Effects of opportunistic algae on the early life history of a habitat-forming fucoid: 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 fucoids 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 fucoid *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.

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 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, Isea 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, we 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 fucoid Hormosira banksii, which is a key structural component of intertidal algal assemblages in New Zealand and southeastern Australia. No other fucoid species in New Zealand is able to provide the same ecosystem services in mid-shore habitats (Schiel 2006), and there are long-lasting impacts on community diversity and productivity following H. banksii removal (Schiel & Lilley 2011, Tait & Schiel 2011). 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, we 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 2 species. Ulva is known to have allelopathic properties that inhibit zygote development (Nelson et al. 2003), so we began by testing whether such effects were evident on H. banksii.

We then tested the effects of the presence of Ulva on the rates of survival and growth of H. banksii in the first 6 wk 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 temperature may differentially affect the 2 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 fucoids, in contrast, 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, can be impaired by elevated nutrient levels (Kevekordes 2001, Bergström et al. 2003). In combination with the presence or absence of Ulva, therefore, we also manipulated temperature and nutrient levels. We expected increased temperature and eutrophication to have a direct detrimental effect on the fitness of the germlings and to stimulate the growth of Ulva, thereby exacerbating its impact on H. banksii.

Finally, we assessed how the interactions between the 2 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 >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, we manipulated the density of Ulva to simulate the biotic consequences of eutrophication scenarios of increasing intensity. We 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.

**MATERIALS AND METHODS**

The experiments were carried out in the facilities of the Edward Percival Field Station in Kaikoura, New Zealand. Settlers of the 2 algal species obtained from adult plants collected in the field were grown on 50 × 50 × 7 mm fibrolite plates. Hormosira banksii settlement density was not manipulated but was kept at ~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 × 25 × 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 ~100 µmol m−2 s−1 under a 12 h light:12 h dark cycle. The plates were submerged throughout the duration of the 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, we were able to test the effects of the experimental factors more accurately.

Expt 1: Impact of Ulva on H. banksii zygote settlement

We 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 2 tanks, each containing 4 plates.

Before the start of the experiment, 32 plates were distributed among 8 tanks (4 plates per tank), each filled with 4 l of seawater. The plates were soaked for 2 d, and successively, 4 of the tanks received 1 l of Ulva zooid solution, while 1 l of seawater was added to the remaining 4 to equalize the volume. All the plates were kept submerged at 17°C for 30 d, and the water was changed twice weekly. After 30 d, the plates seeded with Ulva were examined, and the percentage cover of Ulva was visually estimated using a 5 × 5 cm fine plastic grid divided into 25 sub-quadrats. Eight plates with 53.55 ± 5.55% (mean ± SE) cover of Ulva were selected to represent the treatment with 50% colonized substrates. These were reintroduced into 2 of the tanks originally seeded with Ulva. The remaining unoccupied plates containing Ulva were removed from their tanks and replaced by 8 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 h, all the plates were examined under a binocular microscope, and the number of settled zygotes was estimated in 3 haphazardly chosen 1 cm² areas.

Expt 2: Influence of temperature and nutrients on species interactions

We 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 vs. 20°C); (2) Nutrients (ambient vs. increased concentration) and (3) Culture type (H. banksii monocultures vs. mixed cultures).

We ran the experiment for 6 wk to assess the responses over a longer period of time compared to similar studies reported in the literature (Lotze & Worm 2002, Steen 2004). After 6 wk, however, it was no longer possible to culture H. banksii and Ulva in isolation, as other unwanted species (mainly micro-algae) 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 litre of seawater 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 2 temperature levels. The 2 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, 2 tanks were assigned to each possible combination of nutrient concentration and presence/absence of Ulva, with 4 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 2 d. One litre of H. banksii zygote solution, obtained from ~50 adult plants, was then gently poured over the plates in each tank. After 4 d, 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 2, 4 and 6 wk from the initial monitoring (4 d). At each sampling date, every plate was examined under a binocular microscope, and the number of *H. banksii* germlings was estimated as described for Expt 1. 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 10 individuals randomly selected from each plate. These were detached from the plates and measured length-wise 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 2 species under different combinations of temperature and nutrient levels. The RII is expressed as $\text{RII} = (Bw - Bo)/(Bw + Bo)$, where $Bw$ and $Bo$ 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* ($Bw$), recorded from the plates assigned to mixed cultures of the 2 species, were contrasted with mean values of $Bo$, calculated by averaging the survival rates of *H. banksii* germlings in the monocultures, separately for each combination of temperature and nutrient levels.

### Expt 3: Influence of grazing on species interactions

We tested the impact of grazing by *Lunella smaragdus* on *H. banksii* germlings grown in isolation and in mixed cultures with various densities of *Ulva*. The experiment involved 2 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 2 tanks, each containing 4 plates.

Six medium-sized *L. smaragdus* (average shell length: 22.17 ± 0.41 mm) were collected and allowed to acclimatise to laboratory conditions for 2 wk before being introduced into the experimental tanks. Before the start of the experiment, the plates were soaked for 48 h 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 4 d 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 4 tanks to obtain mixed cultures with a high density of *Ulva*, and 4 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 d to allow the development of *Ulva*. The water was replaced twice weekly. After 30 d, the number of *H. banksii* germlings and percentage cover of *Ulva* were recorded. After this initial period, we started the experiment by adding 1 specimen of *L. smaragdus* to half of the experimental tanks assigned to each culture type.

The abundance of *H. banksii* germlings was monitored 2, 4 and 6 wk 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 RII, describing species interactions relative to *Ulva* density and grazing pressure. Here, $Bo$ represented the average percentage survival of *H. banksii* germlings in the absence of *Ulva*, calculated separately for the 2 levels of grazing pressure.

### Statistical analyses

Zygote abundance data from Expt 1 were analysed using a 2-way 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 the percentage cover of *Ulva* recorded at the conclusion of Expt 2 were analysed using a 4-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 3-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 Expt 3 were analysed using a 3-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 3-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 in accordance with 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).

**RESULTS**

**Expt 1: Impact of *Ulva* on *Hormosira 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. 1), resulting from allelopathy and space pre-emption. The average number of successfully settled *H. banksii* zygotes was ~300 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 attached when there was a 50% cover of *Ulva*.

**Expt 2: Influence of temperature and nutrients on species interactions**

At the start of the experiment, the mean ± SE number of germlings was 306.07 ± 12.35 cm$^{-2}$ (n = 60). After 6 wk, the survival of *H. banksii* germlings was not significantly affected by temperature, nutrient levels or the presence of *Ulva* (Table 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 1B, Fig. 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 4 wk (Fig. 3B). Unexpectedly, *Ulva* also appeared in the *H. banksii* monocultures ~4 wk and maintained percentage covers between 40 and 47% in the 17°C + Nutrients treatment but near zero in all others (Fig. 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 6 wk (Table 1C, Fig. 3A,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 6 wk, the RII ranged from $-0.06 \pm 0.04$ to $0.05 \pm 0.06$ and did not vary significantly with temperature ($F_{1,4} = 0.26, p = 0.63$) or nutrients ($F_{1,4} = 1.17, p = 0.34$).

### Table 1. ANOVA of percentage survival and size of *Hormosira banksii* germlings and percentage cover of *Ulva* spp. recorded at the final sampling date (6 wk) of Expt 2 in different culture types (*H. banksii* monocultures vs. mixed cultures) and under various temperature (17 vs. 20°C) and nutrient (ambient vs. increased concentration) levels. *p < 0.05; **p < 0.01; ***p < 0.001

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<th>B) <em>H. banksii</em> germling</th>
<th>C) <em>Ulva</em> % cover</th>
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Fig. 2. Mean length (+1 SE) of *Hormosira banksii* germlings in (A) *H. banksii* monocultures and mixed cultures with *Ulva* spp. combined across all levels of temperature and nutrient concentration (n = 32), recorded at the end of Expt 2 (after 6 wk), (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 Expt 3 (after 6 wk). The letters above the bars indicate the ranking of the means according to the SNK tests.

Fig. 3. Temporal variation in the mean percentage cover (+1 SE) of *Ulva* spp. in (A) *Hormosira banksii* monocultures and (B) mixed cultures 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.

**Expt 3: Influence of grazing on species interactions**

At the start of the experiment, the average number of germlings was 297.22 ± 12.58 cm$^{-2}$ (n = 48). In the absence of *Ulva*, *Lunella smaragdus* rapidly compromised the survival of *H. banksii* to ~20% after 6 wk.
Our results provide a mechanistic understanding of initial conditions for attachment, settlement and growth which are likely to set the trajectory for the development of fucoid populations. We showed that common, opportunistic algae may benefit from high nutrients and temperature increase and have suppressive effects on the settlement and growth of a dominant fucoid. However, we also observed indirect facilitation of the perennial fucoid by the ephemeral algae moderated through preferential grazing.

*Ulva* may affect *Hormosira 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 fucoid zygotes has been described in other studies (Worm et al. 1999, 2001, Berger et al. 2003, Isæus et al. 2004). In contrast, when unoccupied plates were translocated into tanks previously occupied by Ulva, 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 here we showed that they potentially affect H. banksii in the first 24 h 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 our 6 wk 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 Expt 1. If allelopathy were a major influence, it might be expected to also compromise the survival of settlers, but this was not evident in our 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 germings 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 fucoids, 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 substratum, small germings 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) that 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.

Our study also highlighted the importance of biotic and abiotic influences in regulating the outcome of the interaction between the 2 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). Our 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 Lunella smaragdus showed a marked preference for other ephemeral, disturbance-oriented species, like the brown algae Adenoscytis 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). In addition, we also observed a negative trend in H. banksii survival rates in response to temperature increase, although this was not statistically significant. Nonetheless, such findings are consistent with the results of further laboratory experiments in which we recorded reduced levels of survival for the germings of H. banksii and 2 other fucoids (Cystophora torulosa and Durvillea antarctica) when exposed to a temperature increase of 3°C during the initial 8 wk of their life cycle (T. Alestra & D. R. Schiel unpubl. data). Similarly, recent
field observations and laboratory experiments have shown that the juvenile stages of the fucoïd Scytosiphon lomentaria have a narrow optimal temperature window and are severely affected by temperatures just 2°C above this range (Andrews et al. 2014).

Collectively, our experiments indicate that the strength and direction of fucoïd-epiphemeral 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 2 species in favour of Ulva. Based on our 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 germinals 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 fucoïds (Blanchette et al. 2000). Herbivory may release H. banksii from the competition with Ulva, and the latter species, in the presence of the grazers, may turn out to be an unexpected ally for the fucoïd. As L. smarrgus is by far the dominant grazer in southern New Zealand algal beds, the effects seen in the laboratory are likely to be relevant 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 the ecological role of herbivores. 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 fucoïd-forming species represents a serious obstacle to 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 our findings may extend beyond the individual case of H. banksii, providing useful insights for other investigations.

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