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Feeding rates of common Antarctic gammarid amphipods on ecologically important sympatric macroalgae

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Abstract

Single species feeding trials employing both fresh algal tissues and alginate food pellets containing dried finely ground algal tissues were conducted to examine the relative palatability of sympatric Antarctic macroalgae (three brown and five red macroalgal species) to three common herbivorous gammarid amphipods (*Prostebbingia gracilis* Chevreux, *Gondogeneia antarctica* (Chevreux) Thurston, and *Metaleptamphopus pectinatus* Chevreux). In fresh algal tissue bioassays, both the amphipods *P. gracilis* and *G. antarctica* consumed significantly greater amounts of the red alga *Palmaria decipiens* over all other seven species of macroalgae. The amphipod *M. pectinatus* failed to consume measurable quantities of fresh thalli of any macroalgae and therefore is likely to feed on other resources. In food pellet bioassays, the consumption rates of amphipods fed with eight different species of macroalgae were compared with consumption rates on a highly palatable control green alga. Alginate pellets containing finely ground tissues of *P. decipiens* were consistently the most palatable of any of the macroalgae to *P. gracilis* and *G. antarctica*, while pellets containing the brown algae *Desmarestia menziesii*, *D. anceps* and the red alga *Plocamium cartilagineum* were not consumed by any of the three amphipod species. Regression analysis indicated that feeding rates of the amphipods *P. gracilis* and *G. antarctica* on alginate food pellets were not significantly correlated with known species-specific parameters of macroalgal nutritional quality (%N, %C, C:N ratio, soluble protein, soluble carbohydrate, and lipid). Therefore, differences in amphipod macroalgal palatability are most likely related to other factors including physical and/or chemical deterrents.

Keywords: Amphipoda; Antarctica; *Gondogeneia antarctica*; Herbivory; Macroalgae; *Prostebbingia gracilis*

1. Introduction

Marine mesograzers, which include the conspicuous gastropods, amphipods, and isopods, in addition to a number of lesser taxa, are ubiquitous across a wide suite of marine environments. While some are free living within the water column or are found in association with inert materials such as rock or sand substrata (albeit coated with microbial biofilms and encrusting microorganisms), most are closely associated with living substrates such as macroalgae and seagrasses (Brearley and Walker, 1995; Duffy et al., 2001; Hay and Fenical, 1988; Hay, 1997; Hay et al., 1998; Lippert et al., 2001). These diverse living substrates may provide mesograzers with a variety of resources including

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food, but also potential refuge from predation and/or environmental stress (Duffy and Hay, 1991). Not surprisingly, perhaps because of these resource linkages, a variety of the life history stages of mesograzers appear to be adapted to remain in close association with their living "hosts" (Hay et al., 1990; Sotka et al., 1999).

Macroalgae, while less common around much of Antarctica, are extremely abundant in terms of biomass along the western Antarctic Peninsula (Amsler et al., 1995; Brouwer et al., 1995; Neushul, 1965; Quartino et al., 2001). Commonly associated with a diverse assemblage of epibenthic organisms that encompass a wide range of trophic habits (Iken et al., 1998; Jaźdźewski et al., 1991a,b; Richardson, 1977), peninsular macroalgae are known to provide a significant food resource for grazing sympatric gastropods, annelids, crustaceans, and fish (Iken et al., 1997, 1998, 1999; Iken, 1999). However, different algal species are apparently not consumed in equal frequency to their relative abundance as some species are frequently found in the gut contents of common herbivores whereas others are rarely ingested (Iken et al., 1997; Iken, 1999). Such observations have led to studies focusing on understanding whether chemical defenses mediate these patterns of grazing by sympatric Antarctic herbivorous amphipods (Amsler et al., 1998, 2005; Ankisetty et al., 2004; Fairhead et al., 2005). Despite these recent studies, much remains to be learned about the factors that mediate trophic relationships between Antarctic mesograzers and macroalgae.

Amphipods can be remarkably abundant in macrobenthic communities along the Antarctic Peninsula, in some locations constituting up to 85% of the total macrobenthos when considered in terms of their numerical abundance (Jaźdźewski et al., 1991a,b, 2001). Three of the particularly common neritic amphipods that occur in the coastal waters along the western Antarctic Peninsula include *Prostebbingia gracilis* Chevreux, *Gondogeneia antarctica* (Chevreux) Thurston and *Metaleptamphopus pectinatus* Chevreux (Jaźdźewski et al., 1991a,b, 2001; Richardson, 1977). Occurring in high abundance, *Prostebbingia gracilis* is a widespread circumantarctic amphipod associated with the macroalgal habitats and mainly with *Plocamium cartilagineum* meadows (Y. Huang, personal observations). Its vertical distribution ranges from depths of 4 to 250 m and, in shallow marine habitats surrounding King George Island, its abundance can exceed 25% of the total amphipod community (Chevreux, 1913; Jaźdźewski et al., 1991a,b). *Gondogeneia antarctica* occurs not only along the western Antarctic Peninsula, but is also found on the sub-antarctic islands and in the Magellanic region (Richardson, 1977). Its vertical distribution ranges from the shallow subtidal to depths of 40 m (Thurston, 1972) and it occurs in association with a variety of benthic habitats including muds, sands, gravels, and cobbles, with many of these substrates supporting abundant macroalgae. In the benthic peninsular habitats where *G. antarctica* has been examined, this species may comprise as much as 15–20% of the total amphipod community (Jaźdźewski et al., 1991a,b; 2001; Richardson, 1977). *Metaleptamphopus pectinatus* has been found in shallow depths of the western antarctic sub-region as well as in sub-antarctic waters off South Georgia Island. This species primarily inhabits the mats of epiphytes which occur on the holdfasts of various genera of macroalgae including *Desmarestia* and *Himantothallus* (Thurston, 1972). Richardson (1977) surveyed amphipods associated with the thalli of *Desmarestia anceps* and found that *M. pectinatus* constituted 6–23% of total amphipod abundance over a 1-year period.

The objectives of this investigation were to determine whether differential palatability for sympatric macroalgae occurs in three common antarctic amphipod mesograzers and, if so, whether these patterns are correlated with known parameters of macroalgal nutritional quality.

2. Materials and methods

All organisms were collected within 3.5 km of Palmer Station on Anvers Island, Antarctica (64° 46.5′S, 64°03.3′W; see Amsler et al., 1995 for map). All collections and laboratory assays were conducted between late February and late May 2003.

Three common Antarctic herbivorous amphipod species (see above) were selected for the feeding bioassays. *Gondogeneia antarctica* were collected using hand nets from macroalgal beds in tide pools and the shallow subtidal at Laggard Island (64°48.4′S, 64°00.5′W). These collections were supplemented with animals trapped by the Palmer Station seawater system filters (these animals were quarantined and microscopically examined before use to ensure that they were uninjured). *P. gracilis* and *M. pectinatus* were collected subtidally by divers from *Plocamium cartilagineum* (Linnaeus) P F Dixon and *Desmarestia menziesii* J Agardh, respectively, off Bonaparte Point (64°46.7′S, 64°04.0′W) at depths ranging from 5 to 10 m. Amphipods were maintained in 2-L plastic bottles equipped with openings covered with fine mesh screening and suspended in tanks with flowing ambient seawater (temperature ranges from −1 to 1 °C).

2.1. Fresh thallus bioassays

Eight species of ecologically dominant macroalgae including three representatives of the Phaeophyceae (*Desmarestia menziesii*, *Desmarestia anceps* Montagne, and *Desmarestia antarctica* Moe and Silva) and five representatives of the Rhodophyceae (*Gigartina skottsbergii* Setchell and Gardner, *Iridea cordata* (Turner) Bory, *Myriogramme mangini* (Gain) Skottsberg, *Palmaria decipiens* (Reinsch) Ricker, and *Plocamium cartilagineum*), were collected by divers at depths ranging from 5 to 10 m off Bonaparte Point. Twelve individuals of each macroalgal species were returned to the laboratory and maintained in tanks equipped with running ambient seawater for subsequent feeding bioassays. To examine feeding preferences of herbivorous amphipods for different species of macroalgae, single species feeding trials (non-choice feeding assays) were conducted (Cruz-Rivera and Hay, 2000b). For each amphipod species tested, sixteen 150-mL plastic bottles were filled to the mid-point with seawater, and then into each of eight of these bottles were haphazardly placed fifteen amphipods. Within a given amphipod species, sizes of individuals used in the experiments were similar and based on a mean adult body length (measured from the tip of the rostrum to the base of the telson) determined from a representative field sample of individuals (*P. gracilis*: 6.9 ± 1.0 mm, $n=27$; *G. antarctica*: 8.9 ± 1.2 mm, $n=65$; *M. pectinatus*: 5.0 ± 0.8 mm, $n=38$; mean ± SD). Fresh and completely un-grazed thalli (as evidenced by close visual examination) of each macroalgal species were cut into cross-sectional pieces with similar mass (mass ranged from 2 to 9 mg wet weight for *P. gracilis*; 15 to 38 mg wet weight for *G. antarctica*), blotted to remove excess seawater water, weighed and then individually placed into paired bottles, one with amphipods, and the other without amphipods (control treatment). Using this approach, we were able to calculate the precise consumption rate while negating any potential autogenic effect. Four replicate paired bottles were prepared for each experimental treatment. These were placed in a cold room at Palmer Station and room temperature maintained at 1.5 ± 0.5 °C under ambient photoperiod for a period of 33–45 h. After this time period the pieces of fresh thallus were blotted dry and re-weighed. Amphipod algal consumption rates were calculated as the mean milligram of algae consumed per day per amphipod. The thallus experiments, each consisting of four replicate paired bottles, were repeated three times to yield a total of 12 replicates (including controls) for each macroalgal species. This design in which the replicates were spread over three sets of experiments was used because it was not logistically possible to run all replicates simultaneously and unlike the pellet bioassays (see below) there was no appropriate internal control. Consequently, experimental day was included as a random factor in the statistical analyses.

2.2. Alginate pellet bioassays

In order to eliminate algal morphology (i.e., shape and toughness) as a potential factor influencing palatability to amphipods, alginate pellets containing algal tissues were prepared for each of the eight macroalgal species. Subtidal macroalgae were collected from Bonaparte Point, Hermit Island (64°47.9′S, 64° 00.4′W), and Eichorst Island (64°47.1′S, 64°03.2′W). One individual of each macroalga was freeze dried and then ground into a fine homogenous powder using a mortar and pestle and a commercial coffee grinder. In addition, the filamentous intertidal green macroalga *Cladophora repens* was used as a control feeding stimulant because it is a palatable alga known to be readily consumed by all three species of amphipods (Amsler et al., 2005). This alga was collected by hand from the intertidal and shallow subtidal at Laggard Island. The algal filaments were freeze dried and then ground into a fine powder using a mortar and pestle. Alginate pellets were prepared following the protocols given in Amsler et al. (2005) and Fairhead et al. (2005). Finely ground algal tissues were mixed in 2% alginate solution to a final concentration of 5% algal tissue and then poured into a Petri dish. The mixture was then solidified by slowly pouring cold 1 M $CaCl_2$ solution over the alginate solution. Pellets (10 mm diameter × 2 mm thickness) were punched from the hardened alginate using a cork borer. Amphipod feeding bioassays followed the same protocols as those described above for fresh thalli but with only 10 amphipods (*G. antarctica* and *P. gracilis*) per bottle and 10 sets of replicates. Twenty *M. pectinatus* were placed into each bottle because of their relative small body size. Two of the eight different algal diet treatments and a single control treatment comprised of pellets containing *C. repens* were combined in each experimental treatment. Feeding preference of amphipods was determined by the relative consumption of an experimental algal food as a function of the consumption of the control alginate pellets containing *C. repens* (weight of the consumed treatments divided by weight of the consumed control within each experimental treatment).

From previous feeding experiments using *Gondogeneia antarctica* (C.D. Amsler personal observation, Amsler et al., 2005), patterns of macroalgal consumption varied across different feeding trial days. Hence, to account for such possible temporal differences in consumption rates, we presented amphipods alginate control pellets containing finely ground tissues of the intertidal green macroalga *Cladophora repens* on each day of the feeding trials. As indicated above, *C. repens* is known to be a highly palatable algal food to amphipods both in the field and laboratory (Amsler et al., 2005). By measuring the consumption of pellets containing this control alga as a function of each algal feeding treatment we controlled for both day to day variations in consumption rates and the fact that different algal species were presented to amphipods on different days.

2.3. Statistical analyses

To compare the consumption rates of amphipods for fresh algal thalli among the different dietary treatments and different dates of trials, consumption rate data were analyzed by two-way ANOVA using SAS software (SAS Institute, Cary, North Carolina) followed by Tukey's Honestly Significant Difference (HSD) tests with experimental day as a random factor. Because the alginate pellets in all replicates came from the same preparation, a parametric ANOVA was not appropriate. Therefore, a non-parametric Friedman's test (multiple related samples ANOVA) was performed on these data using SPSS (SPSS Inc., Chicago, Illinois) software followed by multiple *t*-tests using the Bonferroni adjustment for multiple comparisons (General Linear Model, SAS) to compare the percentage of algal pellet consumption among the different dietary treatments. To examine the statistical correlation between amphipod consumption rates and parameters of algal nutritional quality, linear regression analysis was perform using SAS software.

We employed regression analyses to examine whether consumption rates on macroalgal alginate food pellets by the amphipod *Prostebbingia gracilis* and *Gondogeneia antarctica* were significantly correlated with various known parameters of macroalgal nutritional quality. These parameters included percent nitrogen, percent carbon, and the ratio of carbon to nitrogen, as well as levels of soluble protein, soluble carbohydrate, and lipid, all measured in macroalgae collected during the late growing season (Peters et al., 2005). Regression analysis did not include those macroalgal species that either had negative consumption values (*Desmarestia menziesii* and *D. anceps*) or lacked complete nutritional information (*Plocamium cartilagineum*; Peters et al., 2005). Thus, for both amphipods, the macroalgae *D. menziesii* and *P. cartilagineum* were not included in the linear regression analysis. Moreover, in the case of the amphipod *Prostebbingia gracilis* the alga *D. anceps* was not included.

3. Results

3.1. Fresh thallus bioassays

Single species feeding trials indicated that both amphipods, *Prostebbingia gracilis* and *Gondogeneia antarctica*, showed much higher consumption rates of fresh thalli when offered *Palmaria decipiens* over all other seven species of macroalgae (Fig. 1A, B). At the conclusion of each feeding experiment, grazing marks on the edges of the thalli of *P. decipiens* were clearly evident. The third amphipod species tested, *Metaleptamphopus pectinatus*, failed to consume measurable quantities of any of the fresh thalli. *P. gracilis* and *G. antarctica* both consumed significantly ($P<0.0001$) more *P. decipiens* than any of the other seven species of macroalgae presented in feeding trials, respectively (Fig. 1A, B). When comparing consumption rates among different feeding trial days, both amphipod species exhibited significantly different consumption rates of algae on different days (Table 1; $p=0.01$, *P. gracilis*; $p=0.01$, *G. antarctica*). However, the interaction between algal treatments and the different days of the feeding trials had no effect on consumption rates of *G. antarctica* (Table 1; $p=0.78$). This indicates that while the consumption rates of *G. antarctica* fed with the different macroalgal treatments varied from day to day, the difference in consumption rate is mainly influenced by algal palatability. In contrast, the interaction between algal treatments and the different days of the feeding trials significantly influenced consumption rates in the amphipod *P. gracilis* (Table 1; $p<0.001$). Nonetheless, the palatability of *P. decipiens* is still significantly higher than all the other algal species. For both amphipod species, two-way analysis of variance demonstrated that *P. decipiens* was consumed significantly more than all other macroalgae in each feeding trial (Table 1). Thus, we chose to present feeding rate data combined over the 3 consecutive days of feeding trials (see Fig. 1).

Our results based on the fresh thallus consumption of macroalgae indicated that *Palmaria decipiens* is highly palatable to both the amphipods *P. gracilis* and *G. antarctica*. However, consumption rates of amphipods on all other algal thalli did not exhibit significant

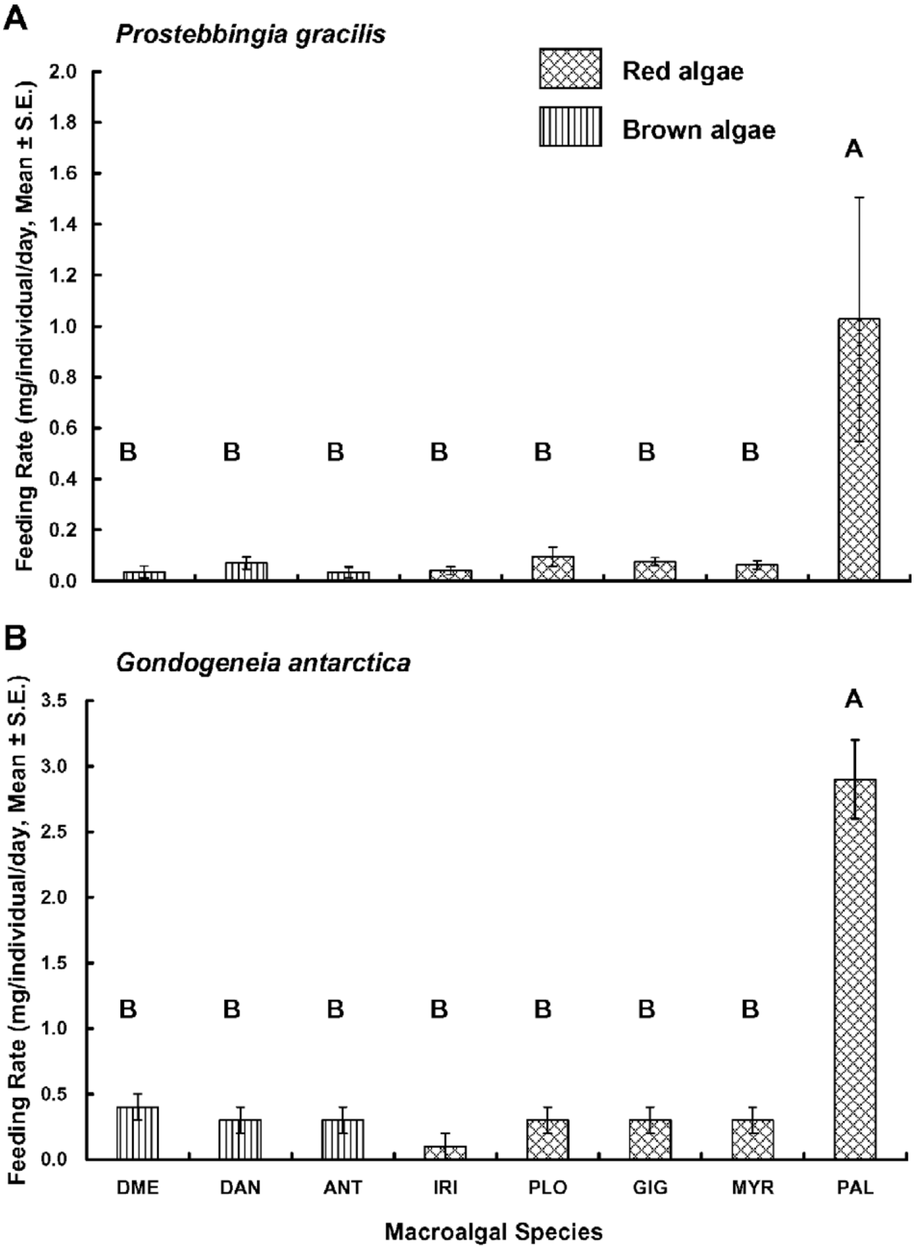

Fig. 1. Results of single species feeding trials offering pieces of fresh thalli of eight Antarctic Peninsular macroalgae to the amphipods *Prostebbingia gracilis* (A) and *Gondogeneia antarctica* (B). Bars represent means ± standard error of mean ($n=12$). Similar letters above bars indicate no statistical differences ($P<0.05$) among the means (two-way ANOVA followed by Tukey's HSD). DME—*Desmarestia menziesii*; DAN—*Desmarestia anceps*; ANT—*Desmarestia antarctica*; IRI—*Iridaea cordata*; PLO—*Plocamium cartilagineum*; GIG—*Gigartina skottsbergii*; MYR—*Myriogramme mangini*; PAL—*Palmaria decipiens*. Data shown are combined across the 3 consecutive days of feeding trials as two-way analysis of variance indicated that statistical groupings of feeding rates did not vary between days for either amphipod species.

variation. In addition, the amounts of these fresh thalli consumed did not differ from zero ($p>0.05$ for *P. gracilis*; $p=0.05$ for *G. antarctica*). Therefore, for these reasons, we were unable to make any inferences about the relative palatability of these other seven macroalgal species.

3.2. Alginate pellet bioassays

The results of alginate food pellet bioassays containing ground thalli of the eight target macroalgae indicated that the amphipod *Prostebbingia gracilis* significantly ($P<0.05$) prefers the macroalgae *Pal-*

Table 1
Two-way analysis of variance comparing consumption rates of amphipods offered eight species of fresh macroalgal thalli

Source of variation		*Prostebbingia gracilis*			*Gondogeneia antarctica*		
	df	SS	*F* ratio	*P*	SS	*F* ratio	*P*
Algal treatments	7	9.88	8.19	<0.0001	75.05	48.97	<0.0001
Trial days	2	1.92	5.59	0.0056	1.97	4.49	0.0145
Algal treatments × trial days	14	16.5	6.84	<0.0001	2.10	0.69	0.7798

maria decipiens, *Myriogramme mangini* and *Gigartina skottsbergii* over the other macroalgae (Fig. 2A, B). The four least preferred macroalgae were consumed at very low levels or not at all. Indeed the brown macroalgae *Desmarestia anceps* and *D. menziesii* had negative consumption values (Fig. 2A). Such negative consumption values resulted when experimental pellets containing a given macroalgae were not consumed by amphipods yet absorbed greater amounts of water over the course of the feeding experiment than did autogenic control pellets (no amphipods present). In terms of net rates of consumption, *P. gracilis* consumed 2- to 10-fold greater amounts of the alginate pellets containing *P. decipiens* than any of the other alginate food pellets (Fig. 2A).

The general feeding patterns of *Gondogeneia antarctica* proffered alginate food pellets are similar but not identical to that of *P. gracilis* (Fig. 3A, B). Alginate food pellets containing *P. decipiens* were significantly ($P<0.05$) preferred over all other macroalgae, with *M. mangini* the next most significantly ($P<0.05$) preferred species. The remainders of the macroalgal species were consumed in very low quantities or not at all (Fig. 3A). In the case of *D. menziesii*, the mean consumption value was negative.

Similar to feeding experiments employing fresh thalli, we detected no consumption of alginate food pellets by *Metaleptamphopus pectinatus*. In many cases these amphipods broke down food pellets into small pieces but this was clearly due to their locomotory activities and not from grazing.

3.3. Correlation analyses of macroalgal nutritional parameters

The results of the regression analyses indicated that for both *P. gracilis* and *G. antarctica* consumption rates were not significantly related to any of the macroalgal nutritional quality parameters (Table 2).

4. Discussion

The results of the fresh thalli bioassays indicate that the amphipods *Prostebbingia gracilis* and *G. antarctica* exhibited their highest consumption rates when grazing on the thalli of the red alga *Palmaria decipiens*. Although the use of single species feeding trials precludes this being directly interpreted as a food preference (Peterson and Renaud, 1989), *P. decipiens* is clearly the most palatable algal food among the eight macroalgal species examined. Differences in these macroalgal consumption rates may be linked to either physical and/or biological factors. In terms of physical factors, algal morphology has been shown to influence the palatability of algae to amphipod grazers feeding on macroalgae occurring on coral reefs (Hay, 1997). The eight macroalgal species presented to Antarctic amphipods represent three distinct morphologies: (1) a high degree of branching and terete branches (*Desmarestia anceps*, *D. menzesii*, and *Plocamium cartilagineum*), (2) moderately high degree of branching and ligulate branches (*D. antarctica*), and (3) no or low level of branching, comprised of one to a few flattened blades (all remaining species). Moreover, some of these macroalgae possess thalli with varying degrees of toughness (Amsler et al., 2005). In the present study, each alga was cut into pieces of similar mass in order to control for interspecific differences in the morphology of thallus edges. The pieces of algae used in the experiments were necessarily of sufficient size to preclude “edge effects.” Given the low rates of consumption by amphipods for all but one of the macroalgal species when presented as relatively large pieces, detection of significant differences in palatability among these species may have been obscured. This outcome precluded any meaningful evaluation of the possible statistical correlation between consumption rates of fresh algae and measures of tissue toughness conducted through penetrometry analyses by Amsler et al. (2005). Nonetheless, it is noteworthy that the most palatable alga by far, *P. decipiens*, is among the lower third of 30 species of Antarctic macroalgae in terms of toughness.

One of the three amphipod species we examined, *Metaleptamphopus pectinatus*, did not consume either fresh thalli or artificial foods of any macroalgae as evidenced by the lack of measurable changes in wet algal mass over the course of the feeding experiments. Moreover, in contrast to the other two amphipods, no

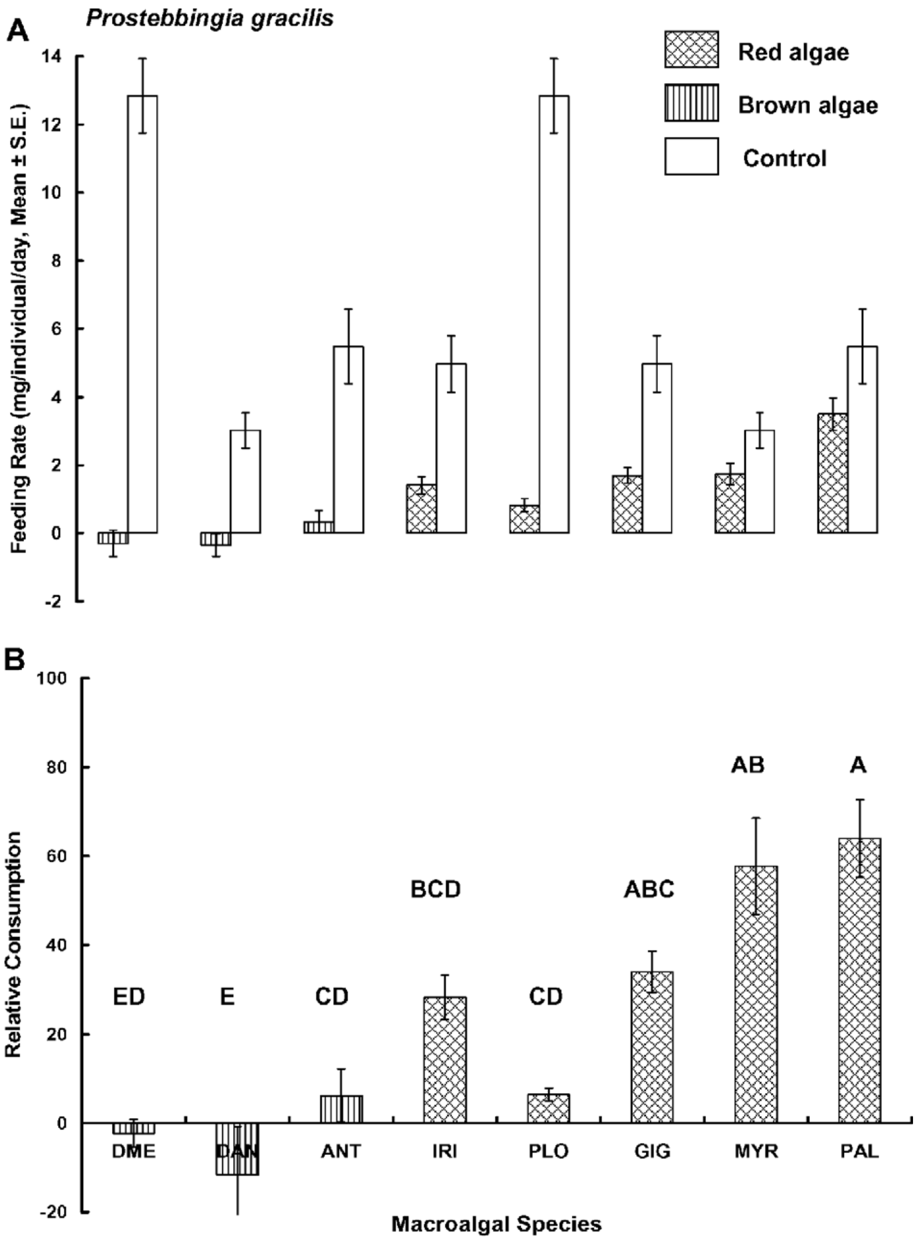

Fig. 2. Results of single species feeding trials offering alginate pellets containing freeze-dried and finely ground thallus tissues of eight macroalgae to the amphipod *Prostebbingia gracilis*. (A) Net consumption rate of *P. gracilis* presented with alginate food pellets containing macroalgal species. Controls consisted of alginate pellets containing the palatable green alga *Cladophora repens*. (B) Relative consumption derived from net consumption rates shown in panel (A). Similar letters above bars indicate no statistical difference ($P < 0.05$) among the means (Friedman's test, multiple related samples ANOVA) followed by multiple *t*-tests using the Bonferroni adjustment for multiple comparisons. Bars represent means ± standard error of mean ($n = 10$). See legend in Fig. 1 for the abbreviations of macroalgae.

discernable algal grazing scars were evident following the feeding trials. This likely indicates that *M. pectinatus* does not exploit macroalgae directly as a food source but rather may graze on epiphytic microalgae such as diatoms that colonize the surfaces of macroalgae. Our results corroborate various reports (Chevreux, 1913; Schellenberg, 1931; Thurston, 1972) that this species inhabits epiphytic mats growing on the holdfasts of brown (*Desmarestia sp.*) and red (Gigartinacea) macroalgae at sites along the Antarctic Peninsula and at South Georgia. Other studies have noted Antarctic amphipods that feed on epiphytes including diatoms, but these studies have focused on diatoms growing on sea ice (Richardson, 1977; Richardson

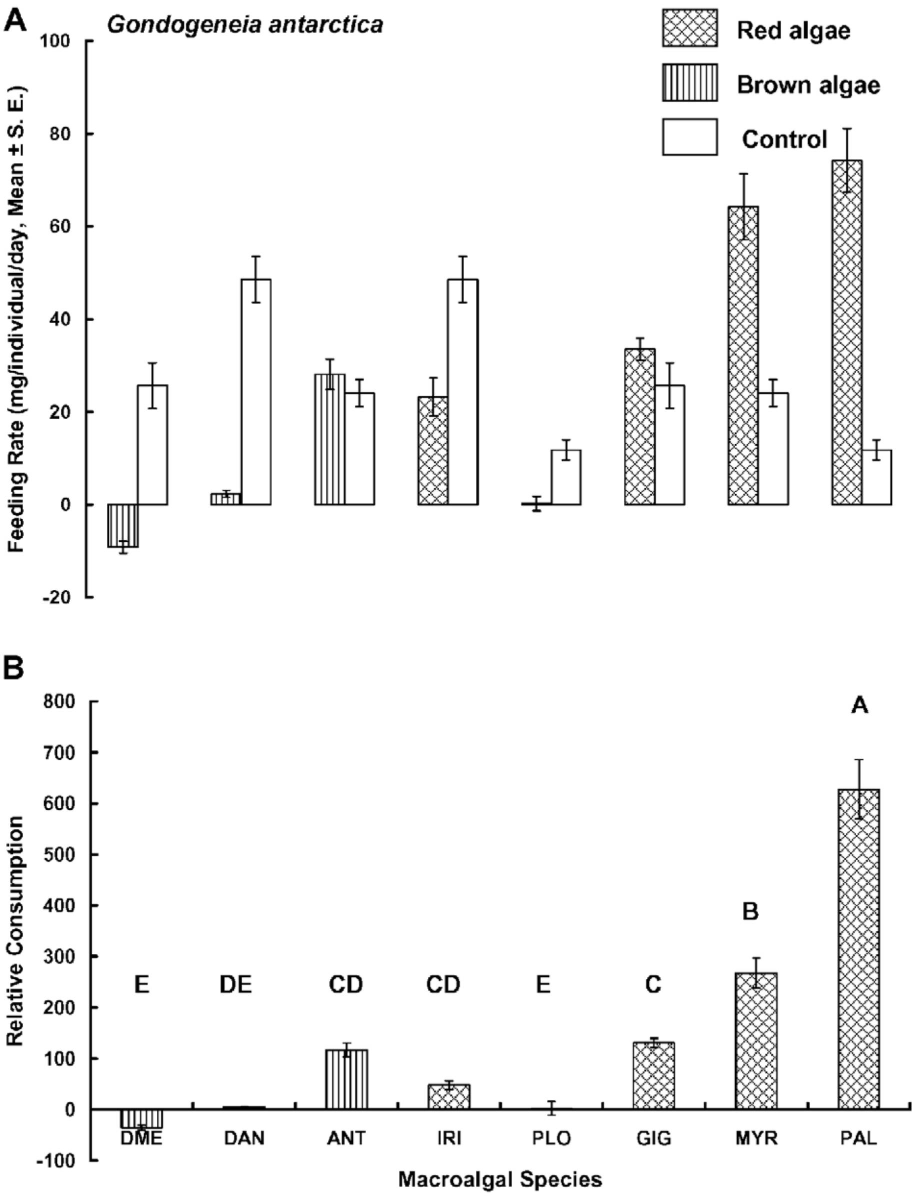

Fig. 3. Results of single species feeding trials offering alginate pellets containing freeze-dried and finely ground thallus tissues of eight macroalgae to the amphipod *Gondogeneia antarctica*. (A) Net consumption rate of *G. antarctica* presented with alginate food pellets containing macroalgal species. Controls consisted of alginate pellets containing the palatable green alga *Cladophora repens*. (B) Relative consumption derived from net consumption rates shown in Fig. 2A. Similar letters above bars indicate no statistical difference ($P < 0.05$) among the means (Friedman's test, multiple related samples ANOVA) followed by multiple *t*-tests using the Bonferroni adjustment for multiple comparisons. Bars represent means ± standard error of mean ($n = 10$). See legend in Fig. 1 for the abbreviations of macroalgae.

and Whitaker, 1979). Amphipods have also been observed to feed on epiphytes growing on subtropical seagrasses (Duffy and Harvilicz, 2001; Mukai and Iijima, 1995).

In order to control for the effects of morphological differences in the edges of fresh thalli, we also conducted amphipod feeding assays using uniformly sized artificial alginate foods impregnated with finely ground algal tissues. While there were small differences in the ranking of consumption rates of macroalgal species between the two amphipod species, similar to the fresh thalli bioassays, both *Prostebbingia gracilis* and *Gondogeneia antarctica* have the highest consumption rates when presented with pellets containing the alga

Table 2
Regression analyses comparing macroalgal nutritional parameters to amphipod consumption rates on macroalgal food pellets (nutritional parameters from Peters et al., 2005)

Nutritional parameter	*n*	Linear equation	r^2	*P*
Prostebbingia gracilis				
N (%)	6	$y=0.5x+2.3$	0.33	0.23
C (%)	6	$y=0.5x+26.9$	0.06	0.65
C:N	6	$y=-1.1x+12.7$	0.16	0.43
Protein	6	$y=0.1x+5.7$	0.002	0.94
Carbohydrate	6	$y=8.3x+11.6$	0.33	0.24
Lipid	6	$y=-1.2x+4$	0.38	0.19
Gondogeneia antarctica				
N (%)	7	$y=0.02x+2.6$	0.27	0.23
C (%)	7	$y=-0.02x+28.9$	0.05	0.62
C:N	7	$y=-0.05x+13$	0.27	0.23
Protein	6	$y=1.3x+30$	0.02	0.80
Carbohydrate	6	$y=0.3x+30.2$	0.04	0.69
Lipid	6	$y=-6.5x+52$	0.34	0.22

Palmaria decipiens. However, in contrast to the fresh thalli bioassays, artificial foods containing ground tissues of the macroalgae *Myriogramme mangini* and *Gigartina skottsbergii* were also consumed at relatively high rates, indeed, in the case of *P. gracilis*, consumption rates of both these algae were statistically indistinguishable from those for *P. decipiens*. The lack of consumption of *M. mangini* and *G. skottsbergii* when presented as fresh thalli suggests that toughness may play some role in its low palatability to amphipods when presented intact. Indeed, *M. mangini* is 11th in terms of toughness and *G. skottsbergii* is the toughest among 30 species of macroalgae examined from the Antarctic Peninsula (Amsler et al., 2005; Peters et al., 2005). It is possible that these amphipods might exploit these macroalgae as a food resource should they be dislodged from the substrate, and subsequently broken down into detritus through grazing activities of macroherbivores and through other natural degradation processes.

Information on the feeding habits of Antarctic benthic omnivores known to include macroalgae in their diets, including the common circumpolar sea star *Odontaster validus* and the Antarctic rockfish *Notothenia coriiceps*, indicates that both *Palmaria decipiens* and *G. skottsbergii* are also palatable to these sympatric macrograzers (Amsler et al., 2005). We found that the amphipod *P. gracilis* also consumes food pellets containing ground tissues of the red alga *Iridea cordata*, a species palatable to the rockfish *N. coriiceps* (Amsler et al., 2005), but chemically defended against the sea star *O. validus* (Amsler et al., 2005) and the sea urchin *Sterechinus neumayeri* (Amsler et al., 1998).

Peters et al. (2005) evaluated a suite of nutritional parameters of 40 species of macroalgae from the Antarctic Peninsula including those examined in the present study. If soluble protein content is considered a proxy for nutritional value (Cruz-Rivera and Hay, 2000a,b), it is clear from our regression analysis that there is no significant correlation between algal nutritional value and consumption rates of amphipods presented with macroalgal food pellets. Nonetheless, it should be noted that in both fresh thalli and alginate pellet assays, *P. gracilis* and *G. antarctica* preferred the macroalga *Palmaria decipiens* which had the highest soluble protein content (9.3% dry weight) among the macroalgal species (soluble protein contents of the remaining macroalgal species ranged from 2.5% to 9.2%, Peters et al., 2005).

A variety of macroalgae are known to harbor defensive secondary metabolites that are deterrent to grazers (Paul et al., 2001; Paul and Puglisi, 2004; Van Alstyne et al., 2001). With respect to the present study, the brown macroalgae *Desmarestia menziesii*, *D. anceps*, and *D. antarctica* and the red algae *Plocamium cartilagineum*, *Myriogramme mangini*, and *Iridea cordata* have been shown to be chemically defended against sympatric herbivores including omnivorous sea stars and fish (Amsler et al., 2005). Four of these macroalgae (*D. anceps*, *D. menziesii*, *D. antarctica*, and *P. cartilagineum*) have been found to be chemically defended against herbivory by the amphipod *Gondogeneia antarctica* (Amsler et al., 2005). In the present study, in both fresh thalli and alginate pellet assays, these same four species of macroalgae were either not consumed at all or consumed in very low quantities by *Prostebbingia gracilis* and *Gondogeneia antarctica*, suggesting that chemical defenses contribute to their lack of palatability.

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