



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

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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. We used a series of laboratory experiments to test short- (48 h) 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 h 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 h. 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. Our 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.

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1. Introduction

Coastal ecosystems worldwide are subjected to considerable and increasing anthropogenic pressure as a result of human demographic trends and activities in both the terrestrial and marine realms (Halpern et al., 2008). Understanding how nearshore systems are affected by multiple anthropogenic perturbations is pivotal to the conservation or restoration of the ecological values and services they provide (Crain et al., 2008, 2009). Human influences at local scales 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 global climate change (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 (Crain et al., 2008; Darling & Côté, 2008; Folt et al., 1999) and understanding how broad scale changes in climate superimpose effects on local, non-climatic processes is one of the more pressing priorities for research and management (Halpern et al., 2008; Harley et al., 2006; Russell & Connell, 2012; Sala et al., 2000).

Because coastal ecosystems are often structured around one or few habitat-dominating species (Bruno & Bertness, 2001), understanding

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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 we tested the effects of combinations of temperature, nutrients and sedimentation on the early life history stages of the habitat-forming fucoids *Hormosira banksii*, *Cystophora torulosa*, and *Durvillaea antarctica*, which dominate intertidal rocky reefs in southern New Zealand. Importantly, these species have no functional equivalents (Schiel, 2006; Taylor & Schiel, 2005), and long-lasting impacts on the structure and productivity of the associated communities have been observed following their loss (Lilley & Schiel, 2006; Schiel & Lilley, 2011; Tait & Schiel, 2011).

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 worldwide have reported a decline in the abundance of fucoids in response to rising temperatures (Smale & Wernberg, 2013; Southward et al., 1995) and to elevated nutrient and sediment regimes (Bellgrove et al., 2010; Eriksson et al., 2002; Mangialajo et al., 2008). Laboratory investigations have highlighted the sensitivity of furoid juvenile stages to altered temperature (Andrews et al., 2014), nutrient (Bergström et al., 2003; Kevekordes, 2001) and sediment levels (Irving et al., 2009; Schiel et al., 2006). However, there have been few, if any, tests of the combined effects of these three factors on the early phases of the life cycle of habitat-forming fucoids. We did a series of laboratory experiments testing the responses of *H. banksii*, *C. torulosa*, and *D. antarctica* to combinations of stressors affecting New Zealand's coastal zone (i.e., increased nutrient and sediment loads; Barr, 2007; Schiel et al., 2006) and temperatures in the range of those predicted in 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 h) phases; 2) survival and growth rates over eight weeks, a period which is significantly longer than most studies reported in the literature. Although laboratory investigations cannot incorporate great natural complexity, our 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, we 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.

2. Materials and methods

2.1. 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 (Schiel, 2006). For each species, a 48-hour experiment was first run and then followed by an 8-week experiment. The experiments were initiated during the period of peak reproduction of each species, when fertile adult plants were releasing gametes in the field. Experiments were done with *H. banksii* during the austral summer 2011 (December 2011–February 2012), and 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, brought to the laboratory and refrigerated at 4 °C for 24 h. The plants were successively exposed to sunlight and warmth to induce gamete release and washed in a bucket containing 18 l of filtered (1 µm) and UV-sterilized seawater to detach the gametes. Given the large disparity in their rates of gamete release, it was difficult to obtain similar settlement densities for all species. Settlement densities in line with those observed in the field in

Kaikoura (Dunmore, 2006; Taylor, 2002) were used (*H. banksii*: ~500 cm⁻², *D. antarctica*: ~1800 cm⁻², *C. torulosa*: ~60 cm⁻²).

Settlers of all species were grown on 50 × 50 × 7 mm fibrolite plates placed in plastic tanks (37 × 25 × 7 cm) filled with filtered (1 µm) and UV-sterilized seawater. The design of all experiments comprised sixteen tanks, each containing four plates. The surface of these plates is covered with tiny pits and concavities which facilitate algal settlement (Dunmore, 2006; Taylor, 2002). Air pumps were used to aerate the tanks and keep the water in motion. Light racks provided illumination at ~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 (Alestra & Schiel, 2014).

Combinations of factors were tested through the manipulation of temperature (ambient vs. increased), nutrients (ambient vs. increased concentration) and sediment levels (present vs. absent). Each combination of treatments was replicated in two separate tanks. In each experiment, the ambient temperature was the maximum sea surface temperature 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). Increased temperatures were 3 °C higher than ambient, consistent with predictions from IPCC (2007) for the end of the 21st century. 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 (Alestra & Schiel, 2014). Within each room, two tanks were assigned to each combination of nutrients and sedimentation. Tanks assigned to different treatments were randomly interspersed in each room. Increased nutrient concentrations were obtained through the addition of 20 µmol N (nitrate and ammonia added at a ratio of 1:1) and 2 µmol P (phosphate) per liter of seawater. This is equivalent to about 0.8 mg N l⁻¹ (nitrate: 0.62 mg l⁻¹; ammonia: 0.18 l⁻¹) and 0.19 mg P l⁻¹. The waters surrounding Kaikoura are known to be relatively nutrient-poor (Alestra, 2014; Guerry et al., 2009) and increased N and P concentrations were selected 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 after the settlement of the reproductive cells of the study species. The sediment was collected in the field, oven-dried, and uniformly distributed over the surface of the plates. 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.

2.2. 48-hour experiments

In the 48-hour experiments we tested the effects of the experimental factors on settlement and early post-settlement phases of the life cycle of each species starting from pre-fertilization stages. Before the start of all 48-hour experiments, each tank was filled with 4 l of seawater and the plates were soaked for two days to ensure that they were saturated with water and to allow water to permeate into all pits and concavities on their surface (Taylor, 2002). The plates were then seeded with 1 l of solution containing the gametes of the study species. The gametes were inoculated into the experimental tanks immediately after being detached from the adult plants. Temperature and nutrient levels were altered before the gametes were introduced into the tanks. The sediment was added to the +Sediment treatments after the initial 24 h of the experiment to allow the zygotes to attach to the plates and not to the sediment grains. After the initial 24 h, the disposition of the tanks in each room was also randomly rearranged.

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