



Habitat choice and predator avoidance by Antarctic amphipods: the roles of algal chemistry and morphology

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ABSTRACT: Habitat choice is an important aspect of community structure. Perhaps the most important factor influencing choice by prey species is predation risk. Predators may directly influence prey habitat choice via consumption or, secondarily, through 'intimidation'. We investigated these forces in the near-shore ecosystem of the western Antarctic Peninsula. This system is dominated by macroalgae and exceedingly abundant amphipods, with the omnivorous fish *Notothenia coriiceps* feeding on both. Amphipod densities are very high on the dominant brown alga *Desmarestia menziesii*, which is both structurally complex and chemically defended from herbivory. Amphipod densities are low on the simply structured alga *Palmaria decipiens*, which is a preferred food of fish and some amphipods. We used these 2 species of algae and plastic and gel algal analogues to experimentally separate the roles of algal structure and chemistry in influencing amphipod habitat preference. In the absence of predators, the amphipod *Gondogeneia antarctica* preferred *Palmaria decipiens* and had no preference between structural analogues. In the presence of predator cues, its preferences changed to *D. menziesii* and the structurally complex analogue. In the absence of predator cues, the amphipod *Prostebbingia gracilis* preferred the chemically defended, structurally complex *D. menziesii* to all other choices, and preferred the structurally complex analogue to the simple one. Both *D. menziesii* and the structurally complex analogue decreased predation risk for *Prostebbingia gracilis*. Based on these results, natural abundances of amphipods are likely driven both by actual predation and the threat of predation (i.e. non-consumptive effects).

KEY WORDS: Predation · Non-consumptive effects · Amphipods · Chemical defense

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INTRODUCTION

Predation risk is pervasive, and predators strongly influence community structure and ecosystem processes (Lima & Dill 1990, Kats & Dill 1998, Preisser et al. 2005). These effects are often mediated indirectly through trophic links (Wootton 1994, Menge 1995, Peckarsky et al. 2008). Removal of predators can result in multi-level trophic cascades that radically shift community structure (Estes et al. 1998). Predation is particularly heavy on small invertebrates, and can be the most important factor regulating densities of phytal invertebrates (Duffy & Hay 1991, 2001).

There are a number of ways in which habitat may provide refuge from predation. These include structural complexity, habitat density, and chemical defenses, each of which may act alone or in concert with other factors.

Habitat preferences of mobile prey may change depending on predation threat (Werner et al. 1983, Lima & Dill 1990, Baumgartner et al. 2003). Assessing predation risk in an aquatic environment, especially when visual signals are limited by turbidity, darkness, or vertical structures such as algae, is often accomplished by detection of chemosensory cues (see e.g. Chivers et al. 1996, Kats & Dill 1998, Wisenden et al. 1999). Chemo-

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sensory detection of predators may be essential when predators are cryptic or adopt an ambush foraging strategy (Ábjörnsson et al. 2000). From waterborne chemical cues, invertebrates can detect and distinguish the type of predator and even perceive what the predator has been eating (Wudkevich et al. 1997, Wisenden et al. 1999). Numerous aquatic invertebrates, including amphipods, demonstrate anti-predator behaviors that reduce actual predation risk (Hay et al. 1990a, Holmlund et al. 1990, Duffy & Hay 1991, Byrnes et al. 2006).

Anti-predator behaviors often impose costs to prey, such as reduced foraging ability or reduced growth rates (McPeck et al. 2001, Byrnes et al. 2006). If these behaviors occur in the absence of actual predation, because of 'intimidation' (changes in behavior due to the presence of a predator alone), they are termed non-consumptive effects (Peckarsky et al. 2008). In terms of affecting prey traits, non-consumptive effects are often overlooked, but may be equally or more important than actual predation risk (Preisser et al. 2005, Pangle et al. 2007, Peckarsky et al. 2008). Furthermore, pronounced changes in community structure can occur when non-consumptive effects cascade down the food chain, having a much larger effect on the prey's resources than on the prey itself (Preisser et al. 2005, Hay 2009).

In tropical systems, algal chemistry has been shown to confer survival value to amphipod inhabitants (Hay et al. 1990b, Duffy & Hay 1991). Herbivores that choose to live on chemically defended hosts can lessen their risk of predation by fish either directly, due to the lack of palatability of the host plant to predators (Sotka et al. 1999), or indirectly, due to infrequent visitation by foraging fish that results in lower probability of being detected and consumed, or inadvertently consumed (Duffy & Hay 1994). In Antarctica, there is a strong inverse correlation between amphipod abundance on an alga in the field and amphipod feeding preference for that same alga measured in the laboratory (Huang et al. 2006, Huang et al. 2007). *Desmarestia menziesii*, for example, harbors high amphipod densities of 20 ind. g^{-1} wet wt (Huang et al. 2007), and this alga contains chemical compounds that render it unpalatable to amphipods, sea stars, and fish (Amsler et al. 1995). In contrast, *Palmaria decipiens* is among the most preferred foods for amphipods (Huang et al. 2006, Amsler et al. 2009a) but has low amphipod abundance of 0.3 ind. g^{-1} wet wt (Huang et al. 2007). The latter alga is also a preferred food item of the omnivorous Antarctic fish *Notothenia coriiceps* (Iken et al. 1997, Iken et al. 1999, Amsler et al. 2005). This observed pattern of amphipod abundance, thus, could be explained as top-down forcing: the amphipods may be displaying predator-

avoidance behavior by seeking chemically defended refugia.

Defensive chemistry is not the only difference between these 2 algal species, however. Structural differences between the species might also play a role. Increases in habitat structural complexity can decrease predation risk for resident mesograzers (Dionne & Folt 1991, Warfe & Barmuta 2004). This decrease may be due to more complex habitats providing more cover for avoiding detection, presenting a physical barrier to the movement of large-bodied fish, decreasing the efficacy of fish strikes, or otherwise inhibiting prey capture. In our study system, the preferred food species, *Palmaria decipiens*, has a simple, blade-like morphology along with low amphipod abundance, whereas the unpalatable *Desmarestia menziesii* is finely branched with high amphipod abundance. Thus, structure and chemistry are coupled for these species, and amphipod choice of a host alga might be due to structural rather than chemical factors.

While some field abundance patterns have been found to be determined solely by amphipod choice (Bell & Westoby 1986), other patterns may arise due to 'plant-mediated differences in susceptibility to predation' (Duffy & Hay 1994). Of course, an amphipod's choice of a host alga may take into consideration the value of the host as a predation refuge, food value, or both. In tropical systems, seasonal patterns of amphipod abundance have been found to be directly determined by differential fish predation on algal species (Duffy & Hay 1994). We know that Antarctic fishes consume amphipods and also some species of algae (Barrera-Oro & Casaux 1990, Iken et al. 1997), but the effects of fish predation on Antarctic community structure have never been studied. If amphipods on *Palmaria decipiens* are disproportionately vulnerable to predation as compared with amphipods on *Desmarestia menziesii*, the observed patterns of abundance in the field may be driven directly by predation and may be independent of any amphipod host-plant preferences.

Here, we investigate the ecology of habitat choice in Antarctic amphipods. We test whether thallus structure or algal chemistry is responsible for host-alga preference. We used 2 species of Antarctic algae, plastic algal analogues, and laboratory-created gel 'algae' to experimentally separate the roles that algal structure and chemistry play in determining habitat preference. Furthermore, we tested whether amphipods demonstrated anti-predator behaviors when exposed to chemosensory cues from the fish predator *Notothenia coriiceps*. Finally, we determined whether the structure or chemistry of host algae increased survival rates of amphipod inhabitants in the presence of a fish predator.

MATERIALS AND METHODS

Ecosystem description. All work was performed from Palmer Station, Anvers Island, off the western Antarctic Peninsula (64° 46' S, 64° 04' W) between March and June 2008. In the waters near Anvers Island, the shallow, near-shore benthos is dominated by macroalgae. Standing biomass of macroalgae in these communities compares to temperate kelp forests, and algae can cover well over 80% of the bottom (Amsler et al. 1995, Brouwer et al. 1995). The brown macroalgae *Desmarestia menziesii* and *D. anceps* are the dominant shallow-water overstory species, averaging 60 to 70% cover at depths of 5 m or less (Amsler et al. 1995).

In these algal forests, amphipods are both ubiquitous and conspicuous, occurring in extremely high densities (Huang et al. 2007). Amsler et al. (2008) estimated amphipod abundances of up to 308 000 and 32 000 ind. m⁻² of benthos in macroalgal forests of *Desmarestia menziesii* and *D. anceps*, respectively. These densities are higher, generally by 2 or 3 orders of magnitude, than amphipod densities found outside Antarctica (Nelson 1980, Amsler et al. 2008). Amphipods can be as important as herbivorous fishes in structuring benthic communities (Brawley & Adey 1981, Duffy & Hay 2000) and are likely to be responsible, via herbivory, for the near-total lack of filamentous macroalgal epiphytes in the Antarctic subtidal ecosystem (Amsler et al. 2009a).

Field collections and animal care. Algae and amphipods were collected by SCUBA divers using fine mesh bags to envelop algal thalli as in Huang et al. (2007). Amphipods utilized for experiments were collected from *Desmarestia anceps* and *Plocamium cartilagineum*, not the species being tested. The amphipod species *Prostebbingia gracilis* and *Gondogeneia antarctica* (size range: 5 to 10 mm) were selected for experimental use due to their abundance in the surrounding environment and their ease of collection and identification. Amphipods were housed in flow-through seawater tanks, within 4 l Nalgene® bottles (Thermo Fisher Scientific) with screened windows to allow water flow and were provided habitat in the form of *D. anceps* and small amounts of *Plocamium cartilagineum*, neither of which are eaten by amphipods (Amsler et al. 2005). These algae, however, may have contained food in the form of diatoms and/or crustacean parts. Amphipods were re-used for pair-wise choice tests, but were not re-used for choice tests after having been exposed to predator cues. Fish were collected either by baited hook and line or baited trap. They were housed in flow-through seawater tanks, fed daily on fresh limpet tissue, and starved for 48 h prior to predation trials to ensure motivation to feed. A total

of 10 fish were housed individually for predation trials and each was used for the 4 predation trial types (see 'Predation trials' below).

Habitat choice experiments. Habitat choice experiments were performed in a cold room at 0°C, in 8 plastic aquaria (19 l) filled with fresh, filtered seawater. To minimize any possible transmission of intra-specific chemical cues, aquaria were scrubbed and copiously rinsed with hot, fresh water between trials. Pair-wise choice tests were conducted for each possible combination of 4 choices: fresh thallus of *Desmarestia menziesii* and *Palmaria decipiens*, and plastic aquarium plants that resembled each species morphologically. For each amphipod species, 8 trials were conducted for each choice pair except in 2 circumstances. (1) If a statistically significant choice ($p < 0.001$) was found after only 4 trials, then further trials were not performed for the sake of expediency. This occurred in 5 of 26 experiments. (2) If we did not find a statistically significant preference for an alga after 8 trials, but thought there may be a trend, we ran 4 more trials for a total of 12. This occurred in 2 cases. The side of the bucket receiving each algal type was randomized. Fresh thalli, both within and between species, were matched by length and wet wt to within 5%. Plastic analogs vs. fresh thalli were matched by length of thallus. Fresh thalli were also tested against Phytigel™ blades (Sigma-Aldrich) containing freeze-dried, powdered algae (see 'Gel 'algae' preparation and trials' below). A total of 14 amphipods (either *Gondogeneia antarctica* or *Prostebbingia gracilis*) were released equidistant from each of the 2 choices over a bare area of tank floor. The number of amphipods on each thallus (a choice) and on the tank walls or swimming (no choice) was counted after 3 h. An initial pilot study, wherein an observer checked tanks each hour for 24 h, indicated that if a choice was going to be made it occurred within 3 h and that amphipods did not change thalli once they had chosen a host-alga. All 14 amphipods often chose the same thallus, indicating that there was no avoidance of conspecifics.

Gel 'algae' preparation and trials. Freshly collected *Desmarestia menziesii* and *Palmaria decipiens* were frozen, lyophilized, and ground to a fine powder (Spectromill-I; Chemplex Industries). Blade-shaped 'algae' were generated from 1.5 g of algae powder (either *D. menziesii* or *P. decipiens*), 0.23 g of Phytigel™, and 30 ml of filtered fresh water (Barnstead Nanopure II) per blade. This recipe resulted in an algal concentration of 25% that of fresh tissue. Phytigel™ is a high-strength agar substitute comprised of edible sugars. The water was heated, and Phytigel™ and the powdered alga were added sequentially to rapidly stirring hot water. The mixture was poured into a blade-shaped mold (18 × 8 cm at widest point)

over a piece of plastic window-screening, which provided structural support (42 grids mm⁻²) (Phifer Pet Screen). Once cooled to 4°C, the gel blades were removed from the molds and hung from pipe cleaners to facilitate their suspension in the amphipod tanks. In this manner, we kept the surface area and shape of the blades constant (resembling a natural *P. decipiens*), while varying the species of powdered alga that each blade contained.

Pair-wise choice trials were performed as described in 'Habitat choice experiments' above. Live algae were matched by thallus length with gel blades. Amphipods chose between each algal species and its gel counterpart, and between 2 gel blades, 1 made with each algal species. Control trials with 2 gel *Palmaria decipiens* blades were performed to see if there was any non-random assorting of amphipods when faced with 2 identical host-alga choices.

Predator cues choice trials. For *Gondogeneia antarctica*, each pair-wise experiment in which *Desmarestia menziesii* or its analogue was not chosen was repeated in the presence of predator cues. *Prostebbingia gracilis* was tested with *D. menziesii* and *Palmaria decipiens* in the presence of predator cues. Due to time constraints imposed by the Antarctic field season, *P. gracilis* was not tested further. In order to provide predator cues, one *Notothenia coriiceps* (mean standard length: 30 cm) was placed in each of the 8 aerated, 19 l seawater aquaria for 12 h. The fish and aerator were then removed, the algal choices added to the water, and amphipods were introduced as in 'Habitat choice experiments' above. Fish were maintained on a diet of limpet tissue to minimize any possibility of potentially confounding conspecific alarm substances (Wisenden et al. 1999).

Predation trials. Ten *Notothenia coriiceps* (mean standard length: 30 cm) were held in separate square plastic tanks (0.8 × 0.8 × 0.6 m) with filtered, flow-through seawater. The outflow pipe was covered by a fine-mesh, amphipod-proof screen, and during experimental trials the incoming seawater flow was halted. The tanks were in an aquarium room maintained at near-ambient seawater temperatures, and water temperature did not appreciably change during the short times the flow was stopped. A single piece of thallus (fresh *Desmarestia menziesii* or *Palmaria decipiens*, or 1 of the 2 plastic analogues) was placed in the center of the tank, shielded from the predator by a plastic cylinder that extended above the water level of the tank. Twenty *Prostebbingia gracilis* were then released over the alga within the tube. The amphipods were given 3 h to settle, and then the number of individuals on the alga was counted. The plastic tube was carefully removed, and the number of amphipods remaining on the alga or elsewhere in the tank was counted after

30 min. No amphipod was used for more than 1 trial. Each fish was used for each of the 4 trials. One fish never fed on amphipods and was excluded from the data analysis. This experiment was attempted with *Gondogeneia antarctica* as well, but the active swimming behavior of this species resulted in all animals being eaten within 2 min of their exposure to a predator.

Data analysis. Data were analyzed with SAS (version 9.2 for Microsoft Windows) (SAS Institute). We used a likelihood ratio test approach (Casella & Berger 2001) to calculate a distribution function for each trial, including both 'choice' and 'no-choice' amphipods (see the supplement at www.int-res.com/articles/suppl/m400p155_app.pdf for full details of the model). The product of this function over the trials yields the likelihood function, from which we calculated maximum likelihood estimates. We then tested the null hypothesis that the number of amphipods on each test alga was equal. The test statistic associated with this approach is y , which has a χ^2 distribution with 1 df (see Table S1 in the supplement for full statistical results). Predation trials were analyzed by blocked single-factor analysis of variance (ANOVA) with the number of amphipods surviving at 30 min as the response variable, algal type as the explanatory variable, and fish number as a blocking factor.

RESULTS

Amphipod host-alga preference in the absence of predator cues

Prostebbingia gracilis preferred *Desmarestia menziesii* over all other host-alga choices (Fig. 1a). In the absence of *D. menziesii*, *P. gracilis* chose *Palmaria decipiens* over its plastic analogue, preferred the *Desmarestia* analogue to the *Palmaria* analogue, and showed no preference between *Palmaria decipiens* and the *Desmarestia* analogue. In the gel algae experiments, *Prostebbingia gracilis* chose *D. menziesii* over gel *Desmarestia*, *Palmaria decipiens* over gel *Palmaria*, and gel *Palmaria* over gel *Desmarestia* (Fig. 2a). Amphipods showed no preference between the 2 gel *Palmaria*. In sum, *Prostebbingia gracilis* preferred *D. menziesii* over all other choices, structured thalli to simple forms, and real algae to analogues.

Gondogeneia antarctica preferred *Palmaria decipiens* to all other choices (Fig. 1b). In the absence of *P. decipiens*, *G. antarctica* chose *Desmarestia menziesii* over its plastic analogue, and showed no preference between *D. menziesii* and the *Palmaria* analogue, nor between the *Desmarestia* analogue and the *Palmaria* analogue. In the gel algae experiments, *G. antarctica*

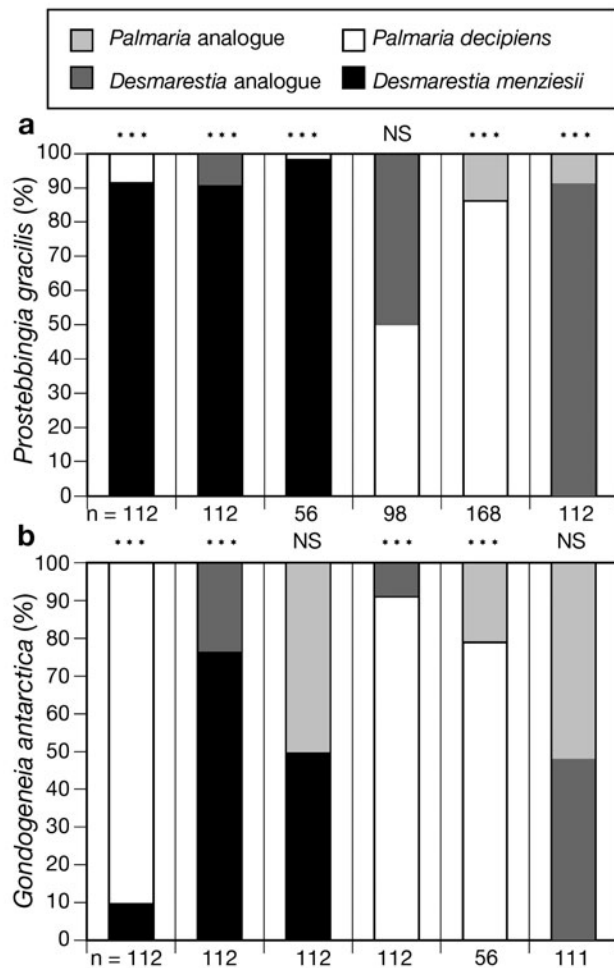


Fig. 1. *Prostebbingia gracilis* and *Gondogeneia antarctica*. Percentage of (a) *P. gracilis* and (b) *G. antarctica* choosing each alga. Each bar is a pair-wise choice trial between 2 of the 4 host structures: *Desmarestia menziesii*, *Palmaria decipiens*, and the plastic analogue of each. P values from χ^2 testing above each bar: *p < 0.05, **p < 0.01, ***p < 0.001. Sample sizes below each bar

tica chose *D. menziesii* over gel *Desmarestia*, and chose gel *Palmaria* over gel *Desmarestia* (Fig. 2b). They showed no preference between *P. decipiens* and gel *Palmaria* and did not show a preference between the 2 gel *Palmaria*. In sum, *G. antarctica* preferred *P. decipiens* to all other choices, and displayed no preference for structural complexity.

Amphipod host-alga preference in the presence of predator cues

In the presence of predator cues, *Gondogeneia antarctica* preferred *Desmarestia menziesii* over *Palmaria decipiens* and the *Palmaria* analogue (Fig. 3). *G. ant-*

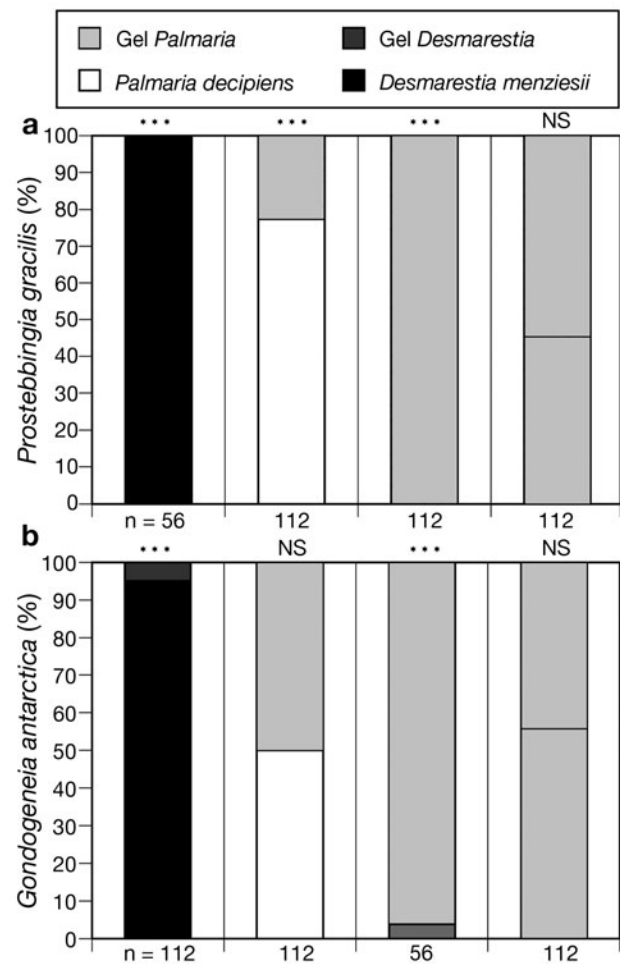


Fig. 2. *Prostebbingia gracilis* and *Gondogeneia antarctica*. Percentage of (a) *P. gracilis* and (b) *G. antarctica* choosing each alga. Each bar is a pair-wise choice trial between 2 of the 4 host structures: *Desmarestia menziesii*, *Palmaria decipiens*, and 2 artificial blade-shaped gel 'algae' containing freeze-dried, ground algae (see Gel 'algae' preparation and trials). For explanation of values and sample sizes, see Fig. 1

arctica also chose the *Desmarestia* analogue over the *Palmaria* analogue, and *Palmaria decipiens* over the *Desmarestia* analogue. In the presence of predator cues, *Prostebbingia gracilis* preferred *D. menziesii* over *Palmaria decipiens* (n = 96, p < 0.0001).

Predator avoidance

After 30 min in an aquarium with a fish predator, more *Prostebbingia gracilis* survived on *Desmarestia menziesii* and the *Desmarestia* analogue than on *Palmaria decipiens* and the *Palmaria* analogue (ANOVA: $F_{3,24} = 8.9$, p < 0.001; Tukey's post hoc, Fig. 4). Survival on real algae vs. their plastic analogues did not differ

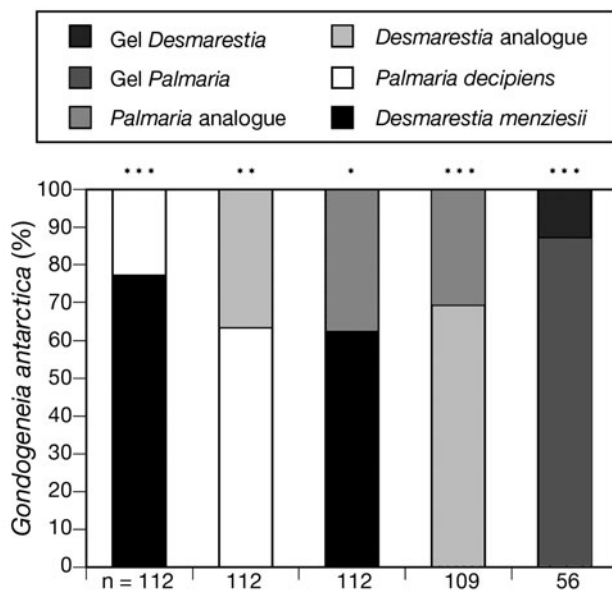


Fig. 3. *Gondogeneia antarctica*. Percentage of amphipods choosing each host algae in the presence of predator cues (see 'Predator cues choice trials'). Each bar is a pair-wise choice test. For explanation of values and sample sizes, see Fig. 1

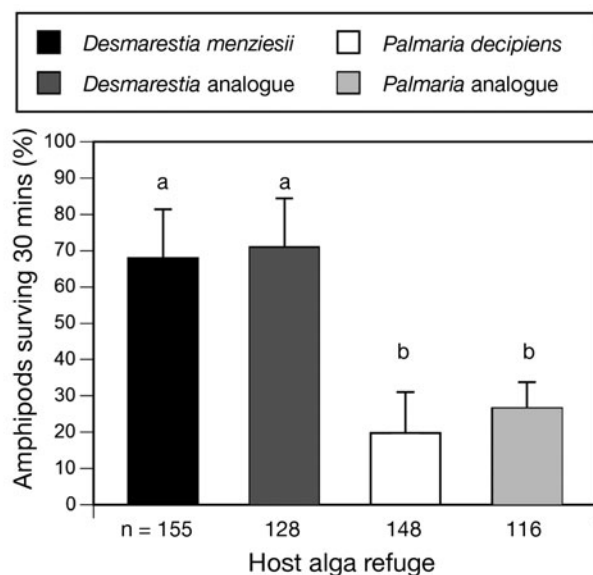


Fig. 4. *Prostebbingia gracilis*. Percentage of amphipods surviving 30 min with a predator, with 1 of 4 host algae as shelter. Host structures are *Desmarestia menziesii*, *Palmaria decipiens*, and plastic analogues of each. Letters indicate statistically significant groupings at $p < 0.05$. Sample sizes are indicated below each bar

(Tukey's post hoc). Individual fish also had a significant effect on survival time (ANOVA: $F_{8,24} = 2.3$, $p = 0.05$). Complex structure, rather than chemistry, seemed to result in higher survival of amphipod prey.

DISCUSSION

Amphipod host-alga preferences

The 2 amphipod species demonstrated different host-alga preferences. *Prostebbingia gracilis* preferred the chemically defended, complexly structured *Desmarestia menziesii* to any other choice. This preference matches with field abundance data, wherein *P. gracilis* abundance on *D. menziesii* was estimated at 41.4 ind. 100 g⁻¹ algae, and only 0.7 ind. 100 g⁻¹ of *Palmaria decipiens* (Huang et al. 2007). *Prostebbingia gracilis* does not eat *D. menziesii* (Huang et al. 2006), so it is likely that this preference is motivated by predator avoidance. *D. menziesii* thallus is rejected by *Notothenia coriiceps*, the dominant fish predator in the system, whereas *Palmaria decipiens* is readily eaten (Amsler et al. 2005). Thus, actual predation risk in the field may be lower for amphipods choosing to live on *D. menziesii*.

When the effect of algal chemistry was suspended by giving *Prostebbingia gracilis* a choice between 2 plastic aquarium plants, the amphipods preferred structural complexity. Complexity of macrophyte growth form is known to reduce fish foraging success (Dionne & Folt 1991, Warfe & Barmuta 2004). Hence, a choice of the more complexly structured aquarium plant may be effective anti-predator behavior. Amphipods are more susceptible to pinfish *Lagodon rhomboides* predation when living on highly branched seaweeds as compared to seaweeds with simpler, 'sheet-like' morphology (Holmlund et al. 1990). The sheet-like algae used in that study, however, differed markedly from *Palmaria decipiens* in having folding and overlapping blades, and the finely branched algae were different from *Desmarestia menziesii* because they were a highly preferred food of the pinfish. Holmlund et al. (1990) suggested that fish may be able to visualize amphipods more easily against branching forms than against the overlapping, sheet-like forms and concluded that both morphology and food preference played a role in amphipod susceptibility to predation. In our experiments, *Notothenia coriiceps* primarily reacted to spontaneous movements of prey or opportunistically mouthed the plants, which often led to prey movements that resulted in predation. Thus, visualization of stationary prey against the host algae may not be a primary detection mode for *N. coriiceps*. Indeed, in Antarctica, where visual signals are often quite limited due to darkness and turbidity, fine-scale visualization of amphipods such as that displayed by tropical pinfish is unlikely to occur.

Gondogeneia antarctica demonstrated a clear preference for *Palmaria decipiens* over any other choice of host algae. Feeding assays indicate that *P. decipiens* is a

highly preferred food source for *G. antarctica* (Huang et al. 2006, Amsler et al. 2009a) but not for *Prostebbingia gracilis* (Amsler et al. 2009b, Aumack et al. 2010), which may explain this difference in host-alga preference. Experimental *P. decipiens* often showed signs of grazing by *G. antarctica* at the end of a 3 h choice trial (J. Zamzow pers. obs.). Field abundance data for *G. antarctica* are 10.8 ind. 100 g⁻¹ of *Desmarestia menziesii* and 5.9 ind. 100 g⁻¹ of *Palmaria decipiens* (Huang et al. 2006). This is a much higher relative preference for *P. decipiens* than observed for *Prostebbingia gracilis*, which does not eat *P. decipiens* (Huang et al. 2006, Huang et al. 2007). This pattern is consistent with our data for algal choice in the face of predation cues. Hence, in the field, amphipod abundances may be due to a combination of feeding preferences and predation pressure causing emigration from *P. decipiens* patches to *D. menziesii* patches. We cannot exclude, however, the possibility that field abundances may be due to higher predation success in *P. decipiens* patches. Field experiments with fish exclusion cages would help to elucidate the reasons for actual population densities.

In contrast to *Prostebbingia gracilis*, *Gondogeneia antarctica* did not show any preference for complex habitat structure when offered 2 plastic aquarium plants in the absence of predator cues. Similar results have been found with Hawaiian amphipods, which showed no preference for complex habitat structure even though it reduced actual predation risk (Russo 1990). Both species did, however, demonstrate a preference for *Desmarestia menziesii* over its plastic analogue. Gut contents of both amphipod species include large numbers of diatoms (C. Aumack, unpubl. data), and this preference for a living alga over a plastic one may be due to diatoms or other food items occurring in conjunction with field-collected algae. The plastic aquarium plants were dried between experiments, and were thus very unlikely to contain any food sources.

Predator cue effects

Invertebrates in general, and amphipods in particular, have been shown to be extremely sensitive to predator cues (Lima & Dill 1990, Kats & Dill 1998, Åbjörnsson et al. 2000). When predators rely on a sit-and-wait strategy, as do *Notothenia coriiceps*, and in low visibility conditions, which are common in Antarctica, detection of chemical signals can be essential for survival of their prey (Chivers & Smith 1998, Åbjörnsson et al. 2000). Whereas in filtered seawater *Gondogeneia antarctica* preferred *Palmaria decipiens* over *Desmarestia menziesii*, in the presence of predator cues they instead chose the chemically defended, morphologically complex *D. menziesii*. Moreover, whereas in

the absence of predator cues *G. antarctica* showed no preference between plastic aquarium plants of differing morphological complexity, in the presence of predator cues *G. antarctica* chose the more complex thallus. These preference shifts can be interpreted as anti-predator behavior, or non-consumptive effects. In the field, *P. decipiens* patches are generally surrounded by large thickets of the more common *D. menziesii* (authors' pers. obs.). *G. antarctica* is an active swimmer, and may be able to escape into nearby *D. menziesii* patches when a predator is sensed. *D. menziesii* grows very densely and thus not only presents a physical obstruction to prey capture and predator movement, but also must inhibit the ability of *N. coriiceps* to visually locate amphipod prey. *Prostebbingia gracilis*, which, unlike *G. antarctica*, does not eat *Palmaria decipiens*, preferred *D. menziesii* both in the presence and absence of predator cues. *P. gracilis* also differs from *G. antarctica* in that it does not swim often, and thus the choice of a suitable host alga may be less labile for *P. gracilis* than for *G. antarctica*. As *P. gracilis* is unlikely to change hosts or escape when a predator is sensed, the adaptive choice for this species may be to remain on the chemically defended, structurally complex *D. menziesii*. This strategy would fit the general pattern of more sedentary amphipods becoming specialized on chemically defended host algae for protection from predation (Duffy & Hay 1994). Non-consumptive effects most often take the form of emigration, reduced activity, or predator-predator facilitation (Preisser et al. 2005). Interestingly, all previous studies with amphipods have shown predator-induced behavioral changes to consist of reductions in activity (reviewed in Kats & Dill 1998) or no response to predator cues (Duffy & Hay 1994). To our knowledge, this is the first study to demonstrate amphipod host switching in response to predator cues. If such host switching is performed by amphipods in the field, it suggests a novel mechanism for avoiding predation.

In the experiments with Phytigel™-based 'algae', we found that both amphipod species, when given identical choices containing *Palmaria decipiens* powder, assorted equally between the 2 gel algae. This lack of preference makes us confident that other tests performed in this study were not affected by any aggregation behavior or 'gregariousness effect' on the part of the amphipods. We found that neither species of amphipod ever preferred the gel *Desmarestia*, even though *P. gracilis* always preferred living *Desmarestia menziesii* to any other choice. Extracts of *D. menziesii* strongly deter *Gondogeneia antarctica* feeding (Amsler et al. 2005), and we speculate that the freeze-drying and/or grinding process probably allows some of these deterrent compounds to leach from the gel *Desmarestia* and thereby render it distasteful to the amphipods.

Predator avoidance

Both chemical defenses and complex morphology of algae have been shown to reduce predator effectiveness against amphipods. Both generalist and specialist grazers are preyed on less often when associated with a chemically defended alga (Duffy & Hay 1991, 1994). Chemical deterrents may reduce the amount of time that a fish spends foraging in an algal patch and thus encountering potential amphipod prey (Duffy & Hay 1994). Since *Notothenia coriiceps* does not eat *Desmarestia menziesii*, the chance of incidental ingestion of an amphipod is low. High structural complexity of an alga may make it harder for fish to detect potential prey, provide a physical obstruction to the predator's body and thus its ability to pursue prey, decrease the efficacy of capture of prey, or increase the likelihood of prey escape. Several studies have demonstrated decreases in predation risk for small invertebrates with increasing habitat complexity (e.g. Dionne & Folt 1991, Warfe & Barmuta 2004). Thus, we expected that survivorship in our predation trials would be highest on the alga with chemical defenses and complex structure, *D. menziesii*, followed by the aquarium plant with complex structure, and that the least effective refuges would be *Palmaria decipiens* and its plastic analogue. We found no difference in survivorship between the 2 algae with complex morphologies, both of which offered superior refuge to the 2 simply structured algae. It seems that the chemical defenses of *D. menziesii* do not increase survivorship of *Prostebbingia gracilis* over that of a complexly structured plastic aquarium plant. While it would have been ideal to have successfully repeated these experiments with *Gondogeneia antarctica*, the active swimming behavior of this species resulted in near-instant mortality for all individuals tested. In the field, the density and abundance of *D. menziesii* are much higher, and an amphipod could swim for many meters through contiguous, dense patches of *D. menziesii* that would hinder fish movement and the visual detection of prey. Thus, active swimming behavior might aid in escape from predation. In a relatively small, confined space with a rather small algal refuge, however, active swimming by the amphipods led to rapid detection and predation by *N. coriiceps*.

Because *Palmaria decipiens* is eaten by *Notothenia coriiceps*, increased predation risk for *Prostebbingia gracilis* on this alga may be due to enhanced detection of amphipods by fish predators, or due to accidental ingestion of amphipods by fishes while eating *P. decipiens*. *P. decipiens* was sometimes partially consumed by fish during the predation trials, thus accidental ingestion of amphipods may have occurred. However, since survivorship on the inedible plastic *Palmaria* analogue could not be statistically distinguished from

the real alga, it seems that enhanced detection is a more likely explanation for increased predation of amphipods on these algae. It is clear from our experiments that structural complexity aids *P. gracilis* in avoiding predation, even in our laboratory-based experiments, where predation risk was very high due to the close proximity of the predator, small thallus size, and lack of alternate refuges. This result concurs with most of the prior research on macrophyte growth forms with respect to predation (Hacker & Steneck 1990, Dionne & Folt 1991, Warfe & Barmuta 2004).

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