Zealand algal beds, the effects seen in the laboratory are likely to be relevant also in natural contexts. In the field, however, the impacts of multiple anthropogenic influences on herbivore populations have the potential both to reduce and increase the importance of their ecological role. For example, human exploitation of intertidal grazers has strong and well documented effects on the structure of algal communities (Castilla 1999, Aguilera & Navarrete 2007). Grazers' metabolism and rates of consumption, on the other hand, are expected to increase under altered climate regimes (Hillebrand et al. 2009, O'Connor 2009).

It is clearly impossible to incorporate great natural complexity into short-term investigations carried out in artificial contexts. Laboratory experiments, however, allow manipulations difficult to perform in the field and provide the opportunity to identify the contribution of selected factors in isolation and to estimate their effects on target organisms. Given the ever increasing human pressure on coastal areas worldwide (Halpern et al. 2008), it is particularly important to have a mechanistic understanding of how organisms respond to altered physical and biotic conditions (Vinebrooke et al. 2004, Crain et al. 2008). In this regard, the limited knowledge of the factors affecting the early demography of numerous key habitat-forming species represents a serious obstacle towards the identification of the causes

of their decline and the development of restoration strategies (Schiel & Foster 2006). Laboratory experiments are powerful tools to fill this knowledge gap (Irving et al. 2009) and the relevance of the findings of this study may extend beyond the individual case of *H. banksii*, providing useful insights for other investigations.

CHAPTER 6

**Impacts of local and global stressors in intertidal habitats:
influence of altered nutrient, sediment and temperature levels on
the early life history of three habitat-forming macroalgae**

6.1. ABSTRACT

As human pressure in coastal areas increases, it is important to understand how key functional components of nearshore ecosystems respond to combinations of global climate changes and local non-climatic stressors. Stressors originating at local scales such as elevated nutrient concentrations and sediment loads are known to contribute to the regression of large habitat-forming macroalgae in temperate rocky reefs. How the persistence of algal beds will be affected by combinations of altered nutrient and sediment regimes and increased temperatures under future global change scenarios is still unclear. Through a series of laboratory experiments I tested short- (48 hours) and long-term (eight weeks) effects of different combinations of nutrient, sediment and temperature on the early life stages of the habitat-forming fucoids *Hormosira banksii*, *Cystophora torulosa* and *Durvillaea antarctica*. A light coating of sediment affected the post-settlement survival of *H. banksii* and *C. torulosa* germlings within 48 hours and reduced growth and survival of all species over eight weeks. Temperatures 3 °C higher than ambient levels during the reproductive season of each species caused increased mortality of the germlings of the three fucoids after eight weeks, but these effects were only evident in the absence of sediment. The cold-adapted *D. antarctica* was particularly susceptible to temperature increase, with reduced germling survival in warmer waters after 48 hours. In the absence of sediment, nutrient enrichment stimulated the growth of *H. banksii* and *C. torulosa*, but caused a decline in the survival and growth of *D. antarctica*. This was probably due to the poor adaptation of *D. antarctica* to laboratory conditions. This study contributes to a better understanding of the impacts of altered physical conditions on important habitat-forming species. My results highlight mechanisms that may well apply in natural contexts, and they reinforce the need for appropriate management of local stressors in order to mitigate the impacts of altered climate conditions.

6.2. INTRODUCTION

Located at the interface between oceans and mainland, coastal ecosystems worldwide are subjected to considerable and increasing anthropogenic pressure, as a result of human demographic trends and activities in both realms (Halpern et al. 2008). Understanding how nearshore systems are affected by multiple anthropogenic perturbations is pivotal to preserve or restore their ecological value and the services they provide (Crain et al. 2008, 2009). Human influences of local dimension such as eutrophication (Smith & Schindler 2009), sedimentation (Airoldi 2003), resource overexploitation (Jackson et al. 2001), and exotic species introductions (Thomsen et al. 2014), have been extensively investigated and their impacts well documented. Local-scale perturbations, however, occur against a backdrop characterized by unprecedented climate change at global level (IPCC 2013). Global-scale phenomena such as ocean warming and acidification manifest their influence at local scales and their impacts are contingent on local conditions (Harley et al. 2006, Helmuth et al. 2010, Russell & Connell 2012). When the resilience of natural systems is eroded by intense anthropogenic pressure at local scales, however, the influence of altered global conditions can potentially be great. For example, recent research in coastal habitats has shown that the combined impacts of seawater eutrophication and acidification (Russell et al. 2009), as well as of overfishing, altered currents and rising temperatures (Ling et al. 2009) can accelerate the transition from kelp beds to states dominated by algal turfs and sea urchins. The compound effects of multiple anthropogenic perturbations, however, remain difficult to foresee (Folt et al. 1999, Crain et al. 2008, Darling & Côté 2008) and understanding how broad scale changes in climate superimpose effects on local, non-climatic processes is one of the most pressing priorities for research and management (Sala et al. 2000, Harley et al. 2006, Halpern et al. 2008, Russell & Connell 2012).

Because coastal ecosystems are often structured around one or few habitat-dominating species (Bruno & Bertness 2001), understanding the impacts of cross-scale stress sources on these key species is essential to predict widespread changes at the community level and beyond (Harley et al. 2006, 2012, Russell & Connell 2012, Wernberg et al. 2012). Here I tested the impacts of particular combinations of temperature, nutrient and sedimentation levels on the early life history stages of the habitat-forming fucoids *Hormosira banksii*, *Cystophora torulosa* and *Durvillaea antarctica*. These canopy-forming macroalgae dominate intertidal reefs around New Zealand across a range of shore heights and wave exposures. Importantly, these species have no functional equivalents (Taylor & Schiel 2005, Schiel 2006; see Chapter 2) and long-lasting impacts on the structure and productivity of the associated communities have been observed following their loss (Schiel 2006, Tait & Schiel 2011a).

Coastal New Zealand is affected by long-term seawater warming trends (IPCC 2013, Schiel 2013) and in many places by high nutrient and sediment loads because of altered land use (Goff 1997, Parfitt et al. 2008). Previous studies have reported a decline in the abundance of various species of fucoids in response to rising temperatures (Southward et al. 1995, Smale & Wernberg 2013) and to elevated nutrient and sediment regimes (Eriksson et al. 2002, Mangialajo et al. 2008, Bellgrove et al. 2010). Laboratory investigations have highlighted the sensitivity of fucoid juvenile stages to altered temperature (Andrews et al. 2014), nutrient (Kevekordes 2001, Bergström et al. 2003) and sediment levels (Schiel et al. 2006, Irving et al. 2009). However, there are few if any tests to date of the combined effects of these three factors on the early phases of the life cycle of habitat-forming fucoids. I did a series of laboratory experiments exposing *H. banksii*, *C. torulosa* and *D. antarctica* to combinations of multiple stressors representative of the current impacts of eutrophication and sedimentation along the coastlines of New Zealand (Schiel et al. 2006, Barr 2007), as well as of

temperatures in the range of what is predicted in the near future as a result of global warming trends (IPCC 2013). For each species, two separate experiments were done to test the impacts of the stressors on: 1) settlement and early post-settlement (48 hours) phases; 2) survival and growth rates over a period of eight weeks, which is significantly longer than most studies reported in the literature (Steen & Rueness 2004, Andrews et al. 2014). Although laboratory investigations cannot incorporate great natural complexity, my experiments were designed to tease out underlying mechanisms and sensitivities that may explain present and future changes in the structure of benthic assemblages dominated by macroalgal canopies. In particular I tested whether the effects of temperature, nutrients and sediment were independent or interactive, and whether the responses of the study species varied depending on their stages of development.

6.3. MATERIALS AND METHODS

6.3.1. Experimental design

The experiments were done at the Edward Percival Field Station in Kaikoura, along the east coast of the South Island of New Zealand. The fucoids *H. banksii*, *C. torulosa* and *D. antarctica* are found in great abundance along local reefs (Taylor 2002, Dunmore 2006, Schiel 2006). For each species I first ran a 48-hour experiment and then an eight-week experiment. These experiments were initiated in correspondence with the period of peak reproduction of each species when fertile adult plants were releasing gametes in the field. The two experiments were first done with *H. banksii* during the austral summer 2011 (December 2011 - February 2012), and successively repeated with *D. antarctica* and *C. torulosa*, during winter (June - August) and spring 2012 (September - November), respectively. To initiate each experiment, reproductive tissue from around ~ 50 plants was collected in the field. Given the large disparity in the rates of gamete release among species (Taylor 2002,

Dunmore 2006), it was difficult to obtain similar settlement densities for each species. Settlement densities in line with those observed in the field in Kaikoura were used (*H. banksii*: ~ 500 cm⁻², *D. antarctica*: ~ 1800 cm⁻², *C. torulosa*: ~ 60 cm⁻²; Taylor 2002, Dunmore 2006).

Settlers of all species were grown on 50 x 50 x 7 mm fibrolite plates housed in plastic tanks (37 x 25 x 7 cm) filled with filtered (1 µm) and UV sterilized seawater. Air pumps were used to aerate the tanks and keep the water in motion. Light racks provided illumination at an intensity of ~100 µmol m⁻² s⁻¹ under a 12:12 hour light:dark cycle. The plates were submerged throughout the experiments to exclude additional stress sources related to aerial exposure (see Chapter 5).

Different combinations of stressors were obtained through the manipulation of temperature (ambient vs. increased), nutrients (ambient vs. increased concentration) and sediment (present vs. absent). In each experiment the ambient temperature was the maximum observed at Kaikoura during the reproductive season of the study species (i.e., 17 °C, 11 °C and 15 °C for *H. banksii*, *D. antarctica* and *C. torulosa*, respectively; Chiswell & Schiel 2001). Increased temperatures were 3 °C higher than ambient temperatures, consistent with the predictions provided by the IPCC (2007) for the end of the 21st century for New Zealand and Southern Australia. Two temperature-controlled rooms equipped with independent thermostats were used to maintain the selected temperature levels throughout the experiments. It was not possible to allocate multiple rooms to the temperature treatments. The two rooms, however, were identical in all respects and the experimental set up (i.e., the positions of tanks, lights and air pumps) did not differ between them (see Chapter 5). Within each room, two tanks were assigned to each possible combination of nutrients and sedimentation, with four plates in each tank. Increased nutrient concentrations were obtained through the addition of 20 µM N (nitrate and ammonia added at a ratio of 1:1) and 2 µM P

(phosphate) per L of seawater, in order to match the values observed in eutrophic coastal areas around New Zealand (Barr 2007). In the tanks allocated to the +Sediment treatment, the plates were covered with a thin layer of sediment collected in the field, oven-dried, and uniformly distributed over their surface. One gram dry weight of sediment, mainly composed of fine sand (grain size: 100-250 μm), was sufficient to cover 100% of the surface of each plate with a thin dusting.

Before the start of all experiments, each tank (16 in total) was filled with 4 L of seawater and the plates were soaked for two days. In the 48-hour experiments, to assess the impacts of the stressors on the earliest phases of the life cycle of the study species, temperature and nutrient levels were altered before the gametes were introduced in the tanks. The gametes of each species were washed from adult plants using seawater, collected in a bucket and immediately inoculated into the experimental tanks to initiate the experiment. One litre of solution containing the reproductive cells of the study species was gently poured over the plates in each tank. The sediment was added to the +Sediment treatments after the initial 24 hours of the experiment to allow the zygotes to attach to the plates and not to the sediment grains.

At the start of the eight-week experiment, water temperature and nutrient concentration in each tank were kept at ambient levels and all plates were sediment-free. One litre of solution containing the reproductive cells of the study species was gently poured over the plates in each tank and the germlings (i.e., post-settlement fertilised stages) were allowed to acclimatize and develop under un-manipulated conditions for four days. After four days the water in each tank was replaced and the initial abundance of the germlings recorded. The manipulation of temperature, nutrient and sediment levels was then initiated. Temperature and nutrient levels were gradually increased over a period of 48 hours. Throughout the

experiments the water was replaced twice weekly and nutrients were re-added to the +Nutrients tanks after each water change.

6.3.2. Sampling and statistical analyses

At the conclusion of each 48-hour experiment all the plates were gently sprayed with seawater to remove the sediment (if present) and any germlings that might be loosely attached. Each plate was then examined under a binocular microscope and the abundance of the germlings was estimated in three haphazardly chosen 1 cm² areas.

In the eight-week experiments, the plates were sampled after two, five and eight weeks from the initial monitoring (four days). At each sampling date, all plates were gently sprayed to remove the dead germlings and the sediment (if present), and examined under a binocular microscope. The abundance of the germlings was estimated in three haphazardly chosen 1 cm² areas and sediment was re-added to the appropriate treatments after the germling count. Percentage survival rates were expressed as the proportional difference in the number of germlings in relation to the abundance recorded in the initial sampling (four days). At the end of the experiments, the mean size of the germlings was also calculated from ten individuals randomly selected from each plate. These were removed from the plates and measured lengthwise using an eyepiece graticule.

At the conclusion of the *H. banksii* eight-week experiment, the photosynthetic status of the germlings in response to the experimental treatments was also assessed using a pulse amplitude modulated fluorometer (Junior PAM, Walz, Germany). This assessed Chlorophyll fluorescence, a relative measure of the photochemistry of Photosystem II, and allowed calculation of the maximum quantum yield, a common indicator of photosynthetic efficiency (Maxwell & Johnson 2000). Germlings were detached from the plates using fine forceps, laid horizontally on a microscope slide and dark-adapted for 15 minutes. The slide was then

enclosed between two circular ring magnets (2 cm diameter). One of these, located above the slide, housed the PAM fiber optic, whose tip was perpendicular to the surface of the slide, at a distance of 2 mm from the germlings. Multiple germlings were placed adjacent to each other, to cover a 2 mm diameter circular area below the fiber optic, and incubated simultaneously. The germlings were exposed to a pulsed measuring beam of weak blue light ($0.15 \mu\text{mol m}^{-2} \text{s}^{-1}$, 450 nm) to measure the ground fluorescence (F_o), followed by a saturating pulse (0.6 seconds, $7000 \mu\text{mol m}^{-2} \text{s}^{-1}$), which raised the fluorescence to a maximum value, F_m . The maximum quantum yield (F_v / F_m) was then calculated as $F_m - F_o / F_m$ (Maxwell & Johnson 2000). Fluorescence analyses could not be repeated with the other fucoids. In the case of *D. antarctica*, this was due to the small size of the germlings, while in the *C. torulosa* experiment technical problems with the fluorometer occurred.

For each species, data of germling abundance (recorded at the conclusion of the 48-hour experiment) and percentage survival and size (recorded at the conclusion of the eight-week experiment), were analysed using a four-way ANOVA with the fixed factors: 1) Temperature (ambient vs. increased); 2) Nutrients (ambient vs. increased concentration); 3) Sediment (present vs. absent) and 4) the random factor Tank (nested within Temperature, Nutrients and Sediment). Since *D. antarctica* germlings did not survive under increased temperature (14 °C) after eight weeks, only the survival and the size of the germlings grown under ambient temperature (11 °C) were analysed, using a three-way ANOVA including the same crossed combinations of the factors Nutrients and Sediment and the random factor Tank. Maximum quantum yield values for *H. banksii* were analysed using a three-way ANOVA with the factors Temperature, Nutrients and Tank (nested within Temperature and Nutrients). The plates assigned to sediment deposition were not used for fluorescence analyses because, due to the strong impact of sedimentation, the size of the germlings was too small.

When the variability among tanks was negligible ($P > 0.25$) pooling procedures were applied according to Underwood (1997). Cochran's C -tests were used to test for homogeneity of variances before each analysis. No transformation was required for any of the response variables. Student-Newman-Keuls (SNK) tests were performed for *a posteriori* comparisons of the means (Underwood 1997).

6.4. RESULTS

In the 48-hour experiments, there were significant effects of sediment burial and temperature, which varied among species, while no effects of nutrient enrichment were detected. When covered with sediment, the abundance of newly settled germlings of *H. banksii* and *C. torulosa* germlings was reduced by approximately 70% ($F_{1,8} = 36.73$, $P < 0.001$; Fig. 6.1A) and 15% ($F_{1,56} = 17.24$, $P < 0.001$, tested against the pooled term Tank + Residual; Fig. 6.1B) compared to the –Sediment treatments, respectively, independently of temperature and nutrient levels. Increased temperature caused a 30% reduction in the abundance of newly settled germlings of *D. antarctica* in the initial 48 hours of their life cycle compared to the ambient temperature treatments ($F_{1,8} = 6.84$, $P < 0.05$; Fig. 6.1C), independently of nutrient and sediment manipulation.

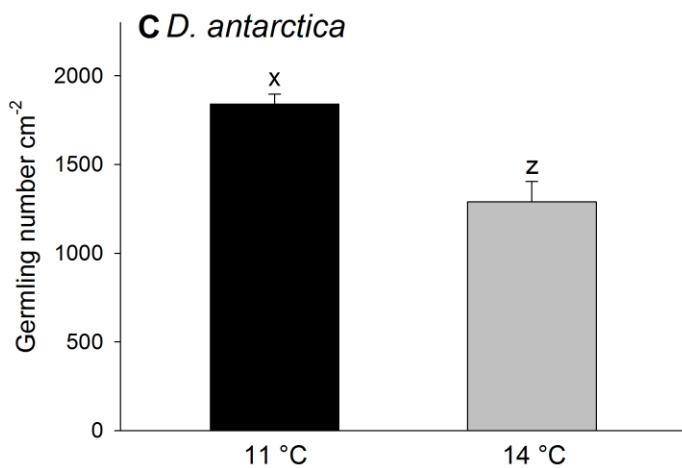
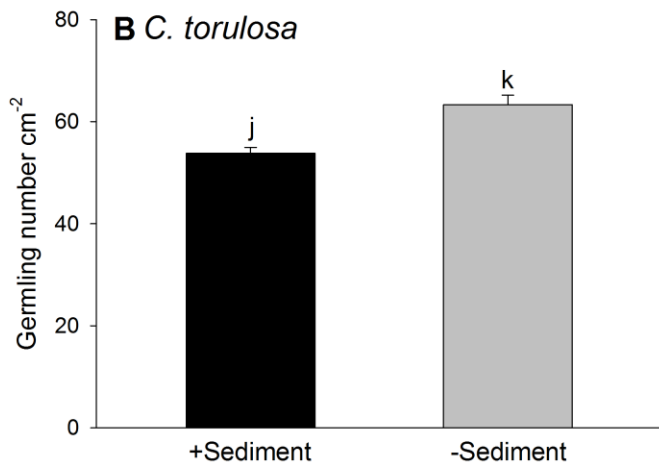
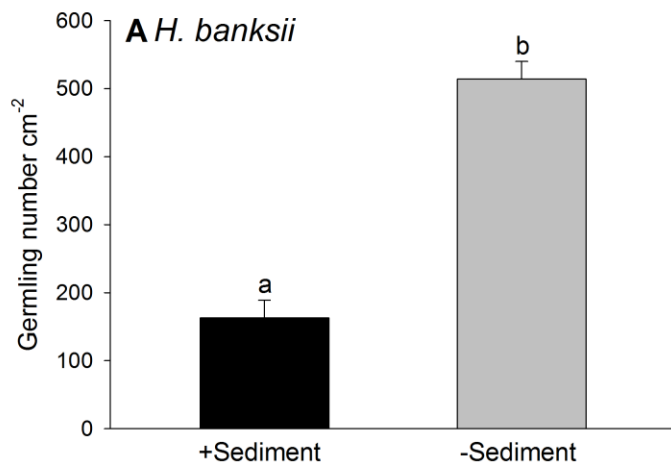


Fig. 6.1. Mean number of *H. banksii* (A) and *C. torulosa* (B) germlings (+SE) at the end of the 48-hour experiments in the presence and absence of sediment, across all levels of temperature and nutrient concentration (n = 32). Mean number of *D. antarctica* (C) germlings (+SE) at the end of the 48-hour experiments under ambient and increased temperature, across all levels of nutrient concentration and sediment deposition (n = 32). The letters show the ranking of the means according to the SNK tests.

In all eight-week experiments there were significant treatment interactions. Survival of all species was reduced by interactive effects of increased temperature and sedimentation, and *D. antarctica* was also affected by nutrient enrichment (Table 6.1). The impact of sediment on *H. banksii* germlings was evident after two weeks and a negative trend in survival rates in response to temperature increase also emerged after five weeks in the –Sediment treatments (Fig. 6.2A). At the end of the experiment there was a significant Temperature x Sediment interaction (Table 6.1A). *H. banksii* germling survival in the absence of sediment was higher at 17 °C (around 44%) than at 20 °C (around 27%). When the plates were covered with sediment, final survival rates were around 1%, with no differences between the two temperatures (Table 6.1A, Fig. 6.2A). In the *C. torulosa* experiment, the impact of sediment was evident after two weeks, as well as the separation between the two temperature levels in the –Sediment treatments (Fig. 6.2B). After eight weeks there was a significant Temperature x Sediment interaction (Table 6.1B). *C. torulosa* germling percentage survival in the absence of sediment was higher at 15 °C (around 48%) than at 18 °C (around 24%). In the presence of sediment, survival was between 4-5%, regardless of temperature manipulation (Table 6.1B, Fig. 6.2B). Survival of *D. antarctica* was affected by a combination of the three factors (Fig. 6.3). This was already evident after two weeks: at this stage germling percentage survival was reduced to less than 3% at 14 °C in the presence of nutrients and sediment (Fig. 6.3B), while the 11 °C –Sediment treatments were clearly separated from the others, with survival rates around 77% and 59% in the absence and presence of nutrients respectively (Fig. 6.3A). Percentage survival in all the other treatments was around 20% (Fig. 6.3A, B). At the conclusion of the experiment, no germlings survived at 14 °C (Fig. 6.3B). Under ambient temperature (11 °C) the –Nutrients –Sediment treatment had the highest survival rates (around

13%), while survival was around 1% under the other combinations of nutrients and sediment (Table 6.1C, Fig. 6.3A).

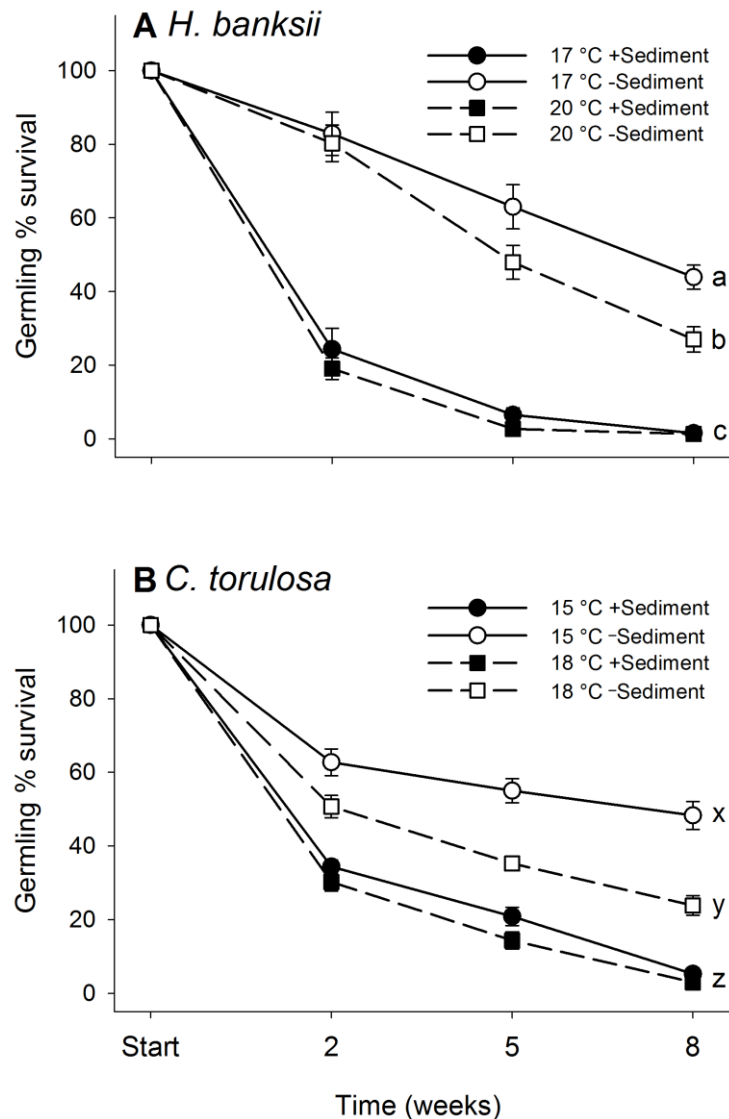


Fig. 6.2. Temporal variation in the mean percentage survival (\pm SE) of *H. banksii* (A) and *C. torulosa* (B) germlings in the eight-week experiments under ambient and increased temperature levels both in the presence and absence of sediment. Data are pooled across temperature levels ($n = 16$). The letters show the ranking of the means according to the SNK tests.

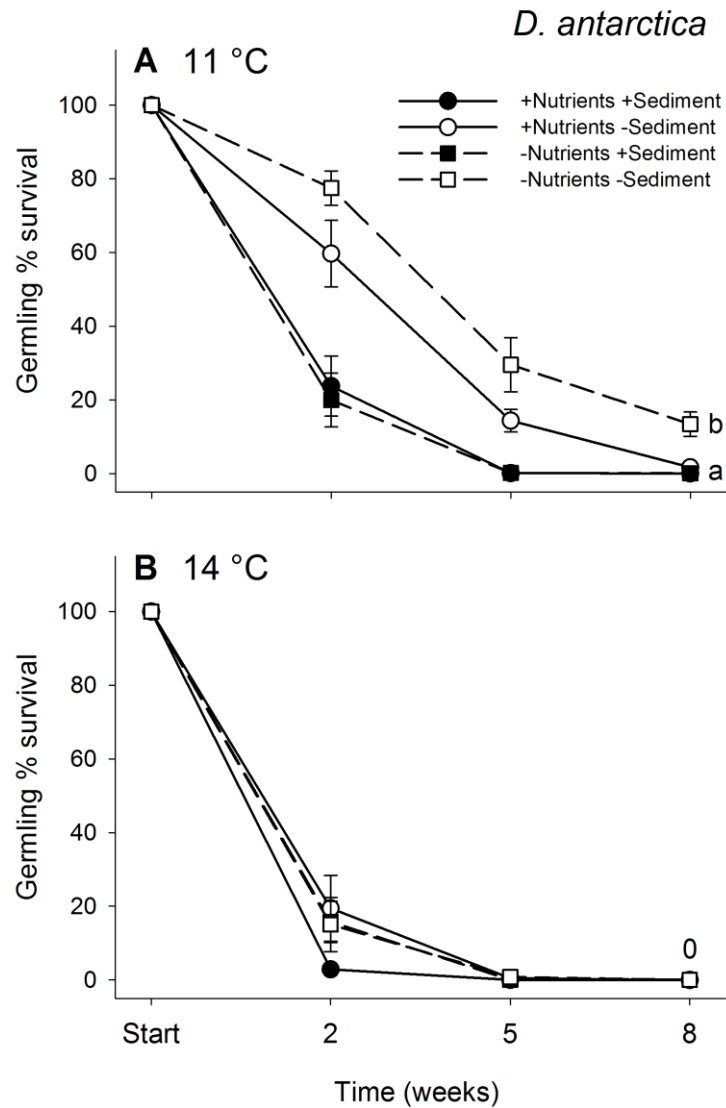


Fig. 6.3. Temporal variation in the mean percentage survival (\pm SE) of *D. antarctica* germlings in the eight-week experiment under all combinations of nutrient concentration and sediment deposition, both at 11 °C (A) and 14 °C (B); $n = 8$. The letters show the ranking of the means according to the SNK tests for the germlings grown at 11 °C. No germlings survived at 14 °C after eight weeks.

Table 6.1. ANOVA on data of percentage survival of *H. banksii* (A), *C. torulosa* (B) and *D. antarctica* (C) germlings after eight weeks. Survival rates of *H. banksii* and *C. torulosa* were tested across different levels of temperature (ambient or increased), nutrient concentration (ambient or increased) and sediment deposition (present or absent). For *D. antarctica*, the analysis tested the effects of nutrients (ambient or increased) and sediment (present or absent) on the survival of the germlings grown under ambient temperature (100% mortality occurred under increased temperature). *P < 0.05; **P < 0.01; ***P < 0.001.

	A. <i>H. banksii</i>			B. <i>C. torulosa</i>		C. <i>D. antarctica</i>			
Source of variation	DF	MS	F	MS	F	Source of variation	DF	MS	F
Temperature (T)	1	1181.64	5.75*	2848.89	10.80*	Nutrients (N)	1	207.28 ^a	11.84**
Nutrients (N)	1	301.89	1.47	213.89	0.81	Sediment (S)	1	442.53 ^a	19.38***
Sediment (S)	1	18530.02	90.15***	16352.02	61.97***	N x S	1	270.28 ^a	11.84**
T x N	1	356.27	1.73	47.27	0.18	Tank (N x S)	4	10.41 ^a	pooled
T x S	1	1113.89	5.42*	1947.02	7.38*	Residual	24	24.91	
N x S	1	301.89	1.47	268.14	1.02				
T x N x S	1	337.64	1.64	66.02	0.25				
Tank (T x N x S)	8	205.5	4.09***	263.89	4.19***				
Residual	48	50.26		63.01					

^aTested against the pooled term Tank + Res (MS = 22.83, df = 28)

For all species, the sizes of the germlings after eight weeks were affected by sediment and nutrients, with no effects of temperature. Sediment deposition limited the growth of all species, independently of nutrient addition (Fig. 6.4). In the absence of sediment, higher nutrient availability stimulated the growth of *H. banksii* (Nutrients x Sediment: $F_{1,8} = 138.14$, $P < 0.001$; Fig. 6.4A) and *C. torulosa* germlings (Nutrients x Sediment: $F_{1,8} = 9.87$, $P < 0.05$; Fig. 6.4B). *D. antarctica* germlings, on the contrary, were larger under ambient nutrient levels when not covered with sediment (Nutrients x Sediment: $F_{1,4} = 8.13$, $P < 0.05$; Fig. 6.4C).

PAM fluorometry confirmed the positive influence of nutrient enrichment on the photosynthetic efficiency of *H. banksii* germlings. Maximum quantum yield values were approximately 25% higher under increased nutrient levels ($F_{1,28} = 30.31$, $P < 0.01$, tested against the pooled term Tank + Residual; Fig. 6.5), independently of temperature manipulation.

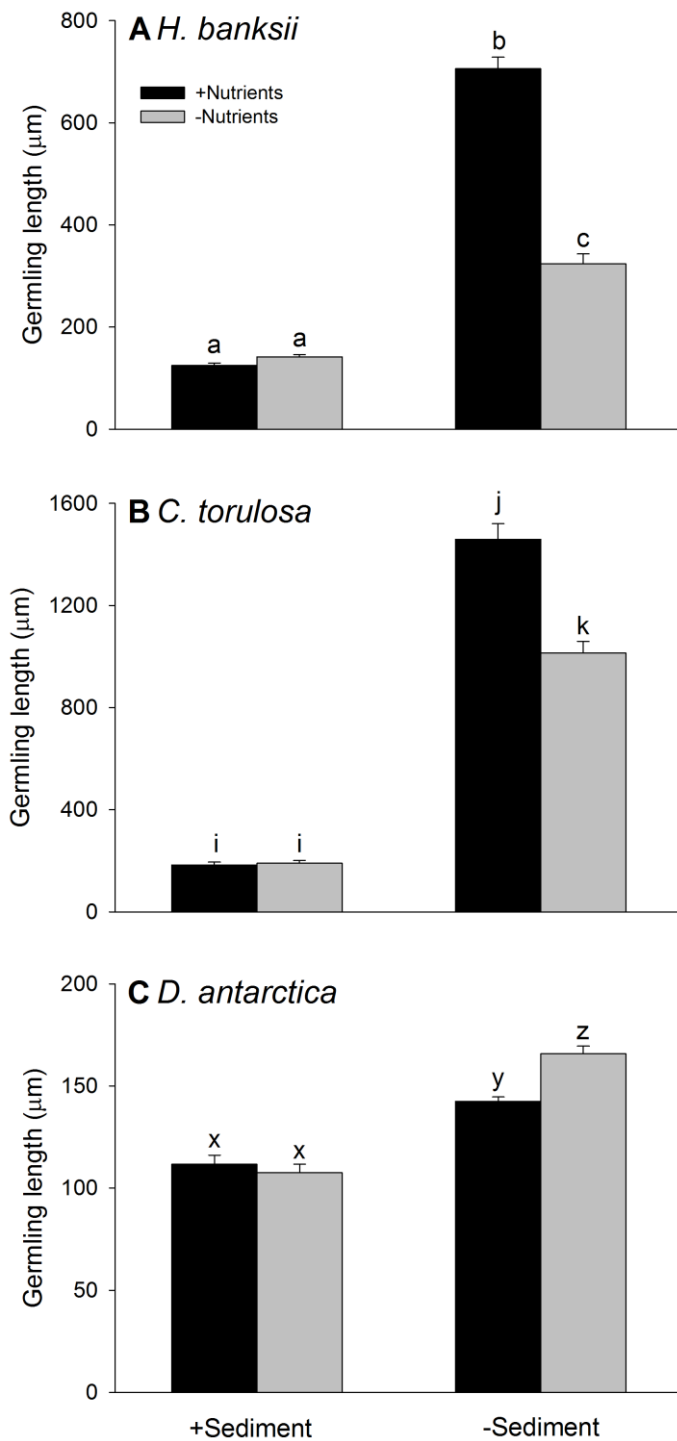


Fig. 6.4. Mean length (+SE) of *H. banksii* (A), *C. torulosa* (B) and *D. antarctica* (C) germlings recorded at the end of the eight-week experiments under ambient and increased nutrient levels, both in the presence and absence of sediment. Data are pooled across temperature levels (n = 16 for *H. banksii* and *C. torulosa*; n = 8 for *D. antarctica*). The letters above the bars indicate the ranking of the means according to the SNK tests.

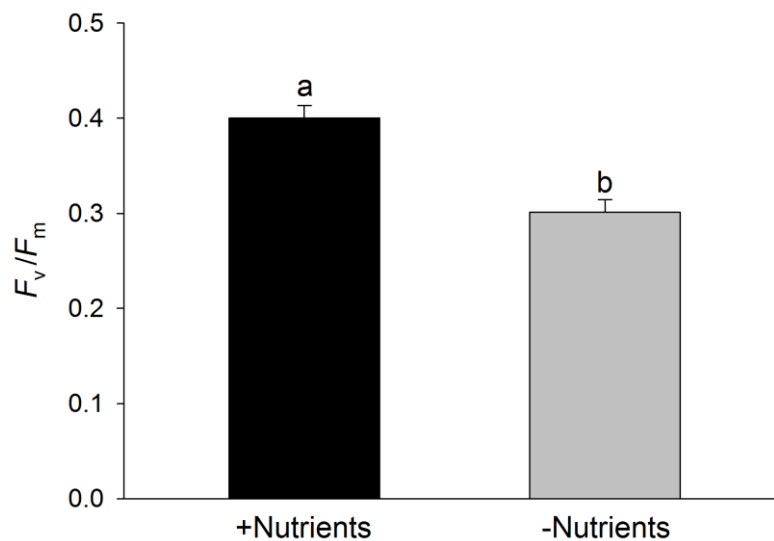


Fig. 6.5. Maximum quantum yield (+SE) of *H. banksii* germlings recorded at the end of the eight-week experiment under ambient and increased nutrient levels. Data are pooled across temperature levels (n = 16). The letters above the bars indicate the ranking of the means according to the SNK tests.

6.5. DISCUSSION

This study showed both independent and combined effects of temperature warming, nutrient enrichment and sedimentation on the survival and growth of three important habitat-forming macroalgae. A fine sediment coating acted as a major barrier to the post-settlement survival and growth of the germlings of all three fucoids, and temperature increase caused higher mortality of all species. Nutrient enrichment was a significant stressor for *D. antarctica*, while *H. banksii* and *C. torulosa* benefitted from increased nutrient availability. These results highlight potential critical thresholds to the persistence of fucoid stands and shed light on the challenges which these important biogenic habitats may face in the near future.

Previous studies have already shown the impacts of sediment on fucoid early life stages (Chapman & Fletcher 2002, Schiel et al. 2006, Irving et al. 2009). My results, in particular, integrate those of Schiel et al. (2006), who observed that a light dusting of sediment reduced

settlement of *H. banksii* by 34% and of *D. antarctica* by 71% relative to controls, and complete cover of sediment prevented attachment altogether. In my study, the germlings of the three furoids were extremely sensitive to sediment deposition in the post-settlement phases. A dusting of sediment for just 24 hours had a significant impact on the germlings of *H. banksii* and *C. torulosa*. This indicates that even short-term sediment disturbance caused, for example, by increased sediment influx following strong rainfalls (Airoldi 2003), may have serious consequences for the replenishment of furoid stands. The effects of sediment escalated greatly with extended periods of burial, reducing the survival of the three species close to zero over eight weeks. When covered with sediment, reduced light availability was clearly an impediment for the germlings, as evidenced by their slow growth rates, but the juvenile stages of other furoids have been shown to be very tolerant to long periods of darkness (Chapman & Fletcher 2002, Irving et al. 2009). Other mechanisms such as altered circulation of water, nutrients and gases, may have contributed to the strong impact of sediment on the study species.

The effects of increased temperature and nutrient levels were subordinate to those of sedimentation (i.e., simple comparative effects; Folt et al. 1999) and were only evident in the absence of sediment, the only exception being the *D. antarctica* 48-hour experiment. Increased nutrient loading often combines with sedimentation to promote the shift from algal forests to simplified systems dominated by ephemeral, opportunistic species in intertidal and shallow subtidal habitats (Eriksson et al. 2002, Gorgula & Connell 2004). In this study there were contrasting responses to nutrient enrichment. Increased nutrient availability stimulated the growth of *H. banksii* and *C. torulosa* and, in the case of *H. banksii*, was also associated with higher levels of fluorescence yield, which indicate a good development of the photosynthetic apparatus (Maxwell & Johnson 2000). Elevated concentrations of ammonium, nitrate and phosphate have been shown to affect critical developmental processes in various

species of furoids, including *H. banksii* (Kevekordes 2001, Bergström et al. 2003), but my experiments indicate that elevated nutrient levels analogous to the levels recorded in some eutrophic coastal areas around New Zealand (Barr 2007) may have a positive effect on the development of *H. banksii* and *C. torulosa*.

Nutrients, on the other hand, had negative effects on survival and growth rates of *D. antarctica*. This is somewhat surprising, because in natural contexts this species is abundantly distributed in upwelling areas with nutrient-rich waters (e.g., West Coast of New Zealand, Menge et al. 1999; Chile, Nielsen & Navarrete 2004). Nonetheless, my results suggest that the early life stages of *D. antarctica* may be particularly sensitive to increased nutrient concentrations when growing under stressful physical conditions. In my experiment, the susceptibility of *D. antarctica* to nutrient enrichment may have increased because of a poor adaptation to laboratory conditions, where the hydrodynamic environment of exposed shores, ideal for this species (Morton & Miller 1968, Taylor 2002), could not be recreated. Even under un-manipulated conditions (i.e., ambient temperature and nutrient levels and no sediment), in fact, *D. antarctica* germlings showed reduced percentage survival (13%) compared to *H. banksii* (44%) and *C. torulosa* (48%), and growth rates about 20 times slower than in the field (Taylor 2002).

While the impacts of sediment and nutrients are well documented, the influence of altered climate conditions on the early demography of habitat-forming macroalgae is still largely unexplored (Harley et al. 2012, Russell et al. 2012, Wernberg et al. 2012). Here water temperatures 3 °C higher than ambient levels reduced germling survival rates consistently across the three study species. The impact of temperature on *D. antarctica* was already evident after 48 hours, as crucial processes such as fertilization and attachment of the zygotes were likely impaired. Reduced post-settlement survival under increased temperatures was highlighted in the eight-week experiments for all species. Although my experiments could

not account for the underlying physiological mechanisms, elevated temperatures may have increased metabolic demands beyond the rates of productivity, and thermally sensitive cellular components such as proteins and membranes may have been affected by prolonged water warming (Davison & Pearson 1996, Eggert 2012). *D. antarctica* was particularly vulnerable to long-term exposure to warmer temperatures, with 100% mortality after eight weeks. Even if probably affected by its poor adaptation to laboratory conditions, these results confirm the elevated susceptibility of this cold-adapted species to increased temperatures, already shown by tests on adult individuals (Cruces et al. 2013).

Increased mortality under elevated temperatures was not associated with reduced growth rates and, in the case of *H. banksii*, fluorescence analyses confirmed that the photosynthetic efficiency of the germlings was not affected by temperature manipulations. Juvenile individuals may not have the same physiological plasticity which allows adult plants to adjust metabolic and photosynthetic rates in order to maximize survival under stressful conditions (Davison & Pearson 1996, Eggert 2012). Furthermore, optimal temperatures for growth and survival do not always coincide. For example, juvenile gametophytes of the kelp *Ecklonia radiata* in Western Australia exhibit maximum growth rates with water temperatures around 20-22 °C, which are well above their thermal optimum for survival (~16 °C; Mohring et al. 2013). Much is still unknown about the thermal physiology of the early life stages of algae. Further research in this area will help to understand how seaweeds respond to climate change and to predict future large-scale distributional shifts (Harley et al. 2012, Russell et al. 2012, Wernberg et al. 2012).

Collectively, the results of this study complement the findings of previous field-based research, enhancing our mechanistic understanding of the influence of anthropogenic stressors of local and global dimensions on critical phases of the life cycle of important components of nearshore systems. In degraded environments, for example, the relative

contribution of increased nutrient and sediment levels to the loss of furoid canopies is often indistinguishable (Mangialajo et al. 2008, Bellgrove et al. 2010). My experiments disentangled the influence of these two factors, showing that the effects of nutrient enrichment were subordinate to those of sedimentation. Altered sediment dynamics are a well recognised issue in coastal areas worldwide (Airoldi 2003; see Chapter 3) and the results of this study constitute further evidence of the threats that they pose to the persistence of algal beds. This study, in addition, provides a mechanistic linkage between predicted climate conditions and algal early demography. Studies correlating sea surface temperature increase with seaweeds' distribution shifts (e.g., Southward et al. 1995, Sagarin et al. 1999) generally ignore the influence of other climatic and non-climatic factors interacting with temperature at local scales (Helmuth et al. 2006a, 2010, Russell & Connell 2012). Here I showed experimentally that despite the proven ability of adult plants to survive long periods of emersion (Morton & Miller 1968), these three furoids may find it hard to adapt to waters 3 °C warmer than the present temperatures at the start of their life cycle. This may represent a serious handicap particularly for *D. antarctica*, which has a narrow reproductive window confined to the coldest months of the year (Hay 1979, Taylor 2002).

This is one of the few studies testing the responses of furoid early life stages to forecasted climate changes (see also Andrews et al. 2014). However, caution is always required when interpreting the results of experiments conducted under artificial, simplified and relatively short-term conditions. The manifestations of climate change are, in fact, far more complex than simple variations in average temperatures (Benedetti-Cecchi et al. 2006, Helmuth et al. 2006a). Furthermore, these three species are also present in warmer waters, for example around the North Island of New Zealand (Morton & Miller 1968), suggesting that processes of physiological acclimatization and genetic adaptation (Breeman 1988, Clark et al. 2013, Jueterbock et al. 2014) may contribute to increasing their thermal tolerance.

Our findings may have wide implications in natural contexts, where reduced recruitment rates of perennial macroalgae under warmer temperatures and elevated sedimentation are likely to be associated with increased interspecific competition from low-lying algal turfs. Turf-forming algae, in fact, thrive under high sediment loads (Airoldi 2003, Gorgula & Connell 2004) and may benefit from increased temperatures (Connell & Russell 2010). This emphasizes the importance of management actions aiming to mitigate the influence of local stressors and to break their synergisms with global scale conditions (Ling et al. 2009, Russell et al. 2009, Falkenberg et al. 2013a). Reducing direct and indirect impacts of sedimentation on habitat-forming macroalgae may prove a key first step to increase the resilience of algal beds in the face of climate change and other human-related perturbations.

CHAPTER 7

General Discussion

7.1. SUMMARY

In this thesis I investigated the impacts of natural and human-related perturbations on intertidal algal assemblages dominated by furoid canopies. In particular, I tested how altered physical and biotic conditions can affect the dominant furoids and assessed potential implications for the structure and functioning of the associated algal assemblages. The impacts of different types of perturbations were tested at different levels of biological organization, from entire assemblages to individual organisms.

A removal experiment was initially set up to test the role of different assemblage components in driving assemblage response to mechanical perturbations of increasing severity (Chapter 2; Table 7.1). This experiment confirmed the key role of the canopy-forming furoids *H. banksii* and *C. torulosa* in this system. Aside from short-lived blooms of ephemeral algae, these dominant furoids were the only taxa to increase their abundance in response to disturbance. This confirmed the limited degree of functional redundancy within this system (Schiel 2006, Tait 2010). The study also provided numerous insights into the patterns of resistance and resilience of understory algal assemblages associated with furoid canopies to increasing disturbance intensities (Chapter 2; Table 7.1).

My subsequent studies (Chapters 3 to 6; Table 7.1) focused on the most abundant components of intertidal algal assemblages along the east coast of New Zealand (i.e., canopy-forming furoids and turf-forming articulated coralline algae) and on the taxa that showed rapid positive responses to disturbance in the initial experiment (i.e., fast-growing ephemeral algae). On the basis of the information about physical and biotic conditions commonly associated with the regression of macroalgal stands (e.g., Benedetti-Cecchi et al. 2001, Eriksson et al. 2002, Berger et al. 2004, Airolidi et al. 2008, Connell et al. 2008, Bellgrove et al. 2010), I expected coralline turfs and ephemeral algae to interact with altered environmental conditions and affect the replenishment and persistence of furoid canopies.

Substrate pre-emption by the turfs did indeed reduce furoid recruitment (Chapters 3 and 4; Table 7.1) and their impacts were compounded by the deposition of sediment on unoccupied substrates (Chapter 3; Table 7.1). I also highlighted further implications of sediment-turf interactions, showing that the accumulation of sediment within articulated coralline algae may limit their photosynthetic capacity, with potential implications for the functioning of assemblages which include a furoid canopy (Chapter 3; Table 7.1).

Ephemeral fast-growing algae responded positively to nutrient enrichment and temperature warming (Chapters 4 and 5; Table 7.1), but had no impact on furoid recruitment in the field (Chapter 4; Table 7.1). Laboratory experiments, however, showed that ephemeral algae may impair settlement and growth of furoid early life stages and that such impacts may be modulated by the action of grazing gastropods (Chapter 5; Table 7.1). In the laboratory, I also tested the influence of different combinations of altered temperature, nutrient and sediment levels on furoid early life history stages (Chapter 6; Table 7.1). I found independent and combined impacts of these stress sources on the survival and growth of three important habitat-forming fucoids. Sediment burial and temperature increase affected all three species, while nutrient enrichment had a negative impact on *D. antarctica* and positive effects on *H. banksii* and *C. torulosa* (Chapter 6; Table 7.1).

Table 7.1. Overview of the findings of the thesis.

Chapter	Physical mechanisms	Negative effects/responses	Positive effects/responses
2	Mechanical perturbations		
	Light intensity	Slow canopy recovery	
	Medium intensity	Reduced growth and/or recruitment of minor understory fucoids	Increased growth of understory conspecific individuals of the dominant fucoids
	High intensity	Delayed canopy recovery Reduced growth and/or recruitment of minor understory fucoids Reduced abundance of non-ephemeral algae	Increased recruitment of the dominant fucoids Increased abundance of ephemeral algae
	Extreme intensity	Delayed canopy recovery Reduced understory diversity (low-shore) Reduced growth and/or recruitment of minor understory fucoids Reduced abundance of non-ephemeral algae Slow recovery of articulated coralline algae	Increased recruitment of the dominant fucoids Increased abundance of ephemeral algae
3, 6	Increased sedimentation	Reduced furoid recruitment Reduced productivity of articulated coralline, with potential implications for assemblage functioning Reduced survival and growth of furoid early life stages	
4, 5, 6	Nutrient enrichment	Reduced survival and growth of furoid early life stages (<i>D. antarctica</i>)	Increased growth of furoid early life stages (<i>C. torulosa</i> and <i>H. banksii</i>) Increased abundance of ephemeral algae
5, 6	Increased temperature	Reduced survival of furoid early life stages	Increased abundance of ephemeral algae

Table 7.1. continued

Chapter	Biological mechanisms	Negative effects/responses	Positive effects/responses
3, 4	Increased abundance of algal turfs	Reduced furoid recruitment Reduced abundance of ephemeral algae (<i>Ulva</i> spp.)	Increased assemblage productivity Increased abundance of ephemeral algae (<i>Colpomenia</i> spp.)
4, 5	Increased abundance of ephemeral algae	Reduced growth of furoid early life stages (<i>H. banksii</i>)	Increased survival of furoid early life stages (<i>H. banksii</i>) because of associational defence from grazing
5	Grazing	Reduced abundance of ephemeral algae (<i>Ulva</i> spp.)	Reduced growth of furoid early life stages (<i>H. banksii</i>)

7.2. ASSEMBLAGE RESPONSES TO DISTURBANCE

Assessing the capacity of natural systems to withstand or recover from perturbations is essential to understanding and predicting the magnitude and ramifications of the impacts of disturbance agents (Connell 1978, Pimm 1984, Sousa 1984, 2001, Pickett & White 1985, Allison 2004). In Chapter 2, I simulated a realistic extinction scenario in macroalgal assemblages with uneven species abundance patterns, and I examined the patterns of resistance and resilience of various assemblage components. Independently of species composition and richness at two sites and shore heights, I found that only two species, the fucoids *H. banksii* and *C. torulosa*, were able to play a dominant structuring role, forming large canopies and modifying the physical features of the habitat. The speed of canopy recovery varied depending on disturbance intensity. Even the lightest disturbance had an impact lasting for at least eighteen months. Following more intense disturbances, the regeneration of the canopies of *H. banksii* and *C. torulosa* was quicker when the mid-canopy was not removed because of the development of conspecific juvenile plants into adult individuals. In all treatments, however, the formation of the canopy relied entirely on the recruitment and growth of *H. banksii* and *C. torulosa*, despite the presence of four other fucoids in the system. This confirms the findings of previous research in the same system (Lilley & Schiel 2006, Schiel 2006, Schiel & Lilley 2007), but contrasts with numerous other studies showing the development of alternative canopies following the removal of the dominant canopy-former elsewhere. The replacement of *Ascophyllum nodosum* by *Fucus* spp., for example, is a classic case which has been well documented at numerous locations (Jenkins et al. 1999a, 2004, Bertness et al. 2002, Petraitis & Dudgeon 2005).

It has been suggested that subordinate members of terrestrial and marine plant communities may act as a filter, influencing the trajectories of recovery of dominant assemblage components following major perturbations (Grime 1998, Viejo et al. 2008). The

influence of understory algae on the dynamics of canopy recovery, however, was very limited in my study. There was no indication of a facilitative role of understory algae towards the dominant fucoids, and negative impacts of understory algae (i.e., turf-forming articulated corallines) on fucoid recruitment were evident only at one shore height at one location.

Increased cover of understory species can also compensate for the decline in community biomass caused by the elimination of the canopy (Miller et al. 2011, Bulleri et al. 2012a, Valdivia et al. 2012). Compensatory dynamics are expected to be particularly influential in species-rich systems, as more diverse communities may express a wider range of responses to perturbations (Yachi & Loreau 1999, Ives et al. 2000, Allison 2004, Aquilino & Stachowicz 2012). For example, the development of a rich understory of kelps and red algae has been shown to maintain high levels of ecosystem net primary production (NPP) despite the reduction of the canopy of the giant kelp *Macrocystis pyrifera* (Miller et al. 2011). In my study, however, there was no evidence that the growth of understory algae may represent a buffering mechanism following the loss of the dominant habitat formers. This was a consistent result at both locations and shore heights investigated, independently of the diversity and composition of understory assemblages. These results confirm that functional replacement following the loss of key species is limited in this system (Schiel 2006, Tait 2010, Tait & Schiel 2011a,b). The absence of compensatory dynamics in intertidal habitats is generally ascribed to the prevalence of environmental forcing due to extreme physical conditions for marine organisms (Bertness & Callaway 1994, Bulleri 2009). This seems to be the case in the intertidal assemblages examined in my study, where most species depend on the amelioration of physical stress by the dominant habitat-formers and are unable to achieve large body sizes (Schiel 2006). Indeed, the species which could have provided functional replacement for the dominant fucoids (i.e., understory fucoids such as *C. torulosa* in the mid-

shore, and *C. retroflexa* and *C. scalaris* in the low-shore) showed reduced rates of growth or recruitment when the overlying canopy was disturbed.

Other components of the understory, however, were generally resistant to disturbances affecting the overlying canopy, and there was little variability in the multivariate structure of understory assemblages when the canopy was experimentally thinned or removed.

Furthermore, when the understory was removed as a consequence of disturbance, its re-assembly occurred more quickly than the regeneration of the overlying canopy. This shows that the capacity of understory assemblages to withstand or recover from perturbations may be to some extent unrelated to the abundance of the canopy.

Previous studies in this same study system have shown that when the canopy is fragmented or lost, flow-on effects resulting in the burn-off of understory algae occur, with a significant loss of diversity and long-lasting impacts on assemblage structure and productivity (Lilley & Schiel 2006, Schiel & Lilley 2007, Tait & Schiel 2011a). This was not evident in my experiment. These contrasting findings may be explained by differences in the size and timing of the experimental manipulations. The study of Lilley & Schiel (2006), for example, was initiated at a similar time of the year as my experiment (winter), but involved the clearance of *H. banksii* canopies from 9 m² plots, areas much larger than the experimental units in my study. Buffering of physical conditions by the surrounding canopies, therefore, may have been less influential. In a further study, Schiel & Lilley (2007) removed different proportions of *H. banksii* canopies from 0.25 m² plots, areas the same size as the experimental units in my study, and observed a decline in richness and cover of understory taxa. This experiment, however, was started in summer. Nonetheless, in my experiment, the recovery of furoid canopies only started after more than one year, which suggests that understory assemblages were probably exposed to stress levels analogous to those in the experiment of Schiel & Lilley (2007) during the warmest months of the year. It is, therefore,

complicated to draw definitive conclusions about the mechanisms underlying such discrepancies. Further repetitions of these experiments through time may help to reconcile and clarify these contrasting patterns (Underwood 1997, 2000).

7.3. IMPACTS OF ALTERED PHYSICAL AND BIOTIC CONDITIONS ON DOMINANT HABITAT-FORMERS

My first experiment (Chapter 2) and previous investigations in the same system (Lilley & Schiel 2006, Schiel 2006, Schiel & Lilley 2007, Tait & Schiel 2011a,b) showed that two dominant canopy-forming furoids are essential to maintaining the structure and productivity of these intertidal algal assemblages and that no other species in the system can provide analogous ecosystem services. This is often the case in a variety of other coastal systems which are structured around one or few habitat-modifying species (e.g., seagrass meadows, mussel beds; Bruno & Bertness 2001, Bruno et al. 2003).

In my subsequent experiments, I investigated how competition by turf-forming articulated corallines, ephemeral opportunistic algae, and altered physical conditions (i.e., increased sedimentation, nutrient enrichment and warmer temperatures) can affect key habitat-formers in the New Zealand intertidal, both separately and in combination (Chapters 3 to 6; Table 7.1). Increased sediment and nutrient loadings are contributing to the spread of turf-forming and ephemeral algae in many places. Mats of articulated corallines, for example, can be very abundant at locations affected by organic pollution and elevated sedimentation (Airoldi 2003, Arévalo et al. 2007, Bellgrove et al. 2010). Fast-growing ephemeral algae, on the other hand, are known to produce extensive blooms in response to nutrient enrichment (Lotze et al. 1999, Lotze & Worm 2002, Steen 2004). In addition, there is increasing concern about the compound impacts of local stress sources (such as sediment and nutrient pollution)

and altered climate conditions on coastal systems (Halpern et al. 2008, Crain et al. 2009, Russell & Connell 2012).

I focused, in particular, on potential impacts of these different physical and biotic stress agents on furoid recruitment and early demography. Juvenile stages are a critical bottleneck in the life cycle of perennial habitat-forming macroalgae because early life stages are more susceptible to consumption, competition and disturbance than adults (Vadas et al. 1992, Schiel & Foster 2006). Previous studies have highlighted the sensitivity of furoid juvenile stages to altered temperature (Andrews et al. 2014) and nutrient (Kevekordes 2001, Bergström et al. 2003) levels. In addition, the attachment and the post-settlement survival of these microscopic stages can be affected by the presence of low-lying algae (Worm et al. 1999, 2001, Bellgrove et al. 2010) and by the accumulation of sediment in the benthic environment (Schiel et al. 2006, Irving et al. 2009). A combination of field and laboratory experiments (Chapters 3 to 6) was used to test the independent and combined effects of nutrients, sediment, temperature and interspecific competition with other algal forms on different phases of the early life history of the dominant furoids in the New Zealand intertidal.

7.3.1. Impacts of sedimentation and algal turfs

Laboratory experiments showed that sediment deposition severely reduced the survival and growth of recently settled germlings of three different furoids (Chapter 6; Table 7.1).

Sediment pre-emptive effects had been shown to impair the settlement of *H. banksii* and *D. antarctica*, as their zygotes tend to attach to the sediment grains and not to the underlying substrate (Schiel et al. 2006). My study highlighted the impacts of sediment deposition on different post-settlement stages of *H. banksii*, *C. torulosa* and *D. antarctica*. A dusting of sediment for only 24 hours reduced the number of *H. banksii* and *C. torulosa* settled germlings by about 70% and 15% respectively. This suggests that even short-term sediment

disturbance caused, for example, by increased sediment influx following strong rainfall and storms (Airoldi 2003, Hurley 2009), may have serious implications for the replenishment of furoid stands. The impacts of sediment deposition were exacerbated by extended periods of burial, with survival rates close to zero for all three species after eight weeks.

The impacts of sediment were also evident in the field (Chapter 3; Table 7.1), where sediment removal from unoccupied substrates increased the cover of *H. banksii* recruits by about 40%. Sediment removal, however, did not facilitate the recruitment of *H. banksii* on surfaces monopolized by mats of turf-forming coralline algae. The use of artificial mimics revealed that the impact of the coralline turfs on *H. banksii* recruitment was due to the physical properties of these complex biogenic habitats. These results show that sediment deposition on unoccupied substrates may override the influence of habitat heterogeneity (Balata et al. 2007), homogenizing furoid recruitment across substrates with different topographic complexity. This experiment also confirms the importance of the structural changes produced by algal turfs in the benthic environment. The physical properties of coralline turfs, for example, are extremely important for the composition of the associated macrofaunal assemblages (Kelaher 2002), while the complex three-dimensional structure of filamentous turfs has been shown to facilitate the spread of the invasive macroalga *C. racemosa* in the Mediterranean Sea by providing safe anchoring to its prostrate stolons (Bulleri & Benedetti-Cecchi 2008). My study provides a further test of the influence of the physical characteristics of the turfs on other benthic organisms, indicating that articulated corallines may affect furoid recruitment by altering the topography of the substrate.

Further implications of the impacts of sediment accumulation in the benthic environment were highlighted using *in situ* and laboratory photorespirometry techniques to assess the contribution of coralline algae to assemblage net primary productivity (NPP), both in the presence and absence of sediment (Chapter 3; Table 7.1). In the field, coralline turf

NPP was around $0.4 \text{ g C m}^{-2} \text{ h}^{-1}$ when loaded with sediment, and about twice as much when sediment was removed. In the laboratory, where NPP was measured across a range of light intensities, coralline turfs fell into net respiration beyond $1000 \mu\text{mol m}^{-2} \text{ s}^{-1}$ when the sediment was present. When free of sediment, however, they were able to maintain their photosynthetic rates above the compensation point across the entire light spectrum.

These results indicate that the accumulation of sediment among their thalli is a clear physical obstruction for articulated coralline algae, limiting their access to the light and potentially inducing photoinhibitive mechanisms. Indeed, the reduced photosynthetic surface emerging from the sediment may not be sufficient for the corallines to maintain their photosynthetic capacity under high light intensities. Since the short incubation periods were probably insufficient to cause photosynthetic damage (Häder & Figueroa 1997, Tait 2010), the dramatic loss of productivity under elevated irradiance in laboratory incubations was most likely caused by a down-regulation of photosynthetic apparatus, known as dynamic photoinhibition. Dynamic photoinhibition is an acclimatization strategy which protects the cells from oxidative damage (Häder & Figueroa 1997) and has been observed in different species of articulated corallines (Häder et al. 1997, Burdett et al. 2014).

Laboratory incubations also showed that when devoid of sediment, coralline algae enhanced the NPP of furoid-coralline assemblages including a furoid canopy at elevated light intensities. On the contrary, when the corallines were loaded with sediment, photoinhibition occurred in the furoid-coralline assemblages at irradiances above $1500 \mu\text{mol m}^{-2} \text{ s}^{-1}$. The importance of the vertical architecture of multilayered algal assemblages in enhancing light use and rates of productivity is increasingly recognized (Binzer et al. 2006, Tait & Schiel 2011b). My results provide further evidence of the importance of synergistic interactions between canopy and understory algae for the efficiency of light use within complex

macroalgal assemblages, and also show how altered physical conditions can impair such mechanisms.

Coralline algae are some of the least productive algae per weight (Littler & Arnold 1982, Tait & Schiel 2011b). However, given their widespread cover on hard substrates in intertidal and subtidal habitats at all latitudes (Nelson 2009), their influence on overall production of hard bottom communities should not be underestimated. Crustose corallines, for example, have been shown to make a larger contribution to organic production on coral reefs than previously thought (Chisholm 2003). My study indicates that when coralline turfs and algal canopies coexist on temperate systems, articulated corallines may enhance the productivity of intact furoid assemblages, but their contribution may depend on light and sediment conditions. Further research is currently increasing our understanding of the contribution provided by coralline algae to carbon cycling and productivity in a variety of systems (Gattuso et al. 2006, Zondervan et al. 2001, Hart & Kench 2007) and of their responses to altered physical conditions, particularly water acidification (Kuffner et al. 2008, Martin & Gattuso 2009, Russell et al. 2009).

7.3.2. Impacts of nutrient enrichment and ephemeral algae

Nutrient enrichment had a less pervasive influence on the dominant furoids *H. banksii* and *C. torulosa* than sedimentation. There was no evidence of direct negative effects of nutrients on *H. banksii* and *C. torulosa* in laboratory (Chapters 5 and 6; Table 7.1) or field contexts (Chapter 4; Table 7.1). In laboratory experiments, nutrients stimulated the growth of *H. banksii* and *C. torulosa* germlings (Chapter 6; Table 7.1). Increased mortality and reduced growth under increased nutrient loads were observed only for the early life stages of *D. antarctica* (Chapter 6; Table 7.1). As discussed in Chapter 6, however, the susceptibility of *D.*

antarctica to nutrient enrichment was probably exacerbated by its poor adaptation to laboratory conditions.

A rapid increase in the abundance of opportunistic, fast-growing algae in response to nutrient enrichment was observed both in the field (Chapter 4; Table 7.1) and in the laboratory (Chapter 5; Table 7.1). Impacts of ephemeral algae on furoid early life stages, however, were only evident in laboratory contexts, where green algae of the genus *Ulva* impaired both the settlement of *H. banksii* zygotes and the growth of the germlings (Chapter 5; Table 7.1). Zygote settlement was reduced by 66% compared to controls when *Ulva* was present on the substrate, confirming the impact of pre-emption of space by ephemeral algae on the attachment of furoid zygotes (Worm et al. 1999, 2001, Berger et al. 2003, Isæus et al. 2004). Interestingly, the abundance of the zygotes was also reduced on unoccupied settlement surfaces housed in experimental tanks previously occupied by *Ulva* (-42% compared to the controls). This was probably due to chemical alterations caused by *Ulva* in the culturing medium (Nelson et al. 2003). These results show that furoid settlement may be impaired both through pre-emptive effects and chemical mechanisms. This shows the role of different mechanisms which may underlie the impacts of ephemeral species on the recruitment of perennial macroalgae.

Once settled on the substrate, *H. banksii* germlings were tolerant to the interspecific competition with *Ulva*, which did not affect their survival rates. The growth of the germlings was, however, slower when the two species were cultured together, probably because of nutrient depletion (Fong et al. 1993) and light attenuation (Brun et al. 2003). A further experiment including herbivorous snails showed that *Ulva* may simultaneously act as a competitor and a facilitator for *H. banksii*. *Ulva* was, in fact, preferentially consumed by the grazers. The association with *Ulva* was, therefore, advantageous for *H. banksii*, despite the competitive cost of reduced growth rates.

Collectively, the results of this series of laboratory experiments (Chapter 5; Table 7.1) contribute to a better mechanistic understanding of initial conditions for attachment, settlement and growth which may affect the most critical phases of the life cycle of important habitat-forming macroalgae. Short-term investigations in artificial contexts, however, cannot incorporate the multitude of physical and biotic factors acting in natural contexts and their patterns of spatial and temporal variability. This was evident in my thesis, because in the field increased covers of ephemeral algae under enhanced nutrient regimes had no impacts on furoid recruitment (Chapter 4; Table 7.1). The first year demography of the furoids *H. banksii* and *C. torulosa* was not affected by organic enrichment within the range of concentrations recorded in eutrophic coastal areas around New Zealand (Barr 2007) and by blooms in the abundance of ephemeral algae during spring.

These results highlight the resistance of furoid assemblages dominated by *H. banksii* and *C. torulosa* to short-term (one year) nutrient stress causing pulses of around three months in the abundance of ephemeral algae during spring. The limited duration of this study, however, did not allow assessment of the long-term impacts of chronic organic pollution, which are likely to cause gradual shifts from perennial to ephemeral algae domination. Such shifts have been clearly shown in large mesocosm experiments in Norway. While the structure of macroalgal assemblages dominated by *Fucus* spp. remained unaffected by nutrient enrichment and blooms of ephemeral algae for a period of three years (Bokn et al. 2002, 2003), a dramatic community shift occurred when the experiment was prolonged for two more years. This caused a decline of furoid canopies and an evident take-over by green opportunistic algae (Kraufvelin et al. 2006).

One of the most interesting findings of Chapter 4 concerned the interactions between ephemeral algae and articulated corallines. Coralline turfs have been previously shown to prevent overgrowing by *Ulva* (Daleo et al. 2006). This was confirmed in my study, as the

cover of *Ulva* in spring in the enriched treatments was around 25% on unoccupied substrates, but only about 1% in the plots dominated by coralline turfs. However, the cover of ephemeral brown algae of the genus *Colpomenia* on the coralline turfs (over 40%) was about twice as much as on unoccupied surfaces (Chapter 4; Table 7.1). This indicates that the spread of ephemeral algae in benthic habitats may not depend only on increased resource availability (e.g., nutrients, light), but also on interspecific interactions with other low-lying algae.

7.3.3. Impacts of increased temperature

Increased water temperatures within the range predicted for the end of the current century (IPCC 2007, 2013) caused increased mortality in the germlings of *H. banksii*, *C. torulosa*, and *D. antarctica* (Chapter 6; Table 7.1) and, in a separate experiment, combined with nutrient enrichment to enhance the growth of ephemeral green algae (Chapter 5; Table 7.1). This suggests that opposite responses to altered climate conditions may contribute to the shift from complex biogenic habitats dominated by macroalgal canopies to simplified systems monopolized by a limited number of stress-tolerant species.

Numerous studies have indicated that low-lying ephemeral and turf-forming algae are likely to proliferate in warmer waters (Lotze & Worm 2002, Steen 2004, Connell & Russell 2010). In one of my laboratory experiments (Chapter 5; Table 7.1), warmer temperatures enhanced the growth of *Ulva*, but only when combined with increased nutrient levels, suggesting that ephemeral, opportunistic algae may take advantage of the combined influence of nutrient pollution and altered climate conditions. Similarly, the results of a recent series of mesocosm experiments have indicated that a combination of increased nutrient and CO₂ concentrations may accelerate the spread of filamentous turfs, which are increasingly dominant in areas previously occupied by kelp forests in southern Australia (Russell et al. 2009, Falkenberg et al. 2012, Falkenberg et al. 2013a,b).

In addition to facilitating the spread of competing species, temperature warming is also likely to have direct negative impacts on large habitat-forming macroalgae. A decline in the abundance of various species of furoids in response to rising temperatures has been observed in different parts of the world (Southward et al. 1995, Smale & Wernberg 2013) and further shifts in the distribution of intertidal furoids are expected to occur because of a warmer climate (Hawkins et al. 2009, Jueterbock et al. 2013). The mechanisms underlying such broad scale changes, however, are not well understood. A recent study (Andrews et al. 2014) showed that the vulnerability of the juvenile stages of the furoid *Scytothalia dorycarpa* to increased temperatures may explain the rapid range contraction of this species in shallow subtidal habitats in southwest Australia. To the best of my knowledge, my laboratory investigations (Chapter 6), along with the study of Andrews et al. (2014), are among the few studies establishing a mechanistic linkage between predicted future conditions and furoid early life history by testing the responses of critical juvenile stages to forecasted climate changes.

Neither my experiment nor the study of Andrews et al. (2014), however, could account for the physiological mechanisms affected by increased temperatures. Much is still unknown about the thermal physiology of the early life stages of algae. This is an area in which further research is required to understand how seaweeds will respond to climate change and to predict future large-scale distributional shifts (Harley et al. 2012, Russell et al. 2012, Wernberg et al. 2012). As discussed in Chapter 6, while future ecological patterns cannot be predicted only on the basis of results obtained under artificial, simplified conditions, laboratory studies are powerful tools to fill the gaps in our knowledge of organism susceptibility to climate change across different life cycle phases (Helmuth et al. 2006a, Russell et al. 2012). My experiments showed the effects of rising water temperatures on the early demography of three important

habitat-forming intertidal macroalgae and may provide useful insights for other studies investigating more complex and realistic scenarios.

7.4. CONCLUSIONS

The results of the research described in this thesis contribute to a better mechanistic understanding of the biotic and physical mechanisms shaping the structure of marine hard bottom communities under increasingly stressful conditions in coastal areas worldwide. Numerous studies have examined assemblage responses to the loss of furoid canopies in intertidal habitats (Benedetti-Cecchi & Cinelli 1992b, Underwood 1998, Jenkins et al. 1999a,b, 2004, Benedetti-Cecchi et al. 2001, Cervin et al. 2005, Lilley & Schiel 2006, Schiel & Lilley 2007). I expanded the findings of this body of research by using a larger set of removal treatments to simulate a realistic gradient of disturbance intensity resulting in the loss of other assemblage components in addition to the canopy. By doing this I was able to assess the influence of both the dominant habitat-formers and of the associated understory on assemblage trajectories of recovery. My results also add to the findings of previous studies which revealed the important functional roles of understory algae associated with furoid canopies in New Zealand intertidal algal assemblages (Tait 2010, Tait & Schiel 2011b).

My research also helps to establish a mechanistic linkage between altered environmental conditions and the loss of complex biogenic habitats such as algal beds. Numerous studies often cannot disentangle the influence of multiple stress sources which simultaneously affect the organisms investigated. For example, increased nutrient and sediment loadings and high abundances of turf-forming or ephemeral algae are often associated with each other in degraded coastal areas (Berger et al. 2003, Gorgula & Connell 2004, Worm & Lotze 2006, Mangialajo et al. 2008, Bellgrove et al. 2010). Similarly, studies ascribing changes in species distribution entirely to variations in climate conditions are likely

to overlook the influence of other relevant factors acting at smaller spatial scales (Helmuth et al. 2006b, 2010, Russell & Connell 2012). This thesis provides an assessment of the response of perennial habitat-forming fucoids to sediment, nutrient and temperature stress, as well as to increased competition with turf-forming or ephemeral algae. Field and laboratory experiments showed the influence of altered physical and biotic conditions on the structure and functioning of benthic assemblages dominated by macroalgal canopies. The relevance of these findings may extend beyond my individual study system, providing insights for other studies investigating the complex mosaic of challenges facing marine coastal systems around the world.

When assessing the relevance of this research, its limitations must also be taken into account. The data presented in this thesis originate from experiments with clear spatial and temporal constraints. Only one of the experiments could be replicated at two locations and monitored for more than one year. To test a wide set of new hypotheses inspired by the first experiment, I concentrated the rest of my field work at one location and integrated it with laboratory tests in order to keep the project easy to manage independently and to complete within the time frame of post-graduate research.

Constraints in the spatial and temporal resolution of experimental investigations are common and well documented issues in ecological research and pose serious limitations to the predictive capacity of numerous manipulative studies (Diamond 1986, Peters 1991, Underwood 1997, 2000). However, insights into the generality of ecological patterns and processes may be gained by integrating the results of separate manipulative investigations (Menge et al. 1986, 1994, Underwood & Petraitis 1993, Petraitis & Dudgeon 1999, Dudgeon & Petraitis 2001, Bertness et al. 2002) and by combining small-scale experiments with correlative studies encompassing larger spatial and temporal scales (Thrush et al. 1997, Worm & Lotze 2006, Hewitt et al. 2007, Foster & Schiel 2010, Bulleri et al. 2011). My work

joins an increasing body of research addressing the loss of complex biogenic habitats in rocky intertidal and subtidal systems worldwide. My hope is that the studies described in this thesis may contribute to a better understating of the causes and the potential implications of this widespread phenomenon.

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Appendix B

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MEPS prepress abstract - doi: 10.3354/meps10932

Effects of algal turfs and sediment accumulation on replenishment and primary productivity of furoid assemblages

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ABSTRACT: As a result of anthropogenic habitat degradation worldwide, coastal ecosystems are increasingly dominated by low-lying, turf-forming species, which proliferate at the expense of complex biogenic habitats, such as kelp and furoid canopies. This results in dramatic alterations to the structure of the associated communities and large reductions in primary productivity. The persistence of turf-dominated systems has been attributed to the impacts of the turfs on the recovery of algal canopies and also to the different susceptibility of canopy- and turf-forming algae to altered physical conditions, in particular increased sedimentation. Here we tested the impacts of turfing geniculate coralline algae and sediment on furoid recovery dynamics and their influence on assemblage net primary productivity (NPP). In the absence of sediments, recruitment of the habitat-forming furoid *Hormosira banksii* on bare substrata was significantly higher than in treatments in which sediments, coralline turfs or turf mimics covered the substratum, indicating that sediment deposition and space pre-emption by algal turfs can synergistically affect the development of furoid beds. NPP of coralline turfs was much less than that of furoid-coralline assemblages, which included a *H. banksii* canopy, and was reduced further by sediment accumulation. When devoid of sediment, however, coralline algae contributed to enhance furoid-coralline assemblage NPP, because of synergistic interactions among the components of the multi-layered assemblage in optimizing light use. Our findings amplify extensive research addressing the global loss of macroalgal canopies and highlight key processes involving sediment accumulation in the benthic environment and effects on the replenishment and productivity of furoid stands.

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Appendix C

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Effects of opportunistic algae on the early life history of a habitat-forming furoid: influence of temperature, nutrient enrichment and grazing pressure

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ABSTRACT: Fragmentation and loss of extensive populations of habitat-forming macroalgae have occurred worldwide as a result of human-driven coastal habitat degradation. Contributing to such declines may be the influence of opportunistic algae, which quickly respond to stresses such as nutrient loading and warmer sea temperatures. The early life stages of furoids are particularly likely to be affected by the combined impacts of altered physical conditions and increased competition with stress-tolerant species. In this study, we examined the interactions between the early life stages of the intertidal furoid *Hormosira banksii* and fast-growing, opportunistic green algae *Ulva* spp. Through a series of laboratory experiments, we tested (1) the impact of *Ulva* spp. on the settlement of *H. banksii* zygotes; (2) the impact of *Ulva* spp. on the rates of post-settlement survival and growth of *H. banksii* germlings under ambient and increased levels of temperature and nutrient concentration; (3) the interactions between the 2 taxa under grazing pressure of the abundant intertidal trochid *Lunella smaragdus*. *Ulva* spp. impaired the settlement of *H. banksii* zygotes, through both physical and chemical mechanisms, and the growth of the germlings; but *Ulva* spp. was also preferentially consumed by the grazers, thereby indirectly facilitating *H. banksii*. In addition, *Ulva* spp. responded positively to increased temperature and nutrients, while we found an indication that post-settlement survival of *H. banksii* may decline with warmer waters. These findings augment extensive field-based research addressing the loss of algal beds and shed light on biotic and physical mechanisms affecting the most critical phases of the life cycle of a key habitat-forming species.

KEY WORDS: Canopy · Competition · Ephemeral algae · Eutrophication · Germlings · Macroalgae · Temperature warming · *Ulva* spp.

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INTRODUCTION

The structure and functioning of many marine ecosystems are shaped by the presence of either a single or a few habitat-forming species (Bruno & Bertness 2001). Well documented examples include canopy-forming macroalgae of the Order Fucales (furoids), which support high levels of diversity and productivity on temperate intertidal rocky reefs worldwide, despite the extreme physical challenges of these

habitats (Chapman 1995, Schiel 2006). It is not surprising, therefore, that the decline of large populations of furoid algae reported worldwide, especially around urbanised areas, has caused great concern and stimulated extensive ecological research (Benedetti-Cecchi et al. 2001, Berger et al. 2004, Irving et al. 2009, Bellgrove et al. 2010).

In degraded environments, slow-growing perennial algae such as furoids can be directly harmed by modified physical conditions (e.g. sedimentation,

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