

# Predation constrains host choice for a marine mesograzer

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**ABSTRACT:** For small sedentary herbivores that inhabit seaweeds, choosing a host that provides adequate nutrition and refuge should be favored by natural selection. Yet, the relative importance of seaweed nutritional value versus habitat quality in driving mesograzer host choice remains poorly understood for most herbivores. Previous work in coastal North Carolina, USA, and 2 tropical locations suggests that amphipods often utilize host seaweeds that offer superior refuge from both omnivorous and carnivorous consumers. Our study was conducted in New Zealand, where carnivores alone are the major consumers of seaweed-dwelling amphipods. We show that the herbivorous amphipod *Aora typica* preferentially utilizes the dictyotalean seaweed *Dictyota kunthii* over a dominant canopy-forming kelp, *Ecklonia radiata*, and that this preferred seaweed host provides a superior refuge from predators in both laboratory and field experiments. There was no difference in *A. typica* feeding preference between *D. kunthii* and *E. radiata*, but *A. typica* grew faster when reared on *E. radiata*. These results suggest that seaweed refuge quality, not nutritional quality, drives *A. typica* host preference and distribution in this system.

**KEY WORDS:** Amphipod · Enemy-free space · Fitness · Plant–herbivore interaction · New Zealand · Seaweed

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## INTRODUCTION

Small marine herbivores (termed mesograzers) are at high risk of predator attack and commonly live on the seaweed they consume. For these mesograzers, choosing a seaweed that provides both adequate nutrition and a refuge from consumers can enhance fitness considerably. However, the relative importance of food value versus habitat value in determining host use remains unclear for most marine herbivores. Determining the factors that contribute to host choice is important because mesograzers are critical components in marine food webs and can dramatically alter benthic community structure, especially when their densities escape control by predators (Tegner & Dayton 1987, Duffy & Hay 2000, Davenport & Anderson 2007, but see Poore et al. 2009).

Superior food quality can drive host choice for mesograzers in cases where one or several seaweed species,

or even different individual seaweeds within a population, maximize fitness (Poore & Steinberg 1999, Cruz-Rivera & Hay 2000, 2003, Taylor et al. 2003). In other cases, marine mesograzers select a host that provides them with superior refuge from predation (Hay et al. 1989, 1990a, Duffy & Hay 1991, 1994, Hay 2009) or physical stresses such as wave action (Sotka 2007).

Seaweeds of superior refuge quality may reduce predation on resident mesograzers by (1) providing deterrent compounds that may be sequestered by mesograzers (Paul & Van Alstyne 1988, Hay et al. 1989, Hay 2009), (2) hiding mesograzers from predators through crypsis (Coull & Wells 1983, Hacker & Steneck 1990, Hacker & Madin 1991, Hultgren & Stachowicz 2008, 2010), or (3) indirectly deterring predators via host chemical defenses that limit predation on both the host and associated mesograzers (Hay et al. 1989, Duffy & Hay 1994, Sotka et al. 1999). For many less mobile mesograzers, food and habitat value are coupled; thus,

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mesograzers may evolve tolerance to chemically rich seaweed hosts that deter large consumers, in order to obtain 'enemy-free space' (Jeffries & Lawton 1984).

For example, off the southeastern coast of the United States, chemical deterrents within *Dictyota menstrualis* suppress feeding by large mobile omnivores like sea urchins and sparid fishes, but have minimal effects on feeding by small resident amphipod and polychaete species (Hay et al. 1987, 1988, Duffy & Hay 1991, 1994, Cruz-Rivera & Hay 2001, 2003). This phenomenon has also been observed in tropical reef communities (Hay et al. 1989, 1990b). At the community level, Taylor & Steinberg (2005) found that mesograzers on 2 temperate Australasian rocky reefs had feeding preferences that differed from those of larger grazers. However, field distributions did not reflect a tendency for mesograzers to inhabit seaweeds of low preference to larger grazers (Taylor & Steinberg 2005). Those authors speculated that this latter result was due to differences in the spatial and temporal distribution of seaweeds in temperate Australasia versus the temperate western Atlantic, and/or the rarity of omnivorous predators at their study sites. Specifically, they pointed out that the fishes preying on mesograzers in their system typically do not eat seaweeds and are thus unlikely to drive mesograzers host distributions toward chemically defended seaweeds that deter large generalist consumers (Taylor & Steinberg 2005).

Here, we investigated the host seaweed preference and distribution of the herbivorous gammarid amphipod *Aora typica* Krøyer, 1845, within a temperate rocky reef system in northeastern New Zealand and evaluated the role of host food value versus refuge value in determining distribution patterns. Using a series of laboratory and field experiments, we asked: (1) Does *A. typica* exhibit host preference among co-occurring seaweeds? (2) Do amphipod–host use patterns change in the presence of predators (via preference and differential predation)? (3) Are host preferences better explained by variation in host nutritional quality and its impact on fitness or by variation in host value as a refuge from predation?

## MATERIALS AND METHODS

**Study sites and organisms.** Unless otherwise stated, all collections and experiments were conducted during January 2007. Organisms were collected near the University of Auckland's Leigh Marine Laboratory at Goat Island, New Zealand (36° 16.1' S, 174° 47.8' E) and nearby in Omaha Cove (36° 17.4' S, 174° 48.6' E). We collected the brown seaweeds *Carpophyllum maschalocarpum* and *Sargassum sinclairii* (Fucales), *Zonaria turneriana* and *Dictyota kunthii* (Dictyotales), and *Eck-*

*lonia radiata* (Laminariales) for use in the present study because they commonly co-occur in the field and are known hosts for the amphipod *Aora typica* (Taylor & Brown 2006). *D. kunthii* was also collected because we observed *A. typica* inhabiting this seaweed in the field and because the seaweed produces diterpene alcohols (De Nys et al. 1993), a class of compounds known to affect the feeding and colonization of amphipods in temperate systems of the western Atlantic (Hay et al. 1987, Duffy & Hay 1994, Sotka & Hay 2002, Sotka et al. 2003). Algae were collected intact from the rocky substrate and housed in buckets supplied with seawater from the Leigh Marine Laboratory's flow-through seawater system until used in assays within 24 h. Seaweeds were identified following Adams (1994). We obtained amphipods from seaweeds collected at Omaha Cove by dipping the seaweeds in freshwater for a few seconds and then returning to saltwater, causing the amphipods to flee the seaweed (Taylor & Steinberg 2005).

Predation rates on *Aora typica* were assessed using the wrasse *Notolabrus celidotus* and the shrimp *Palaeomon affinis* that co-occur with *A. typica* (authors' pers. obs.) and utilize amphipods as a significant prey source (Jones 1984, Taylor 1991, Day 2001). We collected *N. celidotus* by handnet via SCUBA at Ti Point near Leigh, New Zealand. *P. affinis* was captured at Ti Point using minnow traps. Both *N. celidotus* and *P. affinis* were housed in 10 l buckets supplied with seawater from the Leigh Marine Laboratory's flow-through seawater system. Predators were fed freeze-dried krill *Euphausia superba* each morning ad libitum to acclimate them to captivity. One week prior to the start of the predation trials, 1 of the 5 different macroalgal species inhabited by *A. typica* was placed in the predator buckets to further condition them to captive feeding.

**Laboratory: *Aora typica* distribution on potential host seaweeds.** To assess the host preference of *A. typica*, we conducted a multiple-choice colonization assay in the laboratory by simultaneously offering amphipods 5 co-occurring seaweeds (see above subsection) as potential hosts. Individual thalli of each seaweed species were defaunated with a dilute solution (1 ml l<sup>-1</sup>) of insecticide (liquid Sevin 4F, active ingredient 1-naphthyl n-methyl-carbonate; Duffy & Hay 2000), rinsed thoroughly to remove traces of the insecticide, and trimmed to standardize surface area (25.19 ± 0.74 cm<sup>2</sup>). We chose to standardize the surface area of our seaweed plants to equalize amphipod–host encounter probabilities for each seaweed species. Algal pieces were subsequently inserted stipe-first into a small piece of slotted rubber bath mat (2 × 3 cm) and arranged in randomized circular order on the bottom of a 10 l bucket. *A. typica* (15 to 20 adults) were introduced into each trial bucket

and allowed 3 h to colonize the 5 seaweeds and build their membranous tubes.

To assess how predation affects the distribution of *Aora typica* on their host seaweeds (either through a change in preference or differential predation), we set up experiments as described above, but after 2 h we released predators into randomly chosen buckets ( $n = 27$  for fish,  $n = 12$  for shrimp). We allowed predators to forage for the final hour of the experiment, leaving 39 buckets as controls. At the end of the experiment, we removed predators from buckets and carefully removed and rinsed seaweeds with freshwater and scored the number of amphipods inhabiting each seaweed. Amphipods that died during the trial or did not choose a host were noted and excluded from amphipod totals for each bucket. Amphipod distribution patterns were calculated as the percentage of seaweed-occupying *A. typica* on each seaweed species within each bucket. All experimental animals were used only once during our behavioral trials. The effects of algal species on *A. typica* host-use were analyzed using Friedman's test on ranked data followed by Dunn's post hoc test and Bonferroni correction for multiple comparisons. We chose Friedman's test for randomized blocks, to account for dependence within our experimental buckets (i.e. blocks) associated with simultaneously offering seaweed choices (Roa 1992, Sokal & Rohlf 2003). Friedman's test is an appropriate test to use for the short time scale of our experiment, where changes within seaweed tissue due to deterioration or feeding are negligible (Lockwood 1998), and this test has been used in a similar habitat-choice experiment (Sotka 2007). To determine how predators affect amphipod distribution, we compared amphipod distribution patterns in shrimp and fish treatments to the expected distribution in our predator-free treatment using a  $G$ -test for goodness of fit (Sokal & Rohlf 2003).

**Field: *Aora typica* distribution on potential host seaweeds.** Amphipod field distributions are a product of both host preference and differential predation. To assess whether host use patterns observed in our laboratory assays also occurred in the field, we measured amphipod abundance on seaweeds that had been defaunated and out-planted to the field for 48 h. We chose 3 seaweed species for field assays based on *A. typica* colonization preferences in the laboratory (high preference—*Dictyota kunthii* and *Sargassum sinclairii*; low preference—*Ecklonia radiata*; see Fig. 1a). All 3 seaweeds were randomly deployed 15 cm apart. Defaunated seaweed thalli of equal surface area (approximately 150 cm<sup>2</sup>) were attached stipe-first to a 10 cm rope section fastened to a 1 m bar. Bars were deployed at Goat Island ( $n = 7$ ) and Omaha Cove ( $n = 7$ ) for 48 h. During this time, no attempt was made to cage out predators; therefore, 'amphipod abundance'

is a result of both choice and predation. At the end of 48 h, individual seaweeds were carefully bagged *in situ* and returned to the laboratory, where seaweeds were rinsed in freshwater and amphipods were counted. The effects of site location and algal species on the density of *A. typica* (cm<sup>-2</sup> alga) were analyzed with a 2-factor analysis of variance (ANOVA) of log-transformed data, followed by Tukey honestly significant difference (HSD) post hoc tests.

**Laboratory: feeding preferences.** We measured the feeding preference of *Aora typica* for its most preferred (*Dictyota kunthii*) and least preferred (*Ecklonia radiata*; see Fig. 1a) host seaweeds to assess whether palatability explained the differential use of these 2 seaweeds. For each seaweed species, 2 apical pieces of tissue were clipped from the same individual and defaunated by rubbing vigorously. Seaweed pieces were blotted with a paper towel, weighed to the nearest milligram, and placed in 300 ml cups. Each treatment cup ( $n = 20$ ) contained pieces of *D. kunthii* ( $\sim 74 \pm 3$  mg) and *E. radiata* ( $\sim 76 \pm 2$  mg) that were paired to control cups ( $n = 20$ ) containing pieces from the same individual seaweed. Ten amphipods were placed in each treatment cup and covered with shade cloth. Water in both treatment and control cups was refreshed every 12 h by replacing half of the water with clean seawater. After 48 h, we removed amphipods from treatment cups and all seaweeds were blotted and re-weighed. The amount consumed was calculated as:  $[T_i \times (C_i/C_t)] - T_i$ , where  $T_i$  and  $T_f$  are the pre-assay and post-assay blotted wet mass of an alga (respectively) in a treatment replicate, and  $C_i$  and  $C_f$  are the pre-assay and post-assay wet blotted mass of a paired alga (respectively) in an autogenic control replicate. Feeding data were assessed using a paired  $t$ -test.

**Laboratory: food quality of seaweeds.** The ability of *Aora typica* to survive and grow to reproductive maturity on *Dictyota kunthii* and *Ecklonia radiata* was assessed by culturing newly released juveniles on each species. Gravid *A. typica* females were taken from outdoor mixed-algal cultures and kept for 18 d in separate 60 mm diameter Petri dishes containing seawater and a small piece of *Ulva* sp. When most females had released numerous juveniles from their marsupia, juveniles were carefully pipetted into Petri dishes containing seawater with  $5 \times 10^6$  MW polyethylene oxide added at 25 mg l<sup>-1</sup> to reduce entrapment in the surface tension (Sandifer et al. 1975). Four juveniles were taken from each female, with each juvenile added to a Petri dish containing a  $\sim 1$  cm<sup>2</sup> piece of tissue from either *D. kunthii* ( $n = 20$ ), *E. radiata* ( $n = 20$ ), or *Carpophyllum maschalocarpum* (a positive control known to support strong growth and survival in *A. typica*; Taylor & Brown 2006;  $n = 19$ ), or a no-food control containing only a small piece of mesh for the amphipod to

cling to (Chapelle & Peck 1995;  $n = 20$ ). Seawater and seaweed tissue were replaced weekly; or more frequently for seawater if it became discolored due to algal exudates. All amphipods were checked every 2 d until the first ovulating female was observed, after which they were all checked daily. At each observation, deaths and ovulating females were recorded, and seaweed tissue or mesh was moved back next to any amphipods that had lost physical contact with them. On Day 35, surviving amphipods were preserved in 70% isopropyl alcohol, and their lengths were measured from the tip of the rostrum to the rear of the fifth pereonite. Differences among survivorship curves were analyzed by the Wilcoxon test using the SAS procedure LIFETEST (SAS Institute 1990), with post hoc pair-wise comparisons made following Fox (1993). Length of survivors and time to ovulation were analyzed using a 1-factor ANOVA, with multiple comparisons made by a Tukey HSD test.

**Laboratory: refuge quality of seaweeds.** To determine if host preference in *Aora typica* could be associated with improved predator avoidance, we tested the refuge quality of their most preferred (*Dictyota kunthii*) and least preferred (*Ecklonia radiata*) seaweed host (see Fig. 1a). We introduced 15 to 20 amphipods into buckets containing either 5 *D. kunthii* thalli or 5 *E. radiata* thalli of equal surface area and allowed amphipods to colonize seaweed for 2 h before exposure to predators. After 2 h, individual *Notolabrus celidotus* were released into buckets ( $n = 10$ ) and allowed to forage for 1 h, while *Palaemon affinis* ( $n = 6$ ) were allowed to forage overnight because preliminary trials indicated that they foraged much more slowly than the fish. At the end of each trial, we removed seaweed from buckets, rinsed it in freshwater and enumerated surviving amphipods. We compared percent amphipod survival between hosts using a *t*-test.

**Field: refuge quality of seaweeds.** To assess amphipod predation risk when inhabiting *Dictyota kunthii* versus *Ecklonia radiata* in the field, we killed amphipods so that escape from treatments would not be mistaken for removal by predators, tied individuals to a host alga, and deployed these seaweeds with attached amphipods in the field where they would be accessible to the natural suite of predators. We killed amphipods by squeezing their head to induce a cranial contusion. Each amphipod was randomly assigned to the front or back of a seaweed, and its position on a seaweed was determined randomly using a grid laid over the seaweed frond. Both *D. kunthii* and *E. radiata* have a planar structure; thus, 3-dimensional differences were assumed to be negligible. Five amphipods were attached to each seaweed thallus by a sewing thread of matching color (light brown matching the amphipod) wrapped around their abdomen (like a

seatbelt). The thread was pulled tightly so that the amphipod was lying flush against the frond, much as if they were in one of their mucilaginous tubes. A previous experiment assessing seaweed refuge quality in the field had glued amphipods to seaweed surfaces (Duffy & Hay 1994); our method was more time-consuming, but avoided potential chemical or textural effects of the glue on consumer feeding. Individual thalli of *D. kunthii* and *E. radiata* were paired and deployed together on 1 m steel bars at Goat Island ( $n = 6$ ). We placed bars 3 m apart on sandy substrate (5 m depth), in a protected cove for 4 h. We also transported bars ( $n = 6$ ) from the laboratory at Goat Island to the deployment site, deployed them, and immediately retrieved them to determine amphipod loss due to deployment and transport. No amphipods were lost during this process. To control for potential loss due to wave action, we deployed bars ( $n = 6$ ) in a 300 l wave tank. This tank emptied a 30 l bucket of water into the tank from a height of 0.2 m every 160 s, producing a substantial wave surge in the tank. We observed a negligible loss (1 of 79 amphipods) after 4 h due to water movement. To reduce hydrodynamic loss in the field, care was taken to deploy replicates during calm conditions. After 4 h, we enumerated amphipods lost from each seaweed *in situ*. Differences in percentage of *Aora typica* remaining on *D. kunthii* versus *E. radiata* were compared using a *t*-test.

**Field: natural seaweed and amphipod abundances.** In January of 2007 and again in December 2009, we conducted field surveys to assess natural densities of *Aora typica* on the most (*Dictyota kunthii*) and least (*Ecklonia radiata*) preferred seaweeds from our laboratory assays. Individual seaweeds from 0 to 3 m below mean low tide level were haphazardly selected by a diver, cut off 10 mm above the holdfast, and enclosed in a plastic bag ( $n = 10$  in 2007 and  $n = 7$  in 2009). At the laboratory, the seaweeds were washed in freshwater to dislodge associated mobile animals (Taylor & Steinberg 2005), which were retained on a 0.5 mm mesh sieve and preserved in 10% formalin. All *A. typica* were later counted. Seaweeds were shaken to remove excess surface water, and the wet mass was determined ( $\pm 0.1$  g).

Amphipod densities on *Dictyota kunthii* and *Ecklonia radiata* were compared by a *t*-test within each sampling period. Additionally, the 2 resultant *p*-values were combined using Fisher's method as described in Sokal & Rohlf (2003) to give a single *p*-value testing the overall significance of host seaweed species on amphipod field densities.

In 2009, we conducted seaweed abundance surveys to determine the relative likelihood of an amphipod encountering our experimental seaweed species in the field. All seaweeds were counted within 0.25 m<sup>2</sup>

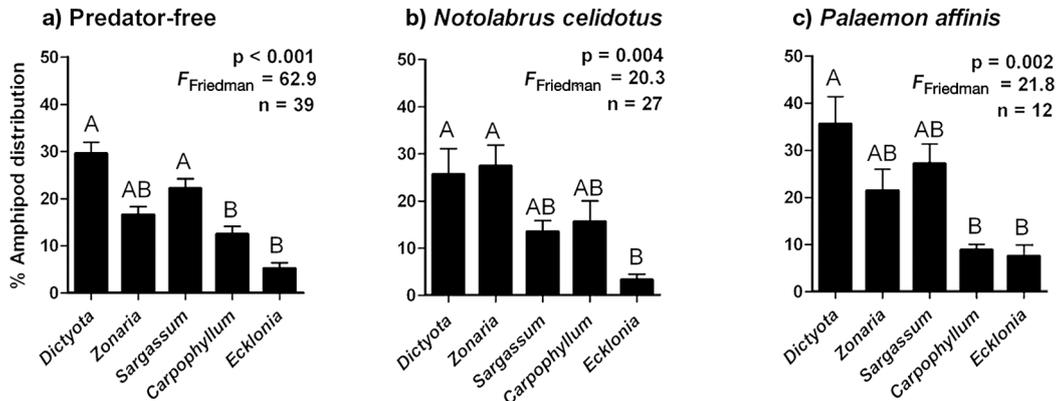


Fig. 1. *Aora typica*. Distribution of the amphipod (mean + SEM) on the co-occurring seaweeds *Dictyota kunthii*, *Zonaria turneriana*, *Sargassum sinclairii*, *Carpophyllum maschalocarpum*, and *Ecklonia radiata* when equal surface areas of each seaweed were available to amphipods in 10 l containers with (a) no predators ( $n = 39$ ), (b) the predatory fish *Notolabrus celidotus* ( $n = 27$ ), or (c) the predatory shrimp *Palaemon affinis* ( $n = 12$ ). Data were analyzed using Friedman's test, followed by Dunn's post hoc test and Bonferroni correction for multiple comparisons. Bars with the same letter are not significantly different within treatments ( $p > 0.05$ )

quadrats haphazardly placed in a zone 0 to 3 m below mean low tide level ( $n = 20$ ). To enable the estimation of seaweed biomass, haphazardly selected individuals of the 5 target species (*Carpophyllum maschalocarpum*, *Ecklonia radiata*, *Dictyota kunthii*, *Sargassum sinclairii* and *Zonaria turneriana*) were collected, shaken dry, and weighed ( $\pm 0.1$  g) ( $n = 10$ ). Seaweed biomasses per unit area were estimated for each seaweed species as the product of average individual seaweed mass ( $n = 10$ ) and average density per unit area ( $n = 20$ ). Averages could not be compared using standard tests (e.g. ANOVA) because there were no replicate 'biomasses per unit area,' so bootstrapping (10 000 runs) was used to identify averages differing significantly at  $p = 0.05$  level (SAS Institute 1990).

## RESULTS

When offered multiple seaweeds as potential colonization sites in laboratory assays (without predators present), the amphipod *Aora typica* preferentially colonized *Dictyota kunthii* and *Sargassum sinclairii*, while occupying *Carpophyllum maschalocarpum* and *Ecklonia radiata* at significantly lower levels (Fig. 1; Friedman's 1-way test,  $p < 0.001$ ). The presence of a predatory fish or shrimp did not significantly affect the distribution patterns ( $G$ -test for goodness of fit,  $p = 0.5$ ). When defaunated seaweeds were placed in the field for 48 h at 2 local habitats, colonization by *A. typica* paralleled patterns seen in the laboratory; at both sites, *A. typica* colonized *D. kunthii* and *S. sinclairii* significantly more than *E. radiata* (Fig. 2).

When *Aora typica* were simultaneously offered their most preferred (*Dictyota kunthii*) and least preferred (*Ecklonia radiata*) host (see Fig. 1a) as food choices,

they consumed similar amounts of each seaweed (paired  $t$ -test:  $p = 0.422$ ,  $n = 20$ ). When confined to single species diets of *D. kunthii*, *E. radiata*, or *Carpophyllum maschalocarpum* (an intermediate preference host) amphipods survived equally well and grew significantly better on the avoided host, *E. radiata*, than on either of the more preferred hosts (Fig. 3a,b). Furthermore, there was no difference in the proportion of *A. typica* females that reached sexual maturity (Fisher's exact test:  $p = 0.37$ ) or the timing of ovulation (Fig. 3c). Thus, physiological performance was not best on the preferred host, so other factors must have selected for host choice.

When *Aora typica* was confined with *Dictyota kunthii* or with *Ecklonia radiata* and exposed to predators in the laboratory, survivorship on *D. kunthii* was 4.5-fold higher with a fish predator and 2.4-fold higher

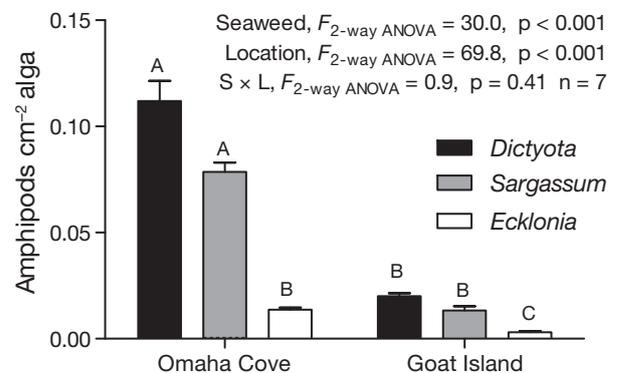


Fig. 2. *Aora typica*. Amphipods (mean + SEM) on *Dictyota kunthii*, *Sargassum sinclairii*, and *Ecklonia radiata* when defaunated and outplanted at 2 field locations for 48 h. Analyzed by 2-way ANOVA, followed by Tukey's honestly significant difference post hoc test. Bars with the same letter are not significantly different ( $p > 0.05$ )

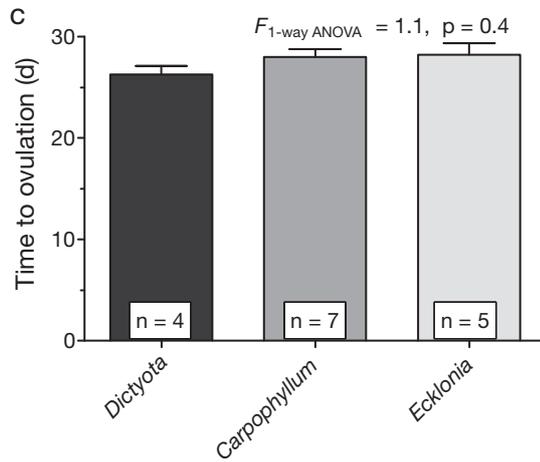
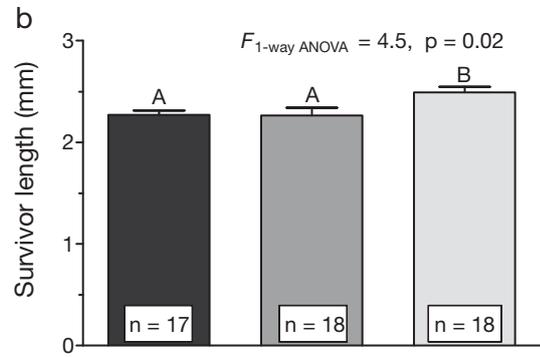
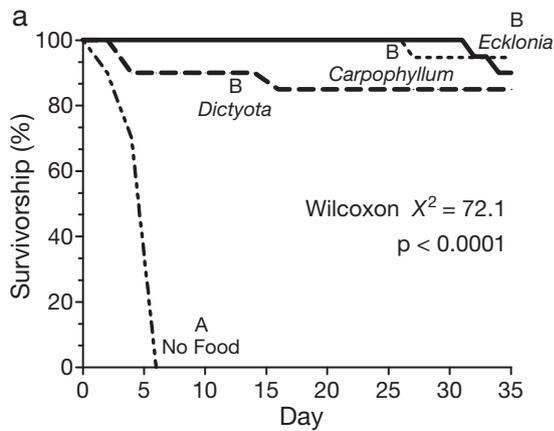


Fig. 3. *Aora typica*. (a) Survival, (b) length at Day 35, and (c) days to ovulation of juveniles (mean + SEM) when raised on 3 co-occurring brown seaweeds. Differing upper case letters indicate treatments that differ significantly according to the test of Fox (1993) (a) or to Tukey's honestly significant difference test (b,c). Initially there were n = 20 amphipods, except for *Carpophyllum maschalocarpum* (n = 19)

with a shrimp predator than when confined on *E. radiata* (Fig. 4). When amphipods were confined on *D. kunthii* versus *E. radiata* in the field and exposed to the natural diversity of consumers occurring there, *A. typica* persistence was 3.7-fold greater on *D. kunthii* than on *E. radiata* (Fig. 5).

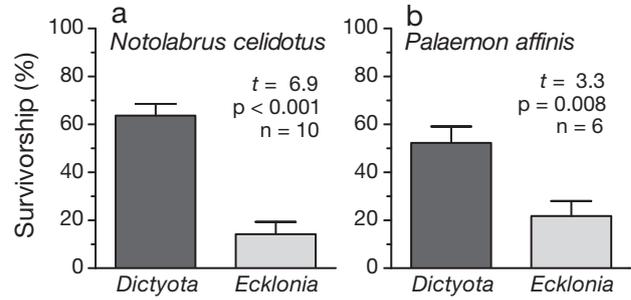


Fig. 4. *Aora typica*. Survival of amphipods (%; mean + SEM) on the seaweeds *Dictyota kunthii* or *Ecklonia radiata* when confined with (a) the predatory fish *Notolabrus celidotus* for 1 h or (b) the predatory shrimp *Palaemon affinis* for 8 h in no-choice laboratory assays. Analyzed by *t*-tests

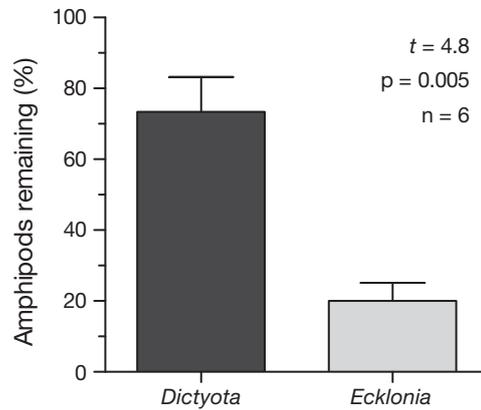


Fig. 5. *Aora typica*. Remaining amphipods (%; mean + SEM) when individuals were killed, tied to *Dictyota kunthii* or *Ecklonia radiata*, and deployed in the field for 4 h. Analyzed by paired *t*-test

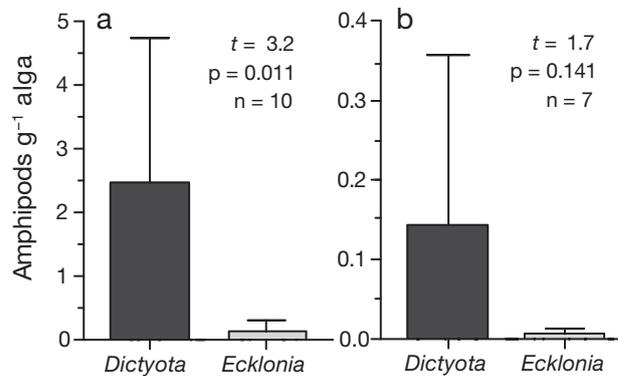


Fig. 6. *Aora typica*. Field abundance of amphipods (mean + SEM) on *Dictyota kunthii* and *Ecklonia radiata* in (a) 2007 and (b) 2009. Analyzed by *t*-test

In the field, *Aora typica* densities were significantly greater on *Dictyota kunthii* than on *Ecklonia radiata* (Fig. 6; combined p-value for the 2 sampling occasions was 0.01 < p < 0.05, calculated following Sokal & Rohlf

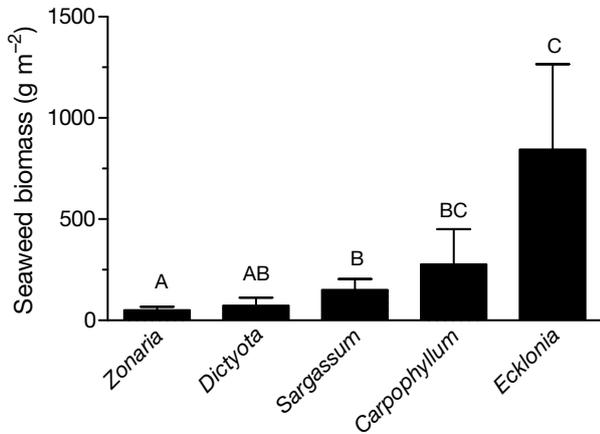


Fig. 7. Seaweed biomass (mean + SEM; *Zonaria turneriana*, *Dictyota kunthii*, *Sargassum sinclairii*, *Carpophyllum maschlocaarpum*, and *Ecklonia radiata*) calculated from independent estimates of individual density ( $n = 20$ ) and individual mass ( $n = 10$ ), with averages differing at  $p < 0.05$  denoted by different upper case letters, as identified using bootstrapping (10000 runs)

2003, p. 794). This distribution was not due to simply colonizing the more common host; biomass of the minimally occupied *E. radiata* exceeds that of *D. kunthii* by 12-fold in the field (Fig. 7).

## DISCUSSION

Despite juvenile *Aora typica* growing significantly better on *Ecklonia radiata*, and surviving and reproducing as well on *E. radiata* as on *Dictyota kunthii*, adult amphipods colonized *D. kunthii* at densities from 4.5- to 8.2-fold greater than those found on *E. radiata* in all laboratory and field experiments (Figs. 1 & 2). These data indicate that seaweed nutritional quality plays a secondary role in shaping the host preference of *A. typica* for these seaweeds, and corroborates a number of studies demonstrating that host preference of many mesograzers is not explicable solely in terms of host nutritional value (Nicotri 1980, Duffy & Hay 1991, Taylor & Brown 2006).

Our results suggest that refuge quality is a major determinant of host preference in *Aora typica*. Survivorship of *A. typica* inhabiting *Dictyota kunthii* versus *Ecklonia radiata* in the laboratory was 2.4-fold higher in the presence of a shrimp predator and 4.5-fold higher in the presence of a fish predator (Fig. 4). In a similar field assay, persistence was 3.7-fold higher on *D. kunthii* (Fig. 5). These patterns could arise if (1) amphipods colonize *D. kunthii* over *E. radiata* regardless of predation risk, and random foraging by predators produces an overall reduction in amphipod density with no change in amphipod relative distribution among host seaweeds, or (2) amphipods colonize

*D. kunthii* over *E. radiata*, and predators reinforce this behavior by selectively removing individuals from *E. radiata*; such selective predation could select for strong host preferences over time.

Our data suggest that predator reinforcement of amphipod behavior is a likely explanation for the colonization patterns we observed, given that both a fish and a shrimp predator foraged more efficiently from *Ecklonia radiata* than from *Dictyota kunthii* (Fig. 4) and that amphipods are 2.7-fold more likely to be consumed from *E. radiata* than from *D. kunthii* in the field (Fig. 5). Thus, predation risk may strongly select for individuals of *Aora typica* that colonize *D. kunthii* and avoid *E. radiata*. Given that *A. typica* prefer *D. kunthii* in the absence of predators (Fig. 1), predator cues appear unnecessary for initiating this colonization behavior.

It is clear that in the presence of predators, survivorship of *Aora typica* is higher on *Dictyota kunthii* than on *Ecklonia radiata* (Fig. 4), yet the mechanism by which *D. kunthii* provides refuge to *A. typica* is unclear. Algal structural complexity can be positively correlated with epifaunal survival (Nicotri 1980, Coull & Wells 1983, Hacker & Steneck 1990, Sotka 2007, Zamzow et al. 2010), but this is not always the case (Holmlund et al. 1990). Furthermore, crypsis through host-plant matching, mimicry, or disruptive coloration can reduce predation in epifaunal species (Hacker & Madin 1991, Merilaita 1998, Hultgren & Stachowicz 2007, 2010). *D. kunthii* and *E. radiata* were 2 of the least structurally complex seaweeds tested, but occupy opposite ends of the host preference range; however, the sometimes overlapping fronds of *D. kunthii* might provide more structural refuge than the more planar fronds of *E. radiata*. In addition, predators may be less efficient foraging on epifauna occupying *D. kunthii* because the alga has small tongue-like protrusions (ligulae) on the surface of reproductive portions of the seaweed; these increase small-scale structural complexity and make amphipods more cryptic or more difficult to attack. These ligulae are easily detached (authors' pers. obs.) and might be incidentally ingested during predation events. This could also deter consumption if *D. kunthii* possesses compounds that are toxic or distasteful to predators of *A. typica*.

*Dictyota kunthii* produces diterpene alcohols (De Nys et al. 1993), and diterpene alcohols from other *Dictyota* spp. deter feeding by large consumers in other systems (Hay et al. 1987, 1988, Cronin & Hay 1996). Furthermore, there are numerous examples of small marine invertebrates gaining refuge from predators by wrapping or covering themselves in chemically defended seaweed (Hay et al. 1990b, Sotka et al. 1999, Stachowicz & Hay 1999, Hay 2009). Whether or not ligulae are ingested during predation events likely

depends on the foraging style of the predator; however, in some seaweeds compounds accumulate on seaweed surfaces (Lane et al. 2009), and their presence alone might impede consumers from foraging on the surface of chemically rich seaweeds. However, because the defensive value of similar metabolites within a chemical class can vary (Kicklighter et al. 2004), assumptions about the function of compounds without rigorous bioassays are questionable.

*Aora typica* preferentially colonizing a dictyotalean seaweed of superior refuge quality is similar to the pattern observed in coastal North Carolina (Duffy & Hay 1991, 1994, 2000), even though there are key differences in the selective forces present in these systems (Taylor & Steinberg 2005). First, in our system, there are few omnivorous grazers akin to those responsible for driving mesograzers onto chemically defended seaweeds in North Carolina. Our system is dominated by both strict carnivores that pick amphipods from host seaweeds and voracious grazers such as urchins that can eliminate seaweeds and create large bare patches (Schiel 1982). Our results suggest that strict carnivores are an important selective force driving *A. typica* to select *Dictyota kunthii* over *Ecklonia radiata* as habitat. However, avoiding seaweeds that are likely to be destructively grazed could also drive host choice as amphipods would risk having their home destroyed by living on highly preferred seaweeds. Previous studies suggest that grazers such as the common sea urchin *Evechinus chloroticus* exhibit a preference for *E. radiata* (e.g. Schiel 1982, Cole & Haggitt 2000, Taylor & Steinberg 2005) and could pose a threat of host seaweed destruction to *A. typica* if they occupied *E. radiata*. However, within our study area, *E. radiata* is by far the dominant seaweed (Fig. 7) and is predictably present year-round, while *D. kunthii* is less common and is seasonal, making it improbable that the amphipod would select *D. kunthii* over *E. radiata* due to either persistence or predictability.

Future work is necessary to identify the mechanism of protection *Dictyota kunthii* offers *Aora typica* (i.e. crypsis/camouflage from predators, reduced dislodgement, or chemically mediated defense), as well as the cues responsible for attracting *A. typica* to *D. kunthii* and signaling its utility as a host seaweed. Understanding the host choice dynamics of Australasian mesograzers is important for gaining insight into mechanisms responsible for mesograzer abundance and distribution patterns under different selective regimes.

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