

Arthropod mesograzers reduce epiphytic overgrowth of subtidal coralline turf

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ABSTRACT: Benthic primary producers such as seaweeds and seagrasses are often inhabited by high densities of small arthropods, but little is known about the impact of these animals on their hosts, which could be positive if they keep them free of fouling epiphytes. We assessed the impact of small arthropods on algal epiphytes growing on coralline algal turf on a shallow, wave-exposed, rocky reef in warm temperate northeastern New Zealand. Plaster blocks impregnated with the insecticide carbaryl were used to reduce arthropod densities (by 96 % relative to unmanipulated controls in the case of amphipods). By the end of the ~3.5 mo experiment total epiphyte cover was 88 % when arthropods were excluded compared to 38 % in unmanipulated controls, a 2.3-fold increase. Brown (*Colpomenia* spp.), green (*Ulva* spp.) and 'filamentous and microscopic' algal epiphyte taxa were responsible for the increase, while the cover of red foliose algal epiphytes decreased slightly. Hyalid amphipods (*Protohyale* spp.) were likely responsible for suppressing the epiphytes, as they were the most abundant arthropod mesograzer taxon and ate both *Colpomenia* spp. and *Ulva* spp. in a laboratory no-choice feeding assay. During the field experiment 2 large storms removed most of the epiphytes that had grown in the mesograzer exclusion treatment. Overall, our results indicate that the amphipods prevented overgrowth of the turf by epiphytes during calm periods. These results provide the first *in situ* cageless example of arthropod mesograzer-exerted control on the abundance and composition of primary producers on a subtidal rocky reef.

KEY WORDS: Amphipod · Epiphyte · Herbivory · Hyalidae · Mesograzer · Storm · Temperate reef · Turf

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INTRODUCTION

Small herbivorous invertebrates (mesograzers) are often highly abundant on seaweeds and seagrasses (Brawley 1992), where they exert strong grazing pressure (Poore et al. 2012). Feeding directly on host tissue can have serious negative consequences for the host macrophyte (e.g. Tegner & Dayton 1987, Reynolds et al. 2012, Poore et al. 2014), but mesograzers more commonly eat epiphytic algae (Bell 1991, Edgar 1991). This should benefit their host, as epiphytes compete with hosts for light and nutrients (van Montfrans et al. 1984) and increase the risk of frond breakage due to drag

(D'Antonio 1985). Thus the potential for mutualism exists between mesograzers and their host macrophytes (Aumack et al. 2011), where the mesograzers derive food in the form of algal epiphytes, along with shelter from predators (Coull & Wells 1983) and wave action (Dommasnes 1968), while the host is kept free of fouling organisms (Duffy 1990, Hay et al. 2004). Mesograzers may even help macrophytes resist vigorous overgrowth by epiphytes responding to anthropogenic eutrophication, an increasingly common stressor in coastal waters (Myers & Heck 2013).

Impacts of small mobile arthropods have generally been examined using mesocosms or cages (e.g.

Brawley & Adey 1981, Duffy & Hay 2000), but these methods suffer from various artefacts such as shading (Lotze et al. 2001) and altered water flow (Kamermans et al. 2002). In response, Poore et al. (2009) developed a cageless poison-based method of reducing densities of amphipods, and potentially other arthropods, in the field. They applied it in a temperate seaweed bed, where they found no impacts of mesograzers on either host or epiphytes. However, the method has since been used in 4 seagrass habitats, with strong impacts of mesograzers on algal epiphytes found in each case (Cook et al. 2011, Myers & Heck 2013, Whalen et al. 2013, Reynolds et al. 2014). The variation in results arising from these studies indicates that similar experiments need to be run in a wide range of coastal benthic habitats before we can generalise about the impact of mesograzers on host macrophytes and their epiphytes, and how this is influenced by properties of the local environment (e.g. depth, wave exposure and sedimentation), the mesograzer assemblage (abundance, taxonomic composition and size structure) and the host macrophytes and their epiphytes (productivity, taxonomic composition and relative susceptibilities to grazing).

Coralline algal turfs occur on shallow hard-bottom habitats worldwide (Nelson 2009, Connell et al. 2014) and host a diverse and highly abundant assemblage of small mobile invertebrates (Taylor 1998, Kelaher & Castilla 2005, Cowles et al. 2009). Coralline algal fronds are calcareous and unpalatable to most mesograzers (e.g. Taylor & Steinberg 2005, Taylor & Brown 2006). It is likely, therefore, that mesograzers instead feed on algal epiphytes growing on the turf (e.g. Kelaher et al. 2001) and that a mutualistic relationship may exist between mesograzers and the turf.

Many temperate reefs are subject to episodic strong wave action, which can overwhelm the effects of herbivores by detaching large numbers of individual macrophytes and/or epiphytes (Anderson & Martone 2014). On the other hand, heavy wave action can benefit algae by reducing the grazing impacts of herbivores through limiting their access or foraging ability (Duggins et al. 2001, Taylor & Schiel 2010).

In this study we tested whether arthropod mesograzers reduce epiphytic overgrowth of subtidal coralline turf in the field using the cageless method of Poore et al. (2009). During the experiment we also quantified wave action in order to determine the relative impacts of large waves and mesograzers on epiphytes.

MATERIALS AND METHODS

Study site

The study site was Kempts Bay (36° 15' S, 174° 45' E), a moderately wave-exposed shallow subtidal rocky reef adjacent to the Cape Rodney–Okakari Point Marine Reserve, in warm temperate northeastern New Zealand. Our experiment was run in patches of coralline turf (almost exclusively *Corallina officinalis*) surrounded by stands of large brown macroalgae (mostly the kelp *Ecklonia radiata*).

Experimental reduction of arthropod densities

The method of Poore et al. (2009) entails impregnating plaster blocks with the insecticide carbaryl (1-naphthyl-*N*-methylcarbamate). In the field the carbaryl is released as the plaster dissolves. Carbaryl contains carbamates, which inhibit the enzyme cholinesterase found in arthropod nervous systems and are particularly toxic to amphipods (Duffy & Hay 2000). Carbaryl does not affect algal growth (Carpenter 1986, Poore et al. 2009) and is often used in marine herbivory experiments to reduce densities of amphipod grazers (e.g. Duffy & Hay 2000, Newcombe & Taylor 2010).

We prepared cylindrical plaster blocks of 350 ml volume in a similar fashion to Poore et al. (2009) using superfine casting plaster and plastic moulds made from 80 mm diameter uPVC pipe with a plastic base. Two types of blocks were produced: 'plaster' blocks contained a mixture of 429 g plaster and 250 ml water, while 'carbaryl' blocks also contained 45 g of carbaryl (80% wettable powder). Blocks were air-dried for ~4 d before use. To ensure that the plaster blocks lasted at least a week at our wave-exposed study site, we protected the bulk of each block from dissolution within a housing, which consisted of a 107 mm length of 80 mm internal diameter uPVC pipe on a plastic base (Fig. 1). Twenty-six 16 mm diameter holes were drilled near the base of the housing to enable the slow release of carbaryl as the bottom end of the plaster block dissolved. Each housing (containing a block) was bolted to a metal rod cemented into the seafloor. A removable cap allowed the replacement of blocks in the field.

Experimental design

Our experiment consisted of 3 treatments: (1) carbaryl (carbaryl-impregnated plaster block in a hous-



Fig. 1. Housing containing a plaster block impregnated with the insecticide carbaryl, which was secured in wave-exposed subtidal coralline turf to reduce arthropod densities

ing) to reduce arthropod density, (2) plaster control (plaster block in a housing) to control for any effects of the plaster and/or housing on algae and (3) unmanipulated control (no block or housing) to provide a natural baseline ($n = 5$ replicates per treatment). Replicates were situated in individual turf patches that were 0.7 to 2.4 m deep at mean low tide, larger than 0.25 m² and separated by at least 2 m. This distance was found by us (pilot study data not shown), and Reynolds et al. (2014), to be beyond the limit of carbaryl effectiveness and is in accordance with other cageless studies in which plots were placed at least 1 to 2 m apart (Poore et al. 2009, Cook et al. 2011, Myers & Heck 2013, Whalen et al. 2013). The experiment began on 1 November 2012 (spring) and continued for 111 d until 19 February 2013 (summer). Blocks were replaced approximately weekly, and on 2 occasions (Days 59 and 96), when wave action prevented access for 14 and 18 d, respectively, blocks had completely dissolved. Water temperatures ranged from 15.2 to 21.7°C during the study.

Wave action

Mean significant wave height (average height of the highest third of all waves counted) per day, used to quantify wave action, was determined from forecast outputs (based on the position 36° 0' S and

175° 5' E) obtained from the 'Pacific Integrated Ocean Observing System' (www.ioos.noaa.gov/regions/pacioos.html, accessed on 5 December 2013) and generated by the model package used in Arinaga & Cheung (2012) utilising Wavewatch III (Tolman et al. 2002).

Faunal composition

To check the effectiveness of the carbaryl treatment, on Day 106 we collected a circular sample (area of 50.3 cm²) of coralline turf and fauna from each replicate using the suction sampler of Taylor et al. (1995). The sample was collected in a 0.2 mm mesh bag and preserved in Glyo-Fixx (Titford & Horenstein 2005). Fauna retained on a 0.5 mm sieve were identified to the lowest practical taxonomic level (usually order or family) and enumerated. Blotted weight of coralline turf (mean per sample), used to standardise amphipod densities for comparison with other studies, was determined from 3 of the unmanipulated control samples after washing algae through a 2 mm sieve (to remove sediment) and blotting it dry.

Algal composition

To quantify algal composition, each replicate was photographed from above, every 1 to 3 wk using a Canon G12 camera with inbuilt flash. Additional closeup photographs were taken to help with algal identifications. The brightness and contrast of photographs was standardised by eye using Adobe Photoshop CS5.1, and an inner circle representing the housing was drawn on unmanipulated controls using ImageJ software. A circle covering 622 cm² of seafloor was then digitally drawn around the housings in each photo-replicate. These circles extended 98 mm from the housing edges, a range over which we (pilot data not shown) and all other cageless studies (Poore et al. 2009, Myers & Heck 2013, Whalen et al. 2013, Reynolds et al. 2014) found carbaryl to strongly reduce amphipod densities. Due to blurred/incomplete photographs, quadrat size on Days 11, 33 and 45 had to be reduced slightly, and several replicates on Days 33 and 85 were not quantified.

Percent coverage of taxa was estimated visually (Dethier et al. 1993) by A. Berthelsen following a training and validation exercise. Visual estimates were compared to measurements obtained using the software ImageJ (a much more time-consuming pro-

cess) until an acceptable level of accuracy was reached ($r^2 \geq 0.7$ with no bias). Taxa in the photoquadrats were classified as follows: (1) filamentous and microscopic algae (identity unknown but included the family Ectocarpaceae and *Ostreopsis siamensis*), (2) the brown alga *Colpomenia* spp. (*C. sinuosa* and/or *C. claytoniae*), (3) the green alga *Ulva* spp., (4) the green alga *Codium fragile*, (5) red foliose algae (including the genera *Hymenena*, *Aphanocladia* and *Gigartina*), (6) coralline turfing algae (mostly *Corallina officinalis*) and (7) sessile invertebrates. Items excluded prior to calculating percentage covers were: sand (transient; averaged 1.4% and never more than 10%), overhanging algae (i.e. holdfast outside the quadrat or growing on housing), marker tape in the unmanipulated control, overhanging housings (occurring if photographs were not taken directly from above), mobile fauna (fish and molluscs) and areas from which turf had previously been removed to sample fauna.

Identification of grazers

Arthropod grazers likely to consume the epiphyte taxa that increased in the carbaryl treatment were identified from the literature (see 'Results'). One of the 2 taxa identified was available in sufficient numbers for a feeding assay. In July 2013 we measured the rate at which hyalid amphipods consumed *Colpomenia* spp. and *Ulva* spp. in a no-choice assay. Hyalids consisted of a mix of *Protohyale rubra* and *P. grenfelli*, as these species could not be separated due to the difficulty of identifying females and juveniles. Amphipods and epiphytes were collected from the study site, and an assay started on the same day. Two large amphipods were added to a plastic bowl containing a pre-weighed piece of algae of 27 to 32 mg blotted weight in 300 ml of seawater. As a control for autogenic weight change, a matching container with tissue from the same algal individual was set up without amphipods ($n = 10$ for each algal taxon and grazing treatment). The feeding assay took place indoors, with a 12 h light:12 h dark regime, and water temperature was kept close to ambient (14°C) using a water bath. The assay ran for ~3 d, but individual grazed replicates and their paired controls were stopped earlier if most of the algae had been eaten. Only 1 amphipod died during the assays, and this was replaced. Algal pieces were then again blotted dry and weighed. Amphipod feeding rates were calculated by scaling for autogenic change as in Taylor & Brown (2006).

Statistical analyses

One-way analysis of variance (ANOVA) in Sigma Plot 11.0 was used to test for differences in densities between faunal groups. Data were tested for normality and homogeneity of variance and were log-transformed to meet these assumptions if necessary. Pairwise multiple comparisons using the Holm-Sidak method were used to investigate significant differences detected by ANOVA. To display temporal changes in epiphyte community composition, a non-metric multidimensional scaling analysis was run on the mean percentage cover of algal epiphytes (defined as all recorded algal taxa except for coralline turfing algae) and sessile invertebrates, using a Bray-Curtis dissimilarity matrix based on square root-transformed data. One-way analysis of similarity (ANOSIM) and post hoc pairwise comparisons were used to test for significant differences in mean algal community composition. Multivariate analyses (Clarke 1993) were conducted with the software package PRIMER v6 (Clarke & Gorley 2006).

RESULTS

Faunal composition

The average density of total arthropods was significantly ($F_{2,12} = 7.65$, $p < 0.01$) reduced in the carbaryl treatment compared to unmanipulated and plaster controls by 87 and 85% (pairwise comparisons: $p < 0.01$ and $p = 0.01$), respectively (Fig. 2). Relative to unmanipulated controls, carbaryl reduced amphipod densities by 96%, ostracods by 81%, isopods by 89% and decapods by 71%. In unmanipulated controls, amphipods comprised 57% of total arthropods, with a mean (\pm SE) density of $22\,874 \pm 6452$ ind. m^{-2} (28 ± 7.9 ind. g^{-1} coralline wet weight). The average total density of non-arthropods (mostly gastropod molluscs, polychaetes and ophiuroids) did not differ significantly between the 3 treatments ($F_{2,12} = 1.60$, $p > 0.1$). In unmanipulated controls, gastropod molluscs were the most abundant non-arthropod taxon ($108\,401 \pm 10\,262$ ind. m^{-2}).

Composition of algal epiphytes

The composition of algal epiphytes (and sessile invertebrates—although the cover of these was never greater than 2% in any 1 replicate) was similar in all treatments at the beginning of the study (ANOSIM:

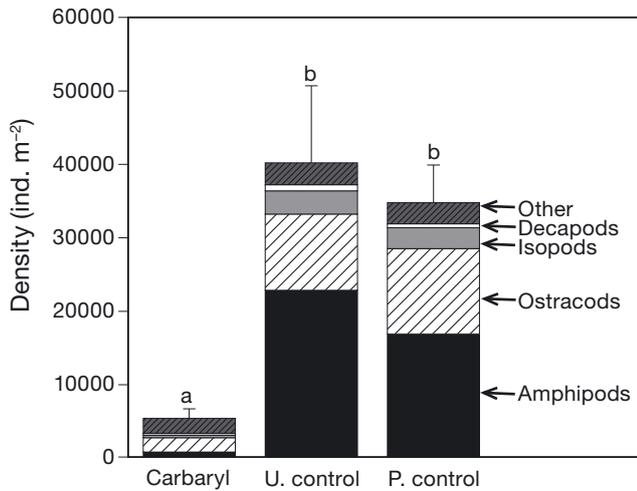


Fig. 2. Mean (+1 SE) densities of arthropod taxa (>0.5 mm) in coralline turf on Day 106 of the study. The 3 treatments are carbaryl, unmanipulated control (U. control) and plaster control (P. control) (n = 5). 'Other' includes tanaids, cumaceans, marine mites, trichopterans, pycnogonids and copepods. Bars labelled with the same lower case letter do not differ significantly ($p > 0.05$) according to Holm-Sidak pairwise comparison

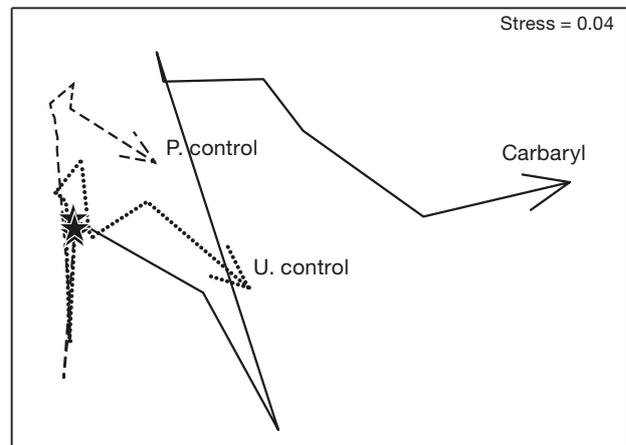


Fig. 3. Non-metric multidimensional scaling plot showing the relative changes in mean epiphyte community composition in a coralline turf habitat over time (star symbols: Day 11; arrows: Day 111). The 3 treatments are carbaryl (solid line), unmanipulated control (U. control) (dotted line) and plaster control (P. control) (dashed line)

$R = -0.07$, $p > 0.5$) (Fig. 3). By Day 45, composition differed significantly between the treatments (ANOSIM: $R = 0.42$, $p < 0.01$), with the carbaryl treatment different to both the unmanipulated and plaster controls (pairwise comparison: $R = 0.62$, $p < 0.01$ and $R = 0.63$, $p < 0.01$), which were not different from each other ($R = 0.08$, $p > 0.1$). Similar differences in composition were present at the study end (Day 111), with the carbaryl treatment significantly different (ANOSIM: $R = 0.72$, $p < 0.01$) from both the unmanipulated and plaster controls (pairwise comparisons: $R = 0.97$, $p < 0.01$ and $R = 1$, $p < 0.01$), and no significant difference detected between the controls ($R = 0.26$, $p > 0.05$). On Day 111 the total mean cover of epiphytes was 88% in the carbaryl treatment compared to 38% in unmanipulated controls, a 2.3-fold difference (Fig. 4A). Mean cover of filamentous and microscopic algae was 63% in the carbaryl treatment versus 11% in unmanipulated controls (Fig. 4B), with the corresponding values being 18.7 vs. 2.6% for *Colpomenia* spp. (Fig. 4C) and 2.5% vs. 0.3% for *Ulva* spp. (Fig. 4D). Conversely, the cover of red foliose algal epiphytes was lower in the carbaryl treatment than in unmanipulated controls (4 vs. 24%; Fig. 4E). The similarity of the plaster control to the unmanipulated control showed that the main effect of the carbaryl treatment was due to the carbaryl rather than to the associated plaster and/or housing. Photographs of a typical replicate of all treatments at Days 45 and 111 are shown in Fig. 5.

Storms

Two large (mean wave height > 3 m) storms with maximum wave heights of 3.7 m (Day 53) and 3.3 m (Day 67) occurred during the study. In comparison, the mean (\pm SE) wave height during the experiment, excluding the days of increased wave height caused by the 2 large storms, was 1.3 ± 0.05 m. The first storm coincided with large decreases in the covers of *Colpomenia* spp., *Ulva* spp., filamentous and microscopic algae and red foliose algae in the carbaryl treatment, and decreases in red foliose algae in both of the control treatments (Fig. 4). During the second storm the epiphytic algal taxa mentioned above remained relatively low in cover.

Grazers responsible

A literature search indicated that of the 15 amphipod families identified in our samples, the Hyalidae (Brawley 1992) and Aoridae (Taylor & Brown 2006) were likely to be mesograzers. At least 2 species of hyalids (*Protohyale grenfelli* and *P. rubra*) and 2 species of aorids (*Aora* sp. and *Microdeutopus apopo*) were present. Mesograzing amphipods (of which 72% were *Protohyale* spp. and 28% aorids) were present in densities of 6007 ± 2209 (SE) ind. m⁻² (equivalent to 7.4 ± 2.7 ind. g⁻¹ coralline blotted wet weight) in unmanipulated controls. In a no-choice

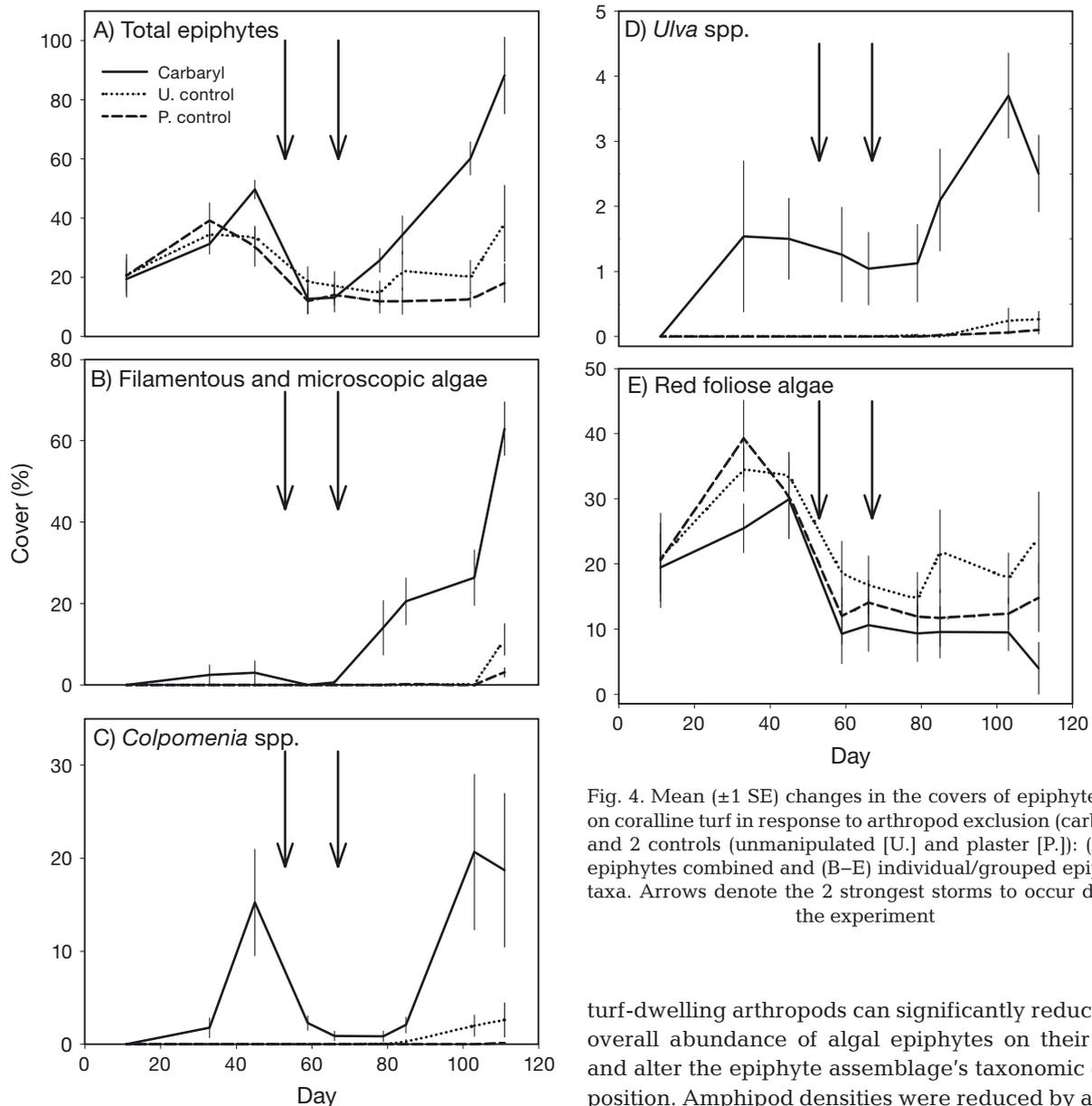


Fig. 4. Mean (± 1 SE) changes in the covers of epiphyte taxa on coralline turf in response to arthropod exclusion (carbaryl) and 2 controls (unmanipulated [U.] and plaster [P.]): (A) all epiphytes combined and (B–E) individual/grouped epiphyte taxa. Arrows denote the 2 strongest storms to occur during the experiment

feeding assay, hyalid amphipods (combination of *P. rubra* and *P. grenfelli*) consumed *Colpomenia* spp. and *Ulva* spp. at average (\pm SE) rates of 1.68 ± 0.45 and 0.26 ± 0.13 mg seaweed blotted weight ind.⁻¹ d⁻¹, respectively. The family Eatoniellidae was the numerically dominant gastropod grazer, with densities of $43\,599 \pm 5882$ (SE) ind. m⁻² in the carbaryl treatment.

DISCUSSION

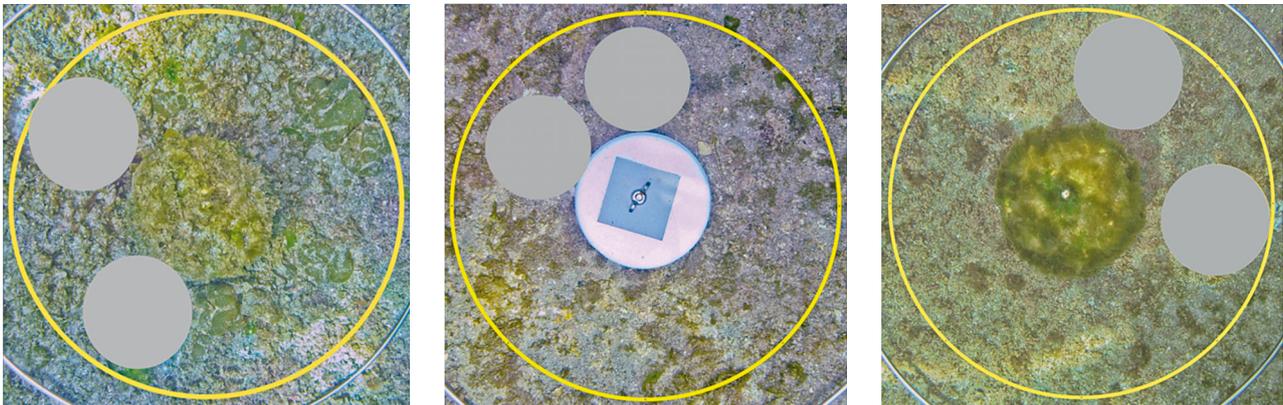
This is the first cageless study to detect strong impacts of arthropod mesograzers in a subtidal temperate reef habitat. We found that small coralline

turf-dwelling arthropods can significantly reduce the overall abundance of algal epiphytes on their host and alter the epiphyte assemblage's taxonomic composition. Amphipod densities were reduced by a similar proportion (>85%) to those reported in other cageless studies (Poore et al. 2009, Cook et al. 2011, Myers & Heck 2013). However, our finding of a large (2.3-fold, or 131%) increase in epiphytic cover following mesograzers exclusion is in contrast with the results of Poore et al. (2009), who found no such impacts in another temperate reef habitat. Although varying in magnitude (with increases in epiphyte cover of 25, 70, 447 and 590% following amphipod exclusion), the results from cageless seagrass studies (Cook et al. 2011, Myers & Heck 2013, Whalen et al. 2013, Reynolds et al. 2014) correspond with ours, suggesting that amphipods play a strong role in controlling epiphyte overgrowth in these 2 habitats, and likely others. Mesograzers exclusion caused an in-

Day 45



Day 111



Carbaryl

U. control

P. control

Fig. 5. Representative photographs of coralline turf on Days 45 (reduced quadrat area) and 111. Arthropod densities were reduced in the carbaryl treatment; the other 2 treatments were controls (unmanipulated [U.] and plaster [P.]). In the unmanipulated control on Day 111 a new housing cap was temporarily placed at the center of the site for the photograph (hence its lack of algal growth). Grey circles mark places from which faunal samples were previously taken

crease in cover of green and brown, but not red, epiphytic algal taxa. Mesograzers impacts on algal composition are often taxon-specific for both the herbivore and primary producer, and thus not easily generalized, although global trends from exclusion experiments are consistent with our result for these broad algal categories (Poore et al. 2012). Results from the cageless experiments, together with those from previous studies using other methods such as field observations (e.g. Tegner & Dayton 1987), mesocosms (e.g. Duffy & Hay 2000, Newcombe & Taylor 2010) and field experiments (e.g. Brawley & Fei 1987, Davenport & Anderson 2007, Poore et al. 2014), clearly show that mesograzers can have a major impact on seaweeds.

It is unclear why arthropod mesograzers had a strong impact on epiphytes in our coralline turf within 45 d but little effect on epiphytes of the brown

seaweed *Sargassum linearifolium* in a similar shallow temperate habitat after 70 d (Poore et al. 2009). It is difficult to meaningfully compare grazing pressure between the studies, due to differences in sampling methods (e.g. sieve mesh size) and potential differences in the taxonomic composition and size-structure of mesograzers communities. However, natural densities of mesograzing amphipods were similar in both studies ($7.4 \text{ ind. } [>0.5 \text{ mm}] \text{ g}^{-1}$ coralline turf vs. $12 \text{ ind. } [>0.3 \text{ mm}] \text{ g}^{-1}$ *Sargassum*). We note that these densities were measured only once during each study, and it is likely they varied over time as has previously been shown for amphipods in subtidal coralline turfs (e.g. Choat & Kingett 1982) and on *Sargassum linearifolium* (e.g. Poore & Steinberg 1999). A possible explanation for the greater response to arthropod exclusion in our study is that our experiment was conducted in spring/summer, seasons

associated with rapid algal growth (King & Schramm 1976, Nelson 2013) and high epiphyte abundance (Dromgoole 1973, Edgar 1983), compared to winter (although see Jennings & Steinberg 1997), when the study by Poore et al. (2009) was conducted. Another factor may have been the greater difference in palatability between host seaweed and epiphytes in our system; coralline algae are much less edible to mesograzers than *Sargassum* (e.g. Taylor & Steinberg 2005).

Gammarid amphipods of the genus *Protohyale* (family Hyalidae) were naturally abundant in subtidal coralline turf and consumed *Colpomenia* spp. and *Ulva* spp. in a feeding assay, strongly suggesting they were responsible for reducing abundances of these epiphytes in nature. Hyalid amphipods are predominantly herbivorous (Brawley 1992) and often eat their algal hosts as well as the epiphytes they support. For example *Protohyale* (= *Hyale*) *rubra* consumed both epiphytic and host macroalgal taxa in a feeding assay (Poore 1994), and greater field abundances of *Protohyale* (= *Hyale*) *nigra* occurred on epiphytised, as opposed to clean, brown seaweeds (Poore et al. 2000). Hyalids, which display species-specific diet preferences, feed on a variety of green, brown and red algal taxa under laboratory conditions (Tararam et al. 1985, Buschmann 1990). *P. rubra*, present in our field/laboratory studies, was similarly found by Poore (1994) to consume epiphytes from the genera *Ulva* and *Colpomenia* in the laboratory. *Protohyale grenfelli*, also present in our field/laboratory studies, is endemic to New Zealand, and no previous studies could be found regarding its diet. *Colpomenia* spp. was consumed at a faster rate than *Ulva* spp. by hyalid amphipods in our feeding assays. Poore & Steinberg (1999) also found high amphipod feeding rates on *C. peregrina*, attributing this to compensatory feeding on this nutritionally poor algal species. However, although feeding assays were carried out on larger algal individuals, we note that the very low densities of *Ulva* spp. and *Colpomenia* spp. in the unmanipulated plots would suggest that much of the mesograzers control is due to consumption of early life-history stages (e.g. Worm & Chapman 1998, Lotze et al. 2001).

Amphipods belonging to the genera *Aora* and *Microdeutopus* (family Aoridae) may also have reduced epiphyte abundances in our field controls. Aorids can be herbivorous: for example, *A. typica*, common in our study region, consumes various algal taxa, including *Ulva* sp., under laboratory conditions (Taylor & Brown 2006), while *Microdeutopus* sp. also eat algae including *Ulva* spp. (Borowsky 1980,

Heckscher et al. 1996). Although isopods, ostracods and decapods were less abundant than amphipods, and taxa within these groups were considered unlikely to be significant grazers of macroalgal epiphytes, they were also negatively impacted by carbaryl and therefore possibly contributed to grazing impacts in our field controls.

Functional redundancy occurs when multiple taxa perform the same ecosystem function. Redundancy has been demonstrated for epiphyte consumption by various arthropod mesograzers (Duffy et al. 2001). In our experiment, extremely abundant herbivorous gastropods of the family Eatoniellidae did not control epiphytes in the absence of amphipods. As eatoniellids have a diet of microalgae and microdetritus (Ponder 1965), rather than larger algal epiphytes, our results may be due to a lack of dietary overlap with amphipods rather than low eatoniellid feeding rates. The inability of other mesograzers to control algal epiphytes when amphipods were absent was also reported by cageless seagrass experiments (e.g. Cook et al. 2011, Myers & Heck 2013, Whalen et al. 2013). This highlights the critical role played by grazing amphipods in the functioning of benthic ecosystems.

Mutualistic interactions, important determinants of ecosystem processes (Hay et al. 2004), are thought to exist between epiphyte-grazing amphipods and host macroalgae (Amsler et al. 2014). Coralline turf fronds are compact and can protect arthropod mesograzers from water motion (Dommasnes 1968) and predation (Coull & Wells 1983) and also provide them with a food source in the form of algal epiphytes. In turn, the mesograzers potentially benefit the coralline by removing epiphytes (present study), which could reduce the growth and reproductive output of the underlying coralline (Konar 1993). It is therefore likely that, by reducing fouling epiphytes, mesograzers maintain the health of coralline turf and could potentially play a role in buffering turfs from the indirect negative impacts of coastal eutrophication (e.g. Myers & Heck 2013).

As in other subtidal habitats (e.g. Dayton & Tegner 1984, Duggins et al. 2003), storm-driven disturbance had strong impacts on algal composition. Covers of red foliose algae, *Ulva* spp. and *Colpomenia* spp. decreased greatly following storms. The rapidity of the loss, and the presence of *Colpomenia* spp. on nearby beaches after storms (A. Berthelsen pers. obs.), indicates that the reduction in epiphyte cover was likely caused by wave action. An alternative explanation is that mesograzers reinvaded carbaryl replicates when wave action prevented replacement of the plaster blocks. However, although reinvasion

probably occurred (Pavia et al. 1999), the rapid consumption of large amounts of epiphytes does not seem likely as blocks also dissolved completely during a weaker storm (Day 96) without similar results. Decreases in epiphyte cover were most apparent at the mesograzers exclusion sites where epiphyte communities were effectively 'reset' (i.e. became more similar to controls), showing that storm disturbance and grazing had similar effects on epiphyte composition and abundance. The mesograzers thus prevented the overgrowth of coralline turf by epiphytes during calm periods.

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