2010

Chemically mediated macroalgal-mesograzer interactions along the Western Antarctic Peninsula

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Recommended Citation

Aumack, Craig Farrar, "Chemically mediated macroalgal-mesograzer interactions along the Western Antarctic Peninsula" (2010). *All ETDs from UAB*. 1058.
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CHEMICALLY MEDIATED MACROALGAL-MESOGRAZER INTERACTIONS ALONG THE WESTERN ANTARCTIC PENINSULA

by

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A DISSERTATION

Submitted to the graduate faculty of The University of Alabama at Birmingham
in partial fulfillment of the requirements for the degree of
Doctor of Philosophy

Birmingham, Alabama

2010

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DEPARTMENT OF BIOLOGY

ABSTRACT

In the following dissertation, we explore benthic communities along the Western Antarctic Peninsula, specifically, interactions between the immense macroalgal and mesograzer assemblages and how these relationships are chemically mediated. Despite the widespread production of various chemical feeding deterrents throughout the macroalgal community, the system supports an abundant and diverse array of crustacean amphipods. Gut content analysis and stable isotopic signatures indicate that filamentous macroalgae and epiphytic diatoms probably play an important role as dietary constituents, despite their visible absence in the sub-tidal zones. Subsequent palatability and extract feeding assays revealed that none of the filamentous macroalgal material found in amphipod guts could be the result of direct grazing on any of the finely branched macrophytes, especially the finely branched rhodophytes which were all determined to be chemically defended against mesoherbivory. However, mesocosm experiments conducted under natural conditions determined that, if grazing pressures were removed, there would be a significant increase in both epiphytic diatom and filamentous algal coverage throughout the macroalgal community. Additionally, there would be a higher incidence of emergent filaments protruding through host macroalgal thalli from invasive endophyte colonies. Likely, the filamentous macroalgal material seen in the gut is the result of continuous amphipod grazing which keep endo/epiphytic biofouling to a minimum. Daytime versus nighttime amphipod density measurements indicate that several amphipod taxa have adopted a nocturnal foraging strategy. Collectively, amphipods are hiding among chemically defended macrophytes during the day while associating with more palatable species at night when the risk of predation from visual predators is decreased. Ultimately, we believe the dominant macroalgae and mesoherbivore assemblages are living in mutualism. The amphipods are taking refuge in the protective confines of chemically defended macrophytes during the day while continuously cleaning both palatable and defended macroalgae of potentially harmful fouling diatoms and filamentous epiphytes at night.

Keywords: Antarctica, amphipods, chemical defenses, herbivory, macroalgae, mutualism

DEDICATION

To my Grandparents, who always encouraged me to strive for the highest levels of education along with my friends and family which continually inspired me along this path.

ACKNOWLEDGEMENTS

I would like to thank my mentor and friend Dr. Charles Amsler, whose supervision, encouragement, and advice assisted me throughout this entire processes. Any success I have in future endeavors will ultimately be a reflection on his mentorship and belief in my scientific abilities. I must also show gratitude to the rest of my committee; Dr. Angus, for attention and guidance regarding statistical analysis; Dr. Bill Baker for his on-ice assistance, supervision, and general encouragement/humor; Dr. Kenneth Dunton for his continual friendship, council, and education regarding science in academia; and Dr. James McClintock for his support, mentorship, and instruction in scientific writing. I would like to praise the entirety of the UAB Chemical Ecology contingent for their constant assistance with a special appreciation of both Maggie Amsler and Philip Bucolo who continually made lab work in both Birmingham and Palmer Station a fun and unique experience. I would also like to thank my friends and family at UAB, Palmer Station, Tuscaloosa, and Port Aransas for making this difficult journey a fun experience. Finally, I would like to acknowledge the National Science Foundation, US Antarctic Program, Raytheon Polar Services, and The Phycological Society of America for their financial and logistical support.

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LIST OF ABBREVIATIONS

ANOVA	Analysis of Variance
$CaCl_2$	Calcium Chloride
C_f	Final weight of autogenic control
C_i	Initial weight of autogenic control
C_g	Amount of total food in digestive tract
cm	centimeter
$\delta^{13}C$	$^{13}C/^{12}C$
$\delta^{15}N$	$^{15}N/^{14}N$
E_f	Final weight of experimental treatment
E_i	Initial weight of experimental treatment
Eqn	Equation
Fig	Figure
g	grams
gDW	grams dry weight

LIST OF ABBREVIATIONS (Continued)

h	hours
I(i)	Importance of dietary item
ind	individuals
kg	kilograms
km	kilometers
L	liters
M	Molarity
m	meters
MeOH	Methanol
μm	micrometers
mg	milligrams
ml	milliliters
mm	millimeters
˚C	degrees Celsius
PAM	pulse amplitude modulation
PAR	photosynthetically active radiation

LIST OF ABBREVIATIONS (Continued)

P_g	Proportion of dietary item in guts
POM	particulate organic matter
R(i)	relative importance of item
SCUBA	self contained underwater breathing apparatus
spp	species
v	volume
wwt	wet weight

INTRODUCTION

Shallow subtidal communities along the western Antarctic Peninsula provide a unique habitat in which to study mesograzer-macroalgal interactions. The benthic community can easily be characterized by the large swaths of macroalgae that constitute a dominating surface coverage, ~85% (Amsler et al. 1995, Brouwer et al. 1995, Quartino et al. 2001, Amsler et al. 2005a), of the benthos with reported biomass measurements averaging between 1.64 - 6.34 kg·m^{-2} (Quartino et al. 2001), attributes comparable to temperate kelp forests (Quartino *et al.* 2001). While extensive research in kelp communities has revealed macroalgae to be a key element to community structure, providing both food (Tegner & Dayton 2000, Cox & Murray 2006, Lauzon-Guay & Scheibling 2006, Rothausler & Thiel 2006) and shelter (Tegner & Dayton 2000, Mai & Hovel 2007, Schmidt & Scheibling 2007), less is known about macroalgal importance along the western Antarctic Peninsula.

Along with the spatial dominance of macroalgae, another unique feature of the environment is the unusually large and diverse array of mesograzers, primarily gammarid amphipods, throughout the community. Some studies have reported densities as high as 50,000 individuals m^{-2} benthos (Jazdzewski *et al.* 2001), while more recent studies have even estimated amphipod densities as high as 300,000 individuals m^{-2} algae (Amsler et al. 2008). Clearly, these estimations indicate the important ecological role amphipods may have in mediating mesograzer-algae interactions. Despite their elevated densities, amphipods appear to have little impact on macroalgae in terms of direct grazing. A comprehensive evaluation of palatability and chemical defenses in western Antarctic macroalgae revealed all the dominant phaeophytes and many of the surrounding rhodophytes are chemically defended against *Gondogeneia antarctica*, one of the most common grazing amphipod species (Amsler et al. 2005a, Huang et al. 2006).

The general unpalatability of local macroalgae to amphipods does not preclude ecological interactions. Although some amphipods associate with sessile invertebrates (Amsler et al. 2009d), most appear to live in association with the dominant macroalgae. However, amphipod distributions throughout algal assemblages are not random. Experiments conducted by Huang *et al.* (2006) demonstrated that there is a strong inverse relationship between amphipod abundance and feeding preference. Chemically defended macroalgal species like the phaeophyte *Desmarestia menziesii* and the rhodophyte *Plocamium cartilagineum* had collective amphipod densities averaging 20.05 and 5.91 inidividuals g^{-1} algae wwt respectively. In contrast, two palatable species of red algae, *Palmaria decipiens* and *Iridaea cordata*, have associated amphipod densities of only 0.26 and 0.10 individuals g^{-1} algae wwt respectively. This phenomenon could be the result of amhipods using chemically defended algae as a refuge from predation. For example, the omnivorous fish *Notothenia coriiceps* is a primary amphipod predator which readily grazes on both *P. decipiens* and *I. cordata* (Iken et al. 1997, Iken et al. 1999) but finds *D. menziesii* unpalatable (Amsler et al. 2005a). In another study, Zamzow *et al.* (2010) showed that in the absence of predators, *G. antarctica* preferred associating with *P. decipiens* but reverted back to *D. menziesii* in the presence of predator cues. Thus, by using chemically defended algae like *D. menziesii* as a host preference over palatable species, amphipods may dramatically increase their own survivorship.

Another unique feature of the western Antarctic Peninsular community in comparison to other macroalgal dominated communities is the relative lack of sub-tidal uniseriate, filamentous macrophytes or fouling epiphytes (Peters 2003, Amsler et al. 2009b). However, despite the lack filamentous epiphytes, there is a wide array of filamentous endophytes throughout the community (Peters 2003, Amsler et al. 2009b). A recent study indicated that eight of 13 macroalgal species, both browns and reds, surveyed from the area almost all had invasive endophytes growing throughout their tissues (Amsler et al. 2009b). Peters (2003) hypothesized that the dense amphipod community, continually grazing on epiphytic material, evolutionarily selected for an endophytic lifestyle. If true, it can be expected that the large assemblage of amphipods would present some evidence of epiphytic grazing in their diets and, if left in the absence of grazers, there would be significantly more epiphytic fouling on macroalgal tissues.

The research herein will enhance our understanding of benthic community dynamics along the western Antarctic Peninsula. Specifically, the roles herbivory may have in mediating the macroalgal community as well as the presence or absence of varying endo/epiphytic species of algae. Equally, the specificity of macroalgae chemical defenses and their uses as anti-grazing deterrents and how these elaborated secondary metabolites may dramatically affect amphipod host selection and behavioral patterns.

Gut content and stable isotopic analysis of dietary constituents in macroalgal associated amphipods

by

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In preparation for *Ecology*

Format adapted for dissertation

Abstract: Shallow sub-tidal communities along the western Antarctic Peninsula can be characterized by their dense macroalgal beds and abundant populations of macroalgal associated amphipods. Despite the large number of mesograzers and abundance of macroalage, direct grazing is, for the most part, unlikely as all the dominant phaeophytes and many of the rhodophytes elaborate secondary metabolite feeding deterrents. What sources were then being used to support the vast amphipod assemblage? We examined this question using two different techniques, gut content analysis and stable isotopic signatures. The $\delta^{15}N$ and $\delta^{13}C$ isotope values revealed that most abundant amphipods in the system are primary consumers whose ultimate carbon source must be derived from some combination of phaeophytic macroalgae, epiphytic diatoms, and endo/epiphytic filamentous, brown algae. Gut contents showed that a large percentage of amphipod diets are comprised of diatoms and macroalgal tissues, both filamentous and multiseriate. Likely, amphipods are routinely cleaning their host macrophytes of potentially harmful epiphytes, including both diatoms and emergent filaments from invasive endophytes. Some prominent amphipod species may even be deriving a percentage of their carbon from both palatable and unpalatable, chemically defended rhodophytes. These results combined with previous studies suggest that many abundant species of mesograzers are, in fact, living in mutualism with their macrophyte hosts. Amphipods are able to seek refuge from predation in the chemical confines of their host macroalgae while continually consuming otherwise potentially harmful epiphytic flora.

INTRODUCTION

Previous studies have shown that benthic macroalgae constitute a dominating percentage, >80%, of the shallow water community in the western Antarctic Peninsula (Amsler et al. 1995, Brouwer et al. 1995, Quartino et al. 2001). Reported biomass measurements as high as 7,000 gDW·m^{-2} (Quartino et al. 2001) are even comparable to temperature kelp forests. However, while extensive research in kelp communities have revealed macroalgae to be a key element to community structure, providing both food (Tegner & Dayton 2000, Cox & Murray 2006, Lauzon-Guay & Scheibling 2006, Rothausler & Thiel 2006) and shelter (Tegner & Dayton 2000, Mai & Hovel 2007, Schmidt & Scheibling 2007) less is known about the importance of macroalgae in western Antarctic Peninsular benthic communities. Recent studies have revealed high abundances and diversities of crustacean mesograzers (especially amphipods) affiliated with the benthic macroalgal communities along the Western Antarctic Peninsula (Nyssen et al. 2002, Huang et al. 2007, Amsler et al. 2008). Reported densities have even been estimated as high as 300,000 individuals m^{-2} algae tissue (Amsler et al. 2008), indicative of the important ecological role amphipods may have in mediating mesograzer-algae interactions. Field studies of amphipod densities have revealed greater abundances of amphipods associated with the unpalatable species of algae (Huang et al. 2007) while non-defended, palatable species are comparably free of amphipods. This is probably the result of amphipods using unpalatable, and possibly chemically defended, algal species as a refuge from predation (Zamzow et al. 2010). Thus, although associations between amphipods and benthic macroalgae are clearly evident, much remains unknown concerning these associations.

Previous studies analyzing Antarctic amphipod gut contents have revealed a diverse array of prospective prey including diatoms, macroalgal filaments and thalli, polychaetes, sponges, cnidarians, inorganic matter, and other crustaceans (Dauby et al. 2001a, 2001b) with the majority being diatoms (and other phytoplankton) and macroalgae. While these initial results indicate a more omnivorous diet, it is still unknown whether the presence of epiphytic material (*i.e.* diatoms) in the guts is the result of host material consumption and incidental ingestion of epiphytes or vice versa. It is important to discern key nutritional sources for these amphipods to further understand the processes mediating mesograzer-macroalgal interactions in near-coastal peninsular benthic habitats. However, despite a variety of techniques developed for food web analysis, there is no one specific technique which can clearly determine preferential food sources without potentially misrepresenting trophic relationships in some ways. As such, we chose to use two different methods for analyzing these trophic interactions.

Basic gut content analysis provides baseline data on the primary materials recently ingested by amphipods at the time of collection as well as a their relative importance toward the recent, overall amphipod diet (Dauby et al. 2001a, 2001b, Graeve et al. 2001). This may be especially important since many endemic Antarctic amphipod species are thought not to have strict trophic tendencies but rather have a broad-spectrum diet and take advantage of many food sources (Dauby et al. 2001b, Dunton 2001). If true, tissue isotopic measurements may be inconclusive as amphipods drift, both between and within species, among different trophic levels and ultimate carbon sources based on long term food availability. However, gut content analysis may still be the most useful method in determining current feeding strategies and monitoring any dietary changes over time.

Unfortunately, gut content data cannot infer which dietary sources are of primary importance toward long term carbon assimilation. Additionally, certain consumed materials like mineral grains and diatom frustules will be unchanged by digestive processes and may, subsequently, have longer residence times in the gut (Dauby et al. 2001b). Unlike gut content observations, stable isotope analyses provide signatures based on actual assimilation of ingested material, and are integrated over longer periods corresponding to tissue generation (growth). The technique involves measuring the $^{13}C/^{12}C$ ($\delta^{13}C$) and $^{15}N/^{14}N$ ratios ($\delta^{15}N$) of consumers and comparing them to those found in food items that comprise their potential diets. Any fractionation between carbon ratios occurs in metabolic processes that retain the heavier isotope. As a result, the stable isotopic signature of any consumer is comparatively close to its ultimate carbon source, ~1‰ for each change in trophic level (DeNiro & Epstein 1978, Peterson & Fry 1987, Dunton 2001, Norkko et al. 2004). Nitrogen ratios are better suited for determining trophic positioning within a food chain based on larger enrichments, ~3.2‰ per trophic level (Nyssen et al. 2002, Post 2002, Moens et al. 2005, Sherwood & Rose 2005, Nystrom et al. 2006), that occur between trophic levels.

Previous studies have used isotopic analysis in Antarctica to successfully elucidate diets of seabirds, seals, krill, and benthic invertebrates (Frazer et al. 1997, Zhao et al. 2004, Quillfeldt et al. 2005, Conlan et al. 2006) but only two studies to date, Dunton (2001) and Cobisier *et al.* (2004), have been exclusively conducted among the shallow sub-tidal regions along the western Antarctic Peninsula. These studies were focused on a broad food web analysis which partitioned all amphipods into one group (unknown number and identity of species used in studies) classified as omnivores and had isotopic signatures close to macroaglae, specifically brown macroalgae in Dunton (2001). However, physiology and previous gut content analysis shows that within the amphipod community there are grazers, carnivores, filter feeders, and detritovores (de Broyer & Jazdzewski 1993, de Broyer et al. 2001). Stable isotopic analysis adds the element of long term nutritional regimes and assimilation of dietary constituents, thus eliminating error caused by the presence of parasitic organisms and indigestible materials such as diatom frustules.

Previous studies have emphasized the influence of brown algal carbon into the western Antarctic Peninsula food web, primarily as detritus, through *Yoldia eightsi* and other deposit feeding bivalves, seastars, limpits, and polychaetes. (Dunton 2001). However, the substantial amphipod assemblage in the area almost certainly contributes as an important carbon conduit to higher trophic levels and must also be linked to large brown macrophytes or other isotopically similar food sources. The widespread elaboration of chemical feeding deterrents in Peninsular brown macrophytes (Amsler et al. 2005a, Fairhead et al. 2005, 2008, 2009c), limited amounts of deposit feeding amphipods (Momo et al. 1998, Huang et al. 2007), and only modest increases in grazing rates by endemic amphipods on partly degraded Antarctic phaeophytes (Reichardt & Dieckmann 1985) indicates, however, that amphipods are probably not significantly using brown macrophytic carbon, degraded or otherwise, as a primary dietary source. We hypothesize that the immense mesograzer assemblage along the western Antarctic

Peninsula is using both epiphytic diatoms and emergent filamentous endo/epiphytes as a nutritional staple.

MATERIALS AND METHODS

Gut Contents:

Fifteen different macroalgal species were collected via SCUBA from February to June, 2007 from the 15 different sites along the surrounding islands near Anvers Island, Antarctic Peninsula (64° 46.5' S, 64° 03.3' W; for map see Amsler 2005, 2009a; Table 1). Each collected individual's thallus was carefully detached from the substrate and gently floated into a mesh collecting bag (<0.5 mm) to minimize loss of associated epifauna (Huang et al. 2007). Once on the surface, macroalgae were submerged in buckets of seawater and immediately transported back to Palmer Station for processing. At Palmer, the macroalgae were repeatedly dunked in seawater to remove all associated mesoherbivores. Amphipods were kept alive and a haphazardly chosen subset taken for dissection and gut content analysis. All amphipod dissections were conducted within 2-3 hours after collection. The digestive tract was usually excised from the body at the esophagus through removal of the mandibles. Once removed, the digestive tract was separated from the midgut glands, opened, and the contents spread on a slide. To prevent desiccation, a bit of silicon grease was applied to edges of the cover slip prior to its insertion on the slide. Gut contents were then analyzed using a Nikon E800 compound microscope equipped with a phase contrast system and epi-fluorescent capabilities (Nikon Inc., Melville, New York, USA).

The relative importance [*R*(i)] of each item in the diet was determined using modified techniques inspired by a "percentage points" method published by Dauby *et al.* (2001b).

The amount of total food in the digestive tract (C_g) was visually quantified and coded using arbitrary scores (4 = ≥75% full, 3 = 50 – 74% full, 2 = 25 - 49% full, 1 = 1 – 24% full, 0 = 0% full). Then every item in the gut was classified to their major taxonomic group (i.e. crustacean parts, algal filaments, diatoms, etc…) whose total proportions (P_g) were determined and scored using a similar coefficient. The importance [I(i)] of item i in the diet of any given species was calculated using the following equation:

$$I(\mathrm{i}) = \sum_{n=1}^{x} C_g(n) * P_g(n)$$

where I(i) is a dimensionless measure, n represents the individual number for the particular speices, and x is the number of samples used in one particular species. Once I(i) was known, the relative importance was computed for each prey item:

$$R(\mathrm{i}) = [I(\mathrm{i}) / \sum_{n=1}^{y} I(\mathrm{n})] * 100$$

where R(i) is the relative importance of item i in the diet and y the number of different items found in the gut.

There are several caveats associated with the resulting percentages to the aforementioned equations. Diatom frustules, mineral grains, and other materials unchanged by the digestive process (or with longer gut residence times) may distort C_g, P_g, and ultimately $R(i)$ (Dauby et al. 2001b). Additionally, these numbers represent the most recent meals for the amphipods collected which may have diel or seasonal fluctuations in their dietary habits.

Isotopic Analyses:

From February to June 2008, macroalgae and associated amphipods were collected from the same area using the same techniques described above. After amphipods were removed from host macroalgae, macroaglal samples were then sectioned into smaller pieces. Algal sections were scraped to remove any epiphytes, weighed, and finally placed into a drying oven. Amphipods, once removed from their host alga, were sorted and placed into separate vials by species rather than individuals, to ensure ample material was collected, and dried. All tissue samples were continually dried in an oven at 60°C until analysis at The University of Texas Marine Science Institute.

All non-algal isotope samples were acidified with 10% HCl to remove carbonates. Acidified samples were then redried at 60°C, and pulverized with either a Wig-L-Bug (Rinn Corp., Elgin, Illinois, USA) or mortar and pestel. Tissue $\delta^{15}N$, $\delta^{13}C$, and %C and %N were determined with a Carlo Erba 2500 elemental analyzer coupled to a Finnegan MAT Delta$^+$ isotope ratio mass spectrometer (CE Instruments, North Carolina, USA). All isotope rations are offered as $\delta^{15}N$ and $\delta^{13}C$ relative to atmospheric N_2 and citrus leaves and bovine liver, respectively, where:

$$\delta^{15}N \text{ or } \delta^{13}C \text{ (‰)} = [(R_{sample}/R_{standard}) - 1] \times 1000$$

and R = either $^{15}N/^{14}N$ or $^{13}C/^{12}C$. Elemental content of samples were calculated using the dry weight, and molar C:N ratios determined.

Statistical Analysis:

A series of t-tests were used to determine any significant intraspecfic differences between the relative importance of varying dietary constituents of amphipods collected from different macrophytes (significance determined at $\alpha = 0.05$; SigmaPlot 11.0, Systat Software Inc., San Jose, CA).

RESULTS

Gut Contents: Gut content analyses were performed on ~520 individuals from 15 different amphipod species with the number for each species ranging from three (*Pontogeneia litoralis*) to 95 (*Gondogeneia antarctica*; Fig. 1). Dietary items were separated into six major groups: diatoms, crustacean parts, filamentous macoalgal material, multiseriate macroalgal material, sponge spicules, and all other unicellular microalgae including items like *Phaeocystis* spp. Other organic matter that were found in the guts but not classified were generally featureless and unrecognizable to any specific taxon. The relative importances of each dietary source to the individual species, regardless of original host algal species, are presented in Figure 1. Figure 2 shows the raw gut content data of eight of the more abundantly dissected amphipod species ($n > 10$, *Jassa* spp. being the exception). Generally, the raw data, without total gut fullness taken into account, is reasonably close to the relative importance of each dietary item. *Paradexamine fissicauda* and *Pontogeneia redfernii* are exceptions, several individuals within those two taxa had high percentages of one food source in a relatively empty guts. Of the general taxa categorized, on an importance value basis, diatoms are the most frequently consumed items across all species analyzed (40.5%), followed by crustacean parts (31%), filamentous macroalgae (11.1%), non-diatomaceous unicellular algae (10.7%), multiseriate macroalgal material (7.1%), and spicules (2.1%).

The relative importance of dietary constituents varied not only between species but, in some cases, within species taken from differing macroalgal hosts. There were significant decreases (average ~20%) in the relative importance of diatoms when collected from the Desmarestalies, larger chemically defended brown algae, than those collectively taken from smaller, bladed red macroalage (i.e. *Gigartina skottsbergii*, *Palmaria decipiens*, *Iridaea cordata*) in three of the most prominent amphipod species; *Gondogeneia antarctica*, *Prostebbingia gracilis*, and *Oradarea bidentata* ($p < 0.01$ for all; Fig. 3). For both *G. antarctica* and *O. bidentata*, the decrease in gut diatom abundance from individuals collected from the large brown algae coincided with a significant (~15% average) increase in macroalgal tissues, primarily filamentous material ($p = 0.04$ and $p = 0.03$, respectively). The relative importance of crustacean parts also substantially increased by an average of 21% in *P. gracilis* and *G. antarctica* and was significantly higher ($p > 0.01$) in *G. antarctica* when taken from Desmarestiales versus the aforementioned reds. No major differences were seen in the relative importance of any other major dietary constituent within species taken from varying macroalgal habitats.

Stable Isotopes: Although there was not much range between algal $\delta^{15}N$ values (1.8 – 6.5‰), we saw a large range in the $\delta^{13}C$ values in the primary producers (Fig. 4). All the large brown macrophytes analyzed (*Desmarestia anceps*, *Desmarestia antarctica*, and *Desmarestia menziesii*) fit within a relatively tight range (-22.7 – -25.0‰), along with the known Antarctic endo/epiphyte *Geminocarpus* spp. (-20.2‰) and epiphytic benthic diatoms (-21.8‰). It should be noted that although the macrophytes were relatively free of any visual epiphytic material, there were likely some diatoms mixed in with the large macrophytic tissues and reasonable amounts mixed with the filamentous algal samples (*Geminocarpus* spp. and *Elachista antarctica*). The chemically defended red macroalgae

(*Plocamium cartilagineum* and *Delisea pulchra*) were much less enriched and ranged between (-31.9 to -35.7‰). *Elachista antarctica*, another known brown endo/epiphyte, had an average $\delta^{13}C$ value of -15.4‰, a value more enriched in ^{13}C than all other algae with exception of *Palmaria decipiens* (-15.2‰), an annual, palatable rhodophyte, commonly infected with *E. antarctica* (Wiencke & Clayton 2002, Bucolo et al. 2011).

Amphipod tissue $\delta^{15}N$ values ranged from 4.7‰ (*Oradarea bidentata*) to 6.7‰ (*Paraphamedia integricauda*; Fig. 5). Based on a previously published standard ~3.2‰ increase per trophic level (Nyssen et al. 2002, Post 2002, Moens et al. 2005, Sherwood & Rose 2005, Nystrom et al. 2006), the amphipods species analyzed generally appear to be primary consumers, though the range of isotopic values on some species (e.g. *Pontogeneia redfernii*) indicates an increasingly omnivorous diet. Tissue $\delta^{13}C$ values were, for the most part, standard and fluctuated between -19.2 to -26.0‰ with the exception of *Paradexamine fissicauda* whose $\delta^{13}C$ was much less enriched at -33.1‰.

DISCUSSION

A study of trophic positioning along the western Antarctic Peninsula, using stable isotopes, indicated that a large contribution of carbon entering nearshore communities is from brown macroalgal detritus (Dunton 2001, Corbisier et al. 2004). The study also suggested that amphipods (species used unknown) were generally omnivorous suspension feeders whose ultimate carbon sources were a mixture of brown macroalgae and phytoplankton POM. While our study did not focus on deposit feeding organisms that are likely adding degraded brown macrophytic carbon to the food web, our data suggest that carbon from isotopically similar epiphytic diatoms and filamentous endo/epiphytes are contributing to the food web via the vast amphipod assemblage. It is likely that amphipods are feeding directly on these palatable algal sources and, within two species analyzed, are feeding directly on both palatable and unpalatable species of red algae as will be discussed later.

Based on previously published $\delta^{15}N$ increases of ~3.2‰ per trophic level for western Antarctic Peninsular fauna (Wada et al. 1987, Dunton 2001), amphipod $\delta^{15}N$ signatures indicate that the seven species collected for isotopic analysis are predominantly primary consumers, despite the presence of crustacean parts and spicules in their guts. It should be noted though that several species whose gut contents indicated a higher relative importance of crustacean parts were not used in the isotopic analyses (i.e. *Atyloella magellanic* and *Bovalia gigantea*). Several amphipod species, including several used in this study, are known to consume their own molts. While the potential isotopic effects are in question, Mateo *et al.* (2008) found little difference between the $\delta^{13}C$ values of whole crustaceans versus those which had been acidified, removing their exoskeleton. This suggests that amphipod consumption of their own molt may have little effects on their isotopic signature. While our $\delta^{15}N$ values of species within the Desmarestales varied slightly from those reported by Dunton (2001), they were analogous to those analyzed in 2002 (R. Dunbar, unpublished). In addition, while Dunton (2001) reports a collective amphipod $\delta^{15}N$ value of 5.6±0.4‰, our amphipod communal measurement was 5.9±0.6‰, the slight difference likely the result of specific species differences. Though the average amphipod species' isotopic signatures are slightly less enriched in ^{15}N than would be expected from strict benthic grazers, the inclusion of some phytoplankton POM, reported as 0.4‰ (Wada et al. 1987, Dunton 2001) would account for this difference.

Typically, consumers have $\delta^{13}C$ value between 0.4 to 1.0‰ higher than their ultimate carbon source (DeNiro & Epstein 1978, Peterson & Fry 1987) and the majority of amphipods measured were within the collective range measured for brown macrophytes, the endo/epiphyte *Geminocarpus* spp., whose samples likely included some epiphytic diatoms, and epiphytic diatoms themselves. Several previous studies have reported the unpalatability of the dominant brown macrophytes (Amsler et al. 2005a, 2009c) to a suite of herbivores, including prominent amphipods (Amsler et al. 2005a). Recent studies have also reported the palatability and increased amphipod grazing rates on 14 different species of western Antarctic endo/epiphytes including 12 species of phaeophytes (Amsler et al. 2009b, Bucolo et al. 2011). Combined with the general lack of deposit feeding amphipods compared to the overall amphipod assemblage (Momo et al. 1998, Huang et al. 2007), the combined gut contents and isotopic data suggest that, collectively, benthic diatoms and endo/epiphyte filaments are a ubiquitous food source throughout the amphipod community and a significant dietary element for the majority of prominent species. Fourteen of 15 species utilized for gut contents had diatoms comprising at least 15% of their total relative dietary importance, while six species had diatoms ≥ 50%. Accidental ingestion and slower residence times of frustules probably inflate these dietary percentages (Dauby et al. 2001b). However, an amphipod exclusion experiment using mesocosms showed significant increases in fouling epiphytes (~50% increase in average coverage), primarily diatoms, over a 6-week period in three of the four macroalgal species used (Aumack et al. 2011).

Amphipod habitat selection among macroalgal species obviously influences their dietary constituents. *Gondogeneia antarctica*, *Prostebbingia gracilis*, and *Oradarea* *bidentata* all had significantly lower percentages of diatoms in their guts when extracted from members of the Desmarestiales versus bladed rhodophytes. This is likely the result of diatom availability on these macroalgae. A study by Amsler *et al.* (2005b) showed that extracts from both *Desmarestia antarctica* and *Desmarestia menziesii* caused 100% mortality in diatoms after 3 days of exposure, though experiments were not conducted in an ecologically relevant manor. In a mesocosm study, Aumack *et al.* (2011) reported no significant increase in diatom epiphytization on *Desmarestia anceps* after a six week incubation in a grazer free environment, the other three macrophytic species used in the study were all significantly more covered with diatoms indicating some production of anti-fouling compounds in *D. anceps*. The natural production of diatom inhibitory metabolites, combined with increased interspecific competition from the large amphipod assemblage associated with the spatially dominant Desmarestiales (Huang et al. 2007) suggests less diatomaceous food availability compared to many bladed red macroalgal species. Subsequently, the diatom percentage in amphipods living on *D. menziesii*, and other spatially dominant Desmarestiales, is likely to be lower compared to amphipods inhabiting other algae.

Along with epiphytic diatoms, filamentous endo/epiphytes are a likely carbon source to the amphipod community. Macroalgal material, both filamentous and multiseriate, comprises a significant portion of the amphipod assemblages' diet, collectively having a relative importance of 18.2% of the total diet. Seven of the 15 species studied had the macroalgal relative importance in the total diet of ≥ 20%, while the gut contents of both *Eurymera monticulosa* (58%) and *Pontogeneia litoralis* (26%) had the relative importance of macroalgae in their total diet greater than any other food source. While the multiseriate material seen in the guts can indicate several different specific algal taxa, filamentous material can only be from limited sources due to the general lack of filamentous algae freely growing in the sub-tidal (Peters 2003). However, surveys have indicated an abundance of filamentous algae growing endophytically throughout the community and at least two species of filamentous epiphytes; *Geminocarpus geminatus* and *Elachista antarctica* (Moe & Silva 1989, Peters 2003, Amsler et al. 2009b). While the enriched isotopic carbon signature of *E. antarctica* (-15.4±0.1‰) indicates it is not a consistent carbon source for most amphipods, *Geminocarpus* spp., along with any associated diatoms, $\delta^{13}C$ values (-20.2±0.4‰) are similar to other larger brown macrophytes and may be a contributing carbon source for many amphipod species along with other, yet uncharacterized, brown epiphyte species. A recent survey by Amsler *et al.* (2009b) reported that many rhodophytes in the western Antarctic Peninsula (*Palmaria decipiens*, *Gigartina skottsbergii*, and *Myriogramme smithii*) all contained <<1 to 0% invasive endophytes growing within their tissues. However, the same survey reported that two species of Desmarestiales (*Desmarestia antarctica* and *Himantothallus grandifolius*) were regularly infected. Aumack *et al.* (2011) showed that when grazing pressures were removed, 14 of 15 *Desmarestia antarctica* individuals had emergent filaments protruding through their thallus from an endophytic colony after six weeks while only 4 of 15 individuals kept with grazers exhibited the same trend. The regular presence of filamentous macroalgal material in the guts of amphipods, combined with the general lack of subtidal filamentous macrophytes in the Western Antarctic, suggest that filamentous epiphytes along with emergent filaments from endophytes are common throughout the community, but go visually undetected as a result of amphipod feeding pressures.

Although most amphipod stable isotope signatures indicate the assimilation of brown algal carbon, some specialists may use red algae, in part, as a dietary source. Several studies have reported the lack of chemical defenses in the pseudo-annual rhodophyte *Palmaria decipiens* (Amsler et al. 2009b, Aumack et al. 2010, Bucolo et al. 2011) and its phaeophytic epiphyte *Elachista antarctica* (Bucolo et al. 2011). However, despite the fact that *P. decipiens* appears not to be chemically defended, many amphipod species do not graze thallus material from the rhodophyte in bioassays (Aumack et al. 2010, Bucolo et al. 2011). The enriched $\delta^{13}C$ value of both *P. decipiens* and *E. antarctica* ($\delta^{13}C$ = -15.2±0.2 and -15.4±0.1‰, respectively) make it unlikely that they significantly grazed by the majority of amphipods in nature as well. The one exception is *Gondogeneia antarctica* ($\delta^{13}C$ = -19.2±0.2‰) which has a noticeably lower average $\delta^{13}C$ value than other amphipods and has been shown to graze both *P. decipiens* and *E. antarctica* in laboratory experiments (Amsler et al. 2009b, Aumack et al. 2010, Bucolo et al. 2011). This suggests that *G. antarctica* is unique, potentially using *P. decipiens* and *E. antarctica* as additional food sources. Previous isotopic measurements of *P. decipiens* by Dunton (2001) and R. Dunbar (unpublished) reveal a less enriched $\delta^{13}C$ value (-19.9±0.1 and -18.3±1.1‰, respectively), increasing the probability that *G. antarctica* is substantially using *P. decipiens* as a dietary source.

Another amphipod, *Paradexamine fissicauda*, appears to eat chemically defended red algae. Gut content analysis from *P. fissicauda* indicate that macroalgal material, both filamentous and multiseriate, had a relative importance of 20%, while the $\delta^{13}C$ values of

P. fissicauda (-33.1±0.4‰) were too low to be a complete assimilation of brown algal carbon. The raw gut content data indicates macroalgae, both filamentous and multiseriate, as near ~55% of the total gut contents when fullness of the gut is not mathematically factored. However, the isotopic signature matches the red algae *Plocamium cartilagineum* (-32.6±0.5‰), an alga that elaborates some of the strongest feeding deterrents in the system (Amsler et al. 2005a, Aumack et al. 2010), along with other structurally similar, chemically defended red algae ($\delta^{13}C$ -32.0 to -36.0‰) determined by both Dunton (2001) and R. Dunbar (unpublished). In a recent study, *P. fissicauda* readily grazed on the fresh thallus of *P. cartilagineum* and its grazing rates increased 20-fold, relative to initial grazing rates, when maintained in aquaria with nothing but *P. cartilagineum* (Amsler et al. submitted). This indicates that *P. fissicauda* is able to both readily graze the defended rhodophyte and to physiologically increase its tolerance to *P. cartilagineum* defenses.

Comparison of amphipods along the western Antarctic Peninsula to less enriched stable isotopic values of amphipods found in both the Weddell Sea, -30.8±0.3‰ (Rau et al. 1991), and the Ross Sea, -27.1 (Wada et al. 1987), imply the significance of brown algal carbon, including diatoms, as an ultimate carbon source to the entirety of the nearshore benthic food web. Although a percentage of brown macrophytic carbon may enter the system as detritus, our data suggest that direct feeding on isotopically similar diatoms and endo/epiphytic filamentous algae are more likely sources for the comparatively enriched carbon values seen throughout the community. The immense amphipod assemblage is a likely an important influence on community structure, both controlling micro- and macroalgal epiphyte populations on their macrophytic hosts and, in doing so, acting as a conduit for brown algal carbon to be integrated into the shallow sub-tidal western Antarctic Peninsular food web.

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Table 1. Number of each amphipod species used in gut content analysis and their respective hosts when captured.

Amphipod Species	Macroalgal Host	No.
Gondogenea Antarctica	*Desmarestia anceps*	7
	Desmarestia menziesii	24
	Gigartina skottsbergii	8
	Gymnogongrus turquetti	3
	Himantothallus grandifolius	5
	Iridaea cordata	19
	Myriogramme mangini	5
	Myriogramme smithii	2
	Palmaria decipiens	9
	Plocamium cartilageneum	9
	Plumariopsis peninsularis	1
	total	92
Metaleptamphous pectinatus	*Desmarestia anceps*	34
	Desmarestia antarctica	2
	Desmarestia menziesii	26
	Himantothallus grandifolius	4
	Iridaea cordata	1
	Plocamium cartilagineum	4
	Plumariopsis peninsularis	4
	total	75
Pontogeneia litoralis	*Desmarestia menziesii*	1
	Gigartina skottsbergii	1
	Halopteris obovata	1
	total	3
Atyloella magellanica	*Desmarestia menziesii*	6
	total	6
Bovallia gigantean	*Desmarestia anceps*	10
	Desmarestia menziesii	19
	Halopteris obovata	1
	Plocamium cartilagineum	1
	total	31
Djerboa forcipes	*Desmarestia menziesii*	9
	Himantothallus grandifolius	1
	total	10
Prostebbingia serrata	*Dendrilla membronas*	1
	Gigartina skottsbergii	1
	Plocamium cartilagineum	2
	total	4
***Jassa* spp.**	*Cystosphaera jacquinotii*	2
	Desmarestia anceps	7
	Desmarestia menziesii	3
	Gigartina skottsbergii	7
	Himantothallus grandifolius	5
	Iridaea cordata	2
	Myriogramme mangini	9
	Plocamium cartilagineum	2
	total	37

Table 1 continued.

Amphipod Species	Macroalgal Host	No.
Oradarea bidentata	*Dendrilla membronas*	1
	Desmarestia anceps	24
	Desmarestia antarctica	7
	Desmarestia menziesii	18
	Gigartina skottsbergii	7
	Gymnogongrus turquetti	3
	Halopteris obovata	1
	Himantothallus grandifolius	1
	Iridaea cordata	3
	Myriogramme mangini	1
	Myriogramme smithii	2
	Plocamium cartilagineum	11
	Pulmariopsis peninsularis	2
	total	81
Paradexamine fissicauda	*Halopteris obovata*	2
	Himantothallus grandifolius	1
	Myriogramme mangini	1
	Picconiella plumosa	1
	Plocamium cartilagineum	13
	total	18
Schraderia gracilis	*Desmarestia menziesii*	1
	Myriogramme mangini	1
	Pantoneura plocamioides	2
	total	4

Amphipod Species	Macroalgal Host	No.
Paraphamedia integricauda	*Desmarestia anceps*	4
	Desmarestia menziesii	19
	Gigartina skottsbergii	3
	Himantothallus grandifolius	1
	Myriogramme mangini	3
	Total	30
Prostebbingia gracilis	*Desmarestia anceps*	21
	Desmarestia antarctica	29
	Halopteris obovata	12
	Myriogramme mangini	2
	Myriogramme smithii	2
	Picconiella plumosa	13
	Plocamium cartilagineum	6
	Pulmariopsis peninsularis	5
	total	90
Eurymera monticulosa	*Desmarestia menziesii*	5
	Myriogramme mangini	1
	total	6
Pondogeniea redfearnii	*Desmarestia anceps*	7
	Desmarestia menziesii	22
	total	29

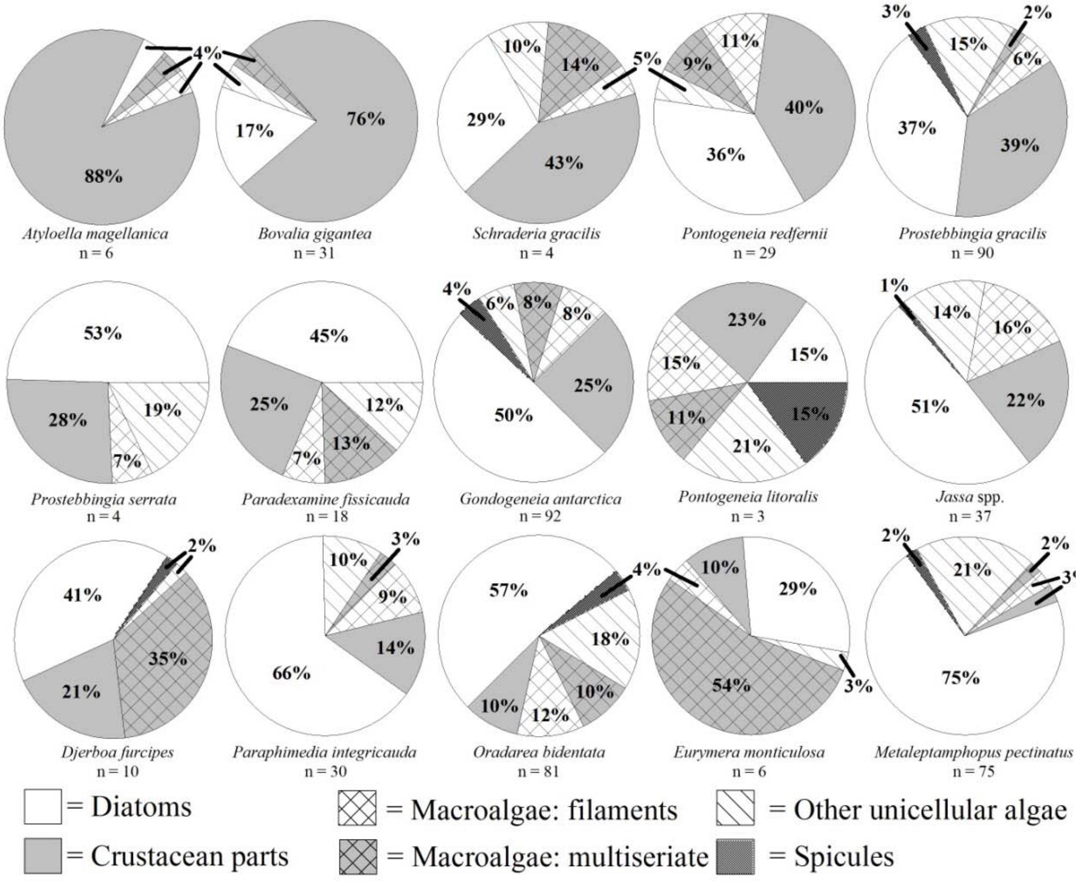

Figure 1: Relative importance [*R*(i)], in terms of percentage, of the six primary food groups found in the digestive tracts of 15 different amphipod species endemic to the western Antarctic Peninsula. *R*(i) calculation based on the intraspecific average percentage of each item (i) found in the guts and the relative fullness of the gut. N represents the number of individuals, per species, used to calculate *R*(i).

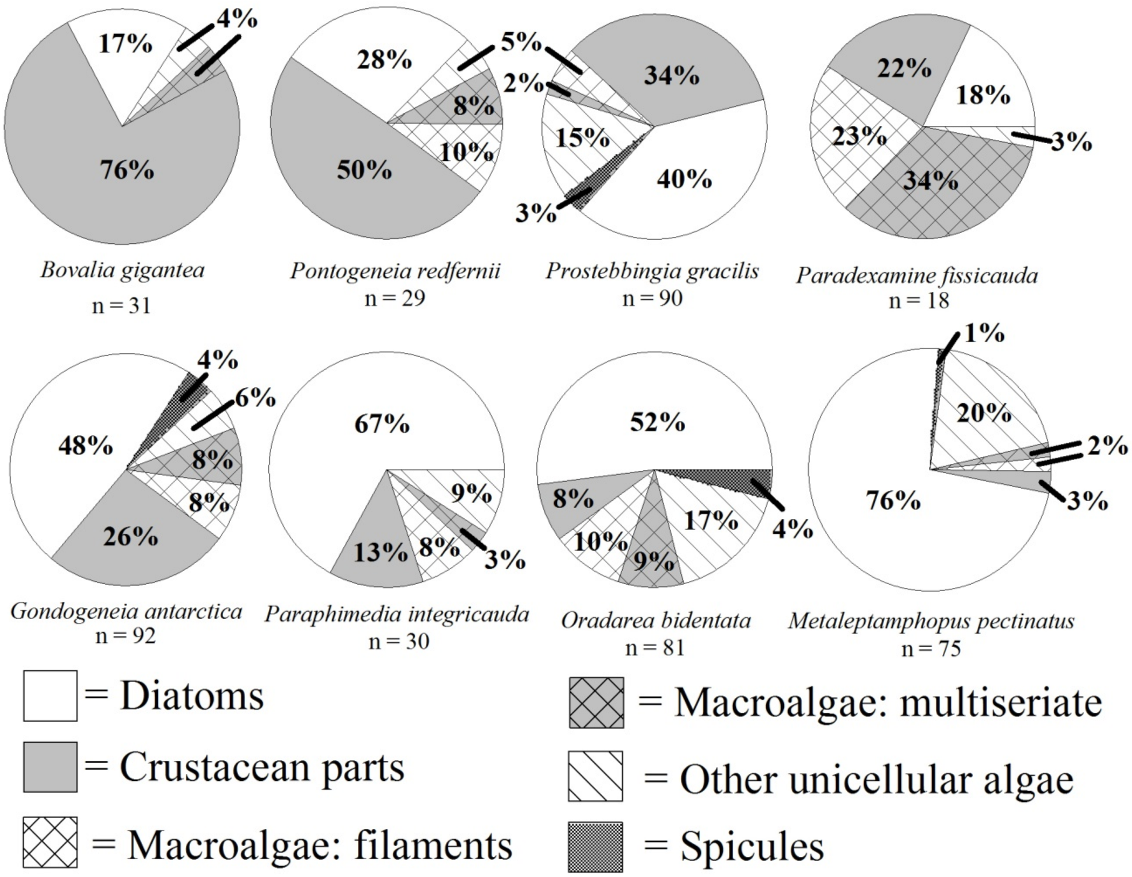

Figure 2: Raw gut content percentages of the six primary food groups found in the digestive tracts of eight different amphipod species endemic to the western Antarctic Peninsula. Only species with a sample size > 10 were used.

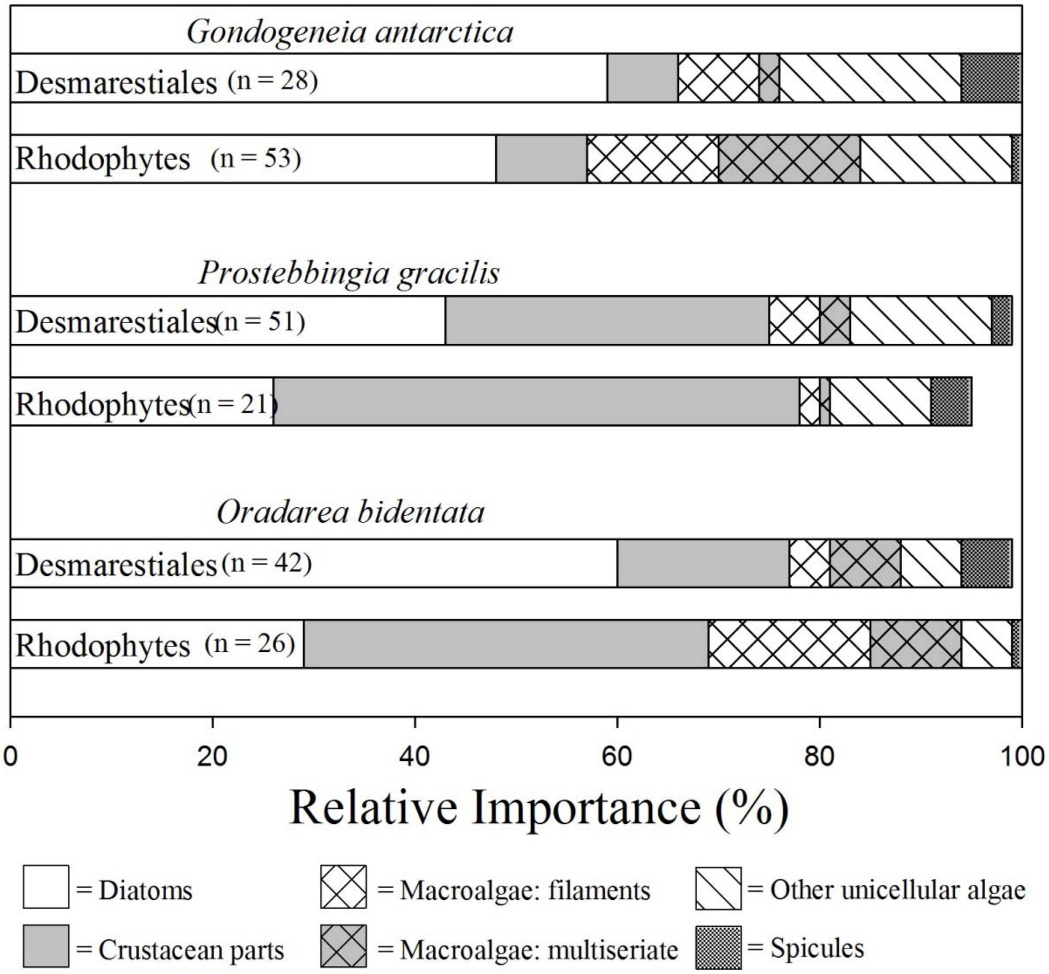

Figure 3: Relative importance [*R*(i)], in terms of percentage, of six primary dietary food groups found in the digestive tracts of three abundant benthic amphipods collected from different macrophyte taxa. Graphs represent intraspecific averages of individuals collected from either chemically defended Desmarestiales or smaller, rhodophytes.

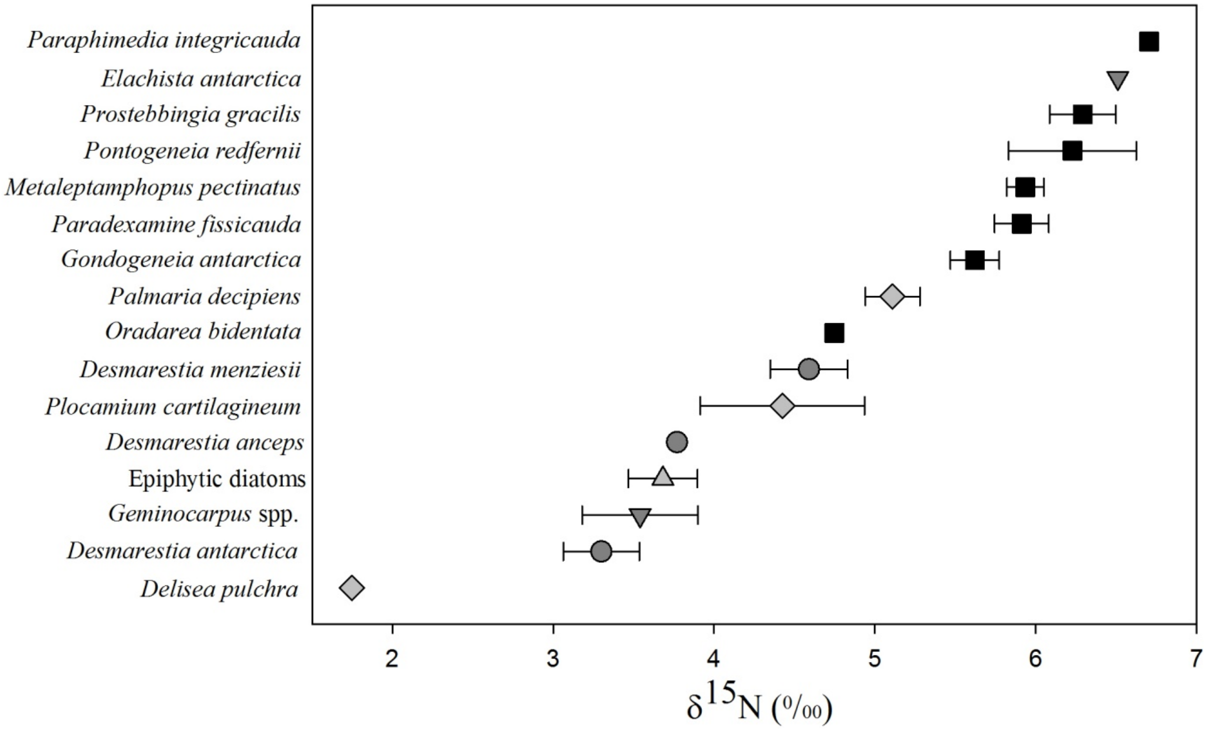

Figure 4: Mean δ^{15}N values of different flora and fauna from the western Antarctic Peninsula. Dark squares (■) represent different amphipod species, shaded circles (●) represent different species of brown macroalgae, shaded diamonds (◆) represent different species of red macroalgae, downward triangles (▼) are different species filamentous endo/epiphyte, and the shaded triangle (△) is an average of various epiphytic diatoms. Note the value for all macrophytes and filamentous endo/epiphytes likely includes epiphytic diatoms. Data are all ± SD.

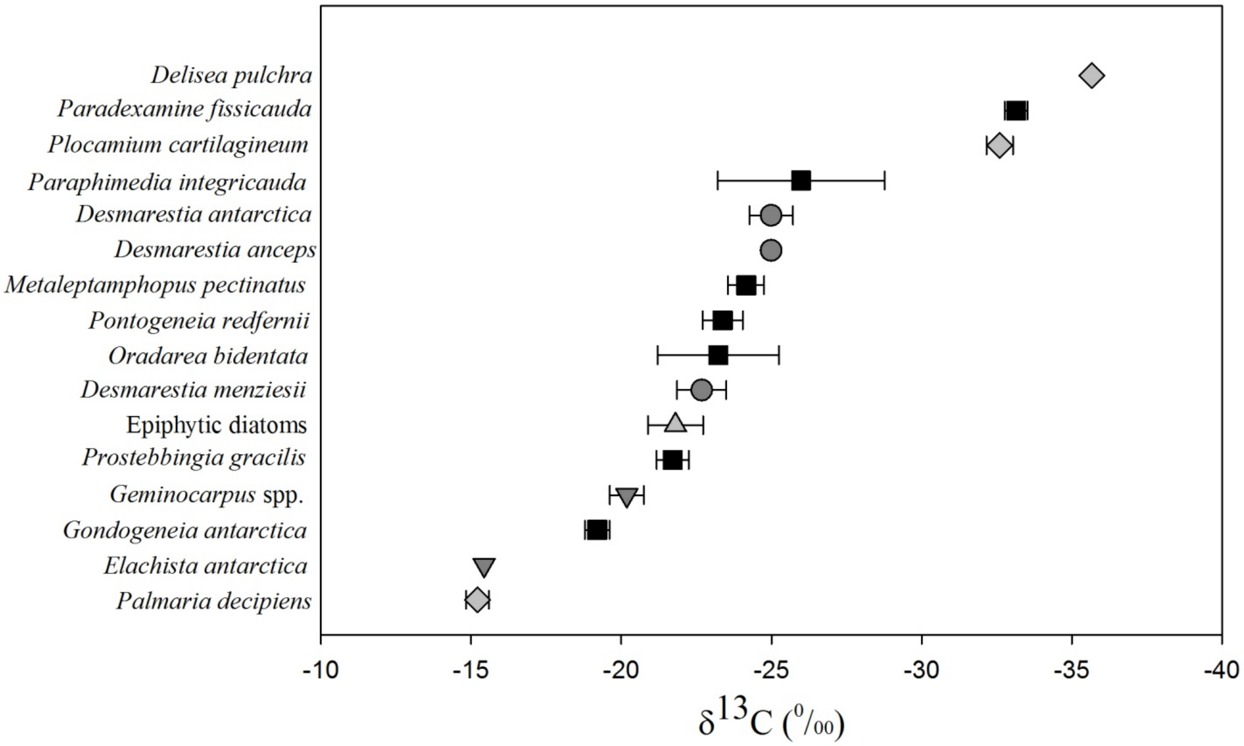

Figure 5: Mean δ^{13}C values of different flora and fauna from the western Antarctic Peninsula. Dark squares (■) represent different amphipod species, shaded circles (●) represent different species of brown macroalgae, shaded diamonds (◆) represent different species of red macroalgae, downward triangles (▼) are different species filamentous endo/epiphyte, and the shaded triangle (△) is an average of various epiphytic diatoms. Note the value for all macrophytes and filamentous endo/epiphytes likely includes epiphytic diatoms. Data are all ± SD.

CHEMICALLY MEDIATED RESISTANCE TO MESOHERBIVORY IN FINELY BRANCHED MACROALGAE ALONG THE WESTERN ANTARCTIC PENINSULA

by

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European Journal of Phycology 45: 19-26

Format adapted for dissertation

Abstract

Along the western Antarctic Peninsula, benthic macrophytic biomass rivals some of the denser algal communities in the world. However, there is a noticeable lack of filamentous epiphytes compared to other algal dominated communities. One possible explanation is that epiphytic species and emerging filaments from profuse endophytes are controlled by grazing pressures from an abundant mesograzer community. Amphipod gut contents from the study area revealed the presence of algal filaments which supports this hypothesis. However, this gut-derived algal material may be from ingestion of any of the several subtidal, finely-branched rhodophyte species which are often inhabited by numerous amphipod mesograzers. Palatability of several of these finely-branched macrophytes (*Halopteris obovata*, the lone phaeophyte in this study, *Cystoclonium obtusangulum*, *Pantoneura plocamioides*, *Picconiella plumosa*, *Plocamium cartilagineum*, as well as the known edible control alga *Palmaria decipiens*) was tested against two of the most abundant amphipod mesograzers, *Gondogeneia antarctica* and *Prostebbingia gracilis*, in a series of fresh thallus feeding assays. Several artificial food bioassays, utilizing artificial foods mixed with algal extracts, were also conducted to test for any chemical grazing deterrents produced by the macroalgae. Results indicate that all the finely branched algae tested were unpalatable to both grazers, most likely due to chemical defenses in the red algae. These results suggest that filamentous material found in amphipod guts is not finely branched rhodophytes despite observation of mesograzers associating with these algae. Possibly, mesograzers of the western Antarctic Peninsula use these chemically defended algae as a refuge from predation and, in turn, graze on

palatable epiphytes, and emergent filaments from endophytes, growing on their host macrophytes.

Introduction

The optimal defense theory suggests that chemical defenses are most often elaborated for protection against larger, more destructive herbivores while tolerance is a better evolutionary strategy when dealing with smaller mesograzers. In terms of fitness, the energetic costs of secondary metabolites, albeit low, may be too great to overcome compared to the physiological benefits attained by defending against the inconsequential tissue damage caused by mesoherbivory (Rhoades 1979). Additionally, in many marine environments, mesograzers populations are controlled by top-down predation (Griffen & Byers 2006, Jephson et al. 2008, Moksnes et al. 2008). Along the western Antarctic Peninsula, however, recent studies have revealed very high densities of grazing amphipods (up to 300,000 individuals m^{-2} benthos, Amsler *et al.,* 2008), suggesting that there may be little to no top-down control over mesograzers by predators. Furthermore, the high abundances of herbivorous amphipods would almost certainly have significant detrimental effects on macroalgal health and fitness if left unhindered. The existence of algal-produced amphipod feeding deterrents (Amsler et al. 2005a, Fairhead et al. 2005, Huang et al. 2006) and the frequent interactions of macroalgae and amphipods (Huang et al. 2007) imply that evolutionary and/or ecological macrophyte-mesograzer relationships are likely to occur in the nearshore benthic marine communities of the western Antarctic Peninsula.

A comprehensive evaluation of palatability and chemical defenses in western Antarctic macroalgae revealed that ~45% of tested macroalgae, including the dominant browns and many abundant reds, were chemically defended against two common macrograzers, the sea star *Odontaster validus* and omnivorous fish *Notothenia coriiceps*. Further analysis revealed that ~60% of the species that were unpalatable to either *O. validus* and *N. coriiceps* were also chemically defended against the abundant omnivorous amphipod *Gondogeneia antarctica* (Amsler et al. 2005a). *Gondogeneia antarctica*, one of the more prolific amphipods found in the shallow (< 20 m depth) benthic community, is most often found in association with the large ecologically dominant brown algae *Desmarestia anceps* Montagne and *Desmarestia menziesii* J. Agardh, as well as with the smaller red algae *Iridaea cordata* (Turner) Bory and *Palmaria decipiens* (Reinsch) R.W. Ricker (Huang et al. 2007). Another abundant omnivorous amphipod, *Prostebbingia gracilis*, is generally found slightly deeper (20-30 m depth) co-occurring with finely branched red algae such as *Plocamium cartilagineum* (Linnaeus) P.S. Dixon and *Pantoneura plocamioides* Kylin (Aumack, personal observation) Gut content analysis indicates that algal filaments make up a significant portion of both these amphipods' natural diets (C. Aumack, unpublished). In fact, the relative percentage of macroalgal material found in the guts of *P. gracilis* doubled when individuals taken from finely branched rhodophytes were analyzed separately from those caught on Desmarestiales (C. Aumack, unpublished). The significant presence of filamentous algal material in amphipod guts is curious since there are very few truly filamentous, non-endophytic, algae present in the western Antarctic Peninsula subtidal zone (Peters 2003, Amsler et al. 2009a). Currently, the filamentous algal species consumed remain unknown, although work is currently in progress to identify them.

The lack of filamentous subtidal algae in the Antarctic marine flora (Peters 2003) is in striking contrast to epiphytes associated with marine macroalgae in tropical and temperate regions (Philippart 1995, Wear et al. 1999, Andreakis et al. 2007). Most of the filamentous algal taxa in the Antarctic subtidal are endophytes, "with up to 100% prevalence in their host populations" (Peters 2003). Peters hypothesized that the extensive mesograzer community affiliated with the Antarctic benthos may forage intensively on small epiphytic algae, but that endophytes escape mesoherbivory because they reside within the tissues of larger macroalgae. Using an omnivorous amphipod as a model grazer, Amsler *et al.* (2009a) confirmed the high palatability of a suite of endophytic species compared to their macrophytic hosts found in the shallow coastal waters of the western Antarctic Peninsula.

It is possible that the filamentous material we found in herbivorous amphipods' guts (C. Aumack, unpublished) are remnants of small, rarely observed algal epiphytes or palatable endophyte filaments emerging from their macroalgal hosts' thallus. Another possibility is that amphipods are feeding on finely branched algae which are close morphologically, albeit not truly filamentous species, to macroalgae found more abundantly in deeper waters (Amsler et al. 1995). Previous research though has shown that fresh thalli from several of these finely branched algae are unpalatable to macrograzers (Amsler et al. 2005a).

The aim of the present study was to determine the palatability of several finely branched Antarctic Peninsular macroalgae to a pair of common sympatric benthic amphipods, *Gondogeneia antarctica* and *Prostebbingia gracilis*, and to determine whether defenses detected against mesoherbivory are chemically mediated.

Materials and methods

Collections: All organisms were collected within 3.5 km of Palmer Station on Anvers Island, west of the Antarctic Peninsula (64° 46.5' S, 64° 03.3'W; for map see Amsler *et al.*, 2005; 2009a). Macroalgae were collected by hand via SCUBA (2 – 30 m) depth between April and June 2007 and 2008. After collection, the algae were kept submerged in buckets of seawater and immediately transported back to Palmer Station for processing. Algae were sorted by species, weighed wet using a portable top loading balance (Ohaus, Pine Brook, NJ, USA) and either frozen at -20°C for extract preparation or segmented into similar sized portions for fresh thallus feeding experiments.

Two herbivorous benthic amphipods common in macroalgal communities along the western Antarctic Peninsula, *Gondogeneia antarctica* and *Prostebbingia gracilis*, were chosen for these experiments based on their considerable abundance (Huang et al. 2007) and previous observations of macroalga material found in their guts (C. Aumack, unpublished). All amphipods were collected subtidally via SCUBA. Divers carefully severed the holdfast of species of macroalgae known to contain high densities of amphipods, typically either *Plocamium cartilagineum* or *Desmarestia menziesii*, and gently floated the alga into a mesh bag with a closeable mouth to minimize resident amphipod loss (Huang et al. 2007). The mesh bag was placed in a bucket of seawater and transported to Palmer Station for processing. The alga was removed from the mesh bag and repeatedly 'dunked' into buckets of saltwater dislodging amphipods, which were then identified and sorted by species. Amphipods were maintained in 2-L plastic bottles, with openings covered by fine mesh screening to prevent amphipod loss and allow water exchange, while floating in tanks supplied with a constant flow of ambient seawater.

Fresh thallus bioassay: *Gondogeneia antarctica* and *Prostebbingia gracilis* were used to test the palatability of five finely branched macroalgae indigenous to the waters of the western Antarctic Peninsula. Four rhodophytes (*Plocamium cartilagineum*, *Cystoclonium obtusangulum* [J.D. Hooker & Harvey] Kützing, *Pantoneura plocamioides*, and *Picconiella plumosa* [Kylin] J. De Toni) and one phaeophyte (*Halopteris obovata* [Hooker F. & Harvey] Sauvageau) were selected for testing. *Palmaria decipiens*, usually a singularly bladed rhodophyte, was chosen as a control species due to its known palatability to *G. antarctica* (Huang et al. 2006, Amsler et al. 2009c). A series of no-choice feeding rate trials were conducted using individual macroalgae and amphipod combinations (Cruz-Rivera & Hay 2000) and comparisons made based on the species-specific amphipod feeding rates on all six macroalgae. For each individual trial, a series of two fresh un-grazed thalli (based on visual examination) pieces from multiple specimens were segmented into similarly sized units, blotted dry, and weighed using a microbalance (Mettler-Toledo Inc., Columbus, OH, USA). Thallus pieces were then independently placed into twenty 250-ml nalgene bottles, ten of which contained one algal piece along with 15 haphazardly chosen *Gondogeneia antarctica* while the other ten contained the paired algal portion but were amphipod free and served as autogenic controls. This technique allowed the calculation of consumption rates while negating any potential autogenic effects. Experiments using *Prostebbingia gracilis* contained 20 individuals per bottle because of their smaller average body size and slower feeding rates compared to *G. antarcitca*. Bottles were allowed to drift in a flow-through seawater aquarium to ensure uniform temperatures. Water within the bottles was replaced at least once every 24 hours to ensure a well oxygenated environment for both the amphipods and algal pieces. Experiments continued until a noticeable change in algal size was visually detected or a period of 96 hours had elapsed. After this period, thallus pieces from each of the bottles were removed, blotted dry, and final wet weights recorded. Amphipod consumption rates were calculated as mean milligram of algae consumed per hour per individual amphipod (mg algae h^{-1} ind^{-1}) corrected for autogenic change using the formula (Eqn. 1);

$$E_i(C_f/C_i) - E_f = \text{Consumption} \tag{1}$$

where E_i and E_f represent the initial and final weights, respectively, of the experimental (with amphipods) treatments while C_i and C_f represent the initial and final weights, respectively, of the autogenic controls.

Processing and extracts: Extraction of chemical constituents from each of the six macroalgal species tested in the fresh thallus bioassays was necessary in order to investigate the extent to which algal secondary metabolites may contribute to predator defense. Algal extracts were prepared following techniques described in Amsler *et al.* (2005). The frozen algal material was submerged in a mixture of dichloromethane:methanol (50:50 v/v) for 24 h rendering a lipophilic extract. The algal material was re-submerged in fresh solvent and the soaking process repeated twice to ensure maximum yield. The same algal material was then soaked in 50% MeOH (v/v) for another three 24-h periods rendering a hydrophilic extract. The three lipophilic and hydrophilic extracts were respectively pooled and dried under reduced pressure using a rotary evaporator (BUCHI Labortechnik AG, Flawil, Switzerland) and freeze dryer

(VirTis, Gardiner, NY, USA). Final extract yields were determined by dividing the combined weight of extract (mg) by the wet weight (g) of the source alga. The resulting value was multiplied by previously published wet weight to volume ratios (Amsler et al. 2005a, Huang et al. 2006) for each species to generate a species-specific extract to volume ratio.

Artificial food preparation: Artificial food pellets were prepared following techniques previously described by Fairhead *et al.* (2005). Food pellets were comprised of 2% alginate powder containing 5% *Cladophora repens* (J. Agardh) Harvey. *C. repens* is an intertidal filamentous chlorophyte in the study area and is readily consumed by the two amphipod species used in this study (Huang et al. 2006). Freeze dried *C. repens* was ground into a fine homogenous powder using a mortar and pestle. Then, specific amounts, based on extract yields, of either lipophilic or hydrophilic extract were dissolved in MeOH and added to *C. repens* powder such that the artificial foods had the same concentration of the extracted compounds as the source algal thallus on a volumetric basis (mg extract per ml). Once extracts were dissolved onto the *C. repens* powder, the MeOH was dried off under reduced pressure. Dried powders were then added to separate 100 mm plastic petri dishes and covered with 2% alginate solution and stirred to form two homogenous solutions, one with algal extracts and one control without any extract but with an equal amount of MeOH used to dissolve extracts for the treated pellet. The mixture was then gelled cold using 1 M $CaCl_2$ and refrigerated until used in assays. A cork borer was then used to cut 1-cm diameter disks for use in the amphipod feeding assays.

Food pellet bioassays: One each control and extract food pellet was weighed prior to insertion into 250-ml nalgene bottles. Ten of these bottles contained 15 haphazardly chosen *Gondogeneia antarctica* while the other ten, paired bottles were amphipod free serving as autogenic controls. In experiments using *Prostebbingia gracilis*, 20 individuals were placed into bottles to adjust for its smaller average body size and slower feeding rate compared to that of *G. antarctica*. All bottles were allowed to drift in a flow-through seawater aquarium until a noticeable change in pellet size or structural integrity was observed, generally between 18-36 h. In longer experiments, seawater was replaced after 24 h to ensure a well oxygenated environment for the amphipods. Both control and extract pellets were then removed from the bottles, and re-weighed. Anti-grazing potential of macroalgae secondary metabolites was determined by calculating wet mass change difference between the extract and control disks in the amphipod containing bottle adjusted for autogenic changes as determined from the amphipod-free bottle as described in the fresh thallus assays (Eqn. 1).

Statistical analysis: Amphipod consumption rates on individual fresh thalli sections were determined by adjusting the final wet weight based on changes in the subsequent autogenic control and using a series of 1-sample t-tests comparing the mean feeding rate to 0 ($\alpha < 0.05$; SAS 9.2, SAS Institute Inc., Cary, NC, USA). Changes between feeding rates on fresh thallus pieces were determined using a set, one for each amphipod species, of one-way analysis of variance (ANOVA) and Tukey multiple-comparison tests to examine significant differences ($\alpha < 0.05$; SAS 9.2). Choice experiments involving consumption of the alginate control and extract pellets were analyzed using a Wilcoxon signed ranks test. This is a non-parametric one-way equivalent of a paired-samples t-test designed for related samples with a standard level of significance set at $\alpha < 0.05$ (SPSS 10.0, SPSS Inc., Chicago, IL, USA).

Results

Fresh thallus bioassay: Results from the fresh thallus bioassays indicate that neither amphipod species, *Gondogeneia antarctica* nor *Prostebbingia gracilis*, grazed on any of the finely branched macroalgae species examined in this study. Mean consumption rates of both amphipods on all finely branched macroalgae species used in this study were not significantly different from 0 (Fig. 1, $P > 0.05$). *G. antarctica* had significantly different feeding rates on the six algal species ($F_{4,45} = 10.41$, $P < 0.0001$) but the only alga it consumed was *Palmaria decipiens*, the bladed alga used in this study as a control.

There were no significant differences in consumption on any of the algae tested, including *Palmaria decipiens*, by *P. gracilis* (Figure 1, $F_{4,45}= 1.02$, $P = 0.405$). The consumption rates on all species were not found to be significantly different from 0 ($P > 0.05$).

Food pellet bioassays: Control pellets were consumed significantly faster than pellets with either lipophilic or hydrophilic extracts of *Pantoneura plocamioides*, *Picconiella plumosa*, *Cystoclonium obtusangulum*, and *Plocamium cartilagineum* (Fig. 2). The lipophilic extract from *P. cartilagineum* appears especially effective in deterring herbivory by *G. antarctica*. Artificial food pellets with extracts from *Halopteris obovata*, the finely branched brown macrophyte, were more heavily grazed than the control pellets, though not significantly ($P > 0.05$). There were no significant differences in *G. antarctica* consumption of control pellets versus those with either hydrophilic or lipophilic extracts from *Palmaria decipiens* ($P > 0.05$; Fig. 2).

Similar results were observed in artificial food pellet bioassays using *Prostebbingia gracilis*. Significant differences were seen between control pellets and those with either lipophilic or hydrophilic compounds for two of the finely branched red algal species, *Picconiella plumosa* and *Cystoclonium obtusangulum* ($P < 0.05$; Fig. 3). Pellets with lipophilic extracts from *Pantoneura plocamioides* and from *Plocamium cartilagineum* were also significantly less consumed than control pellets. However, hydrophilic extracts from these two algae did not significantly deter feeding by *P. gracilis* (Fig. 3). Lipophilic and hydrophilic extracts from both *Palmaria decipiens* and *Halopteris obovata* did not significantly deter feeding. In fact, *P. gracilis* consumed significantly more of the alginate pellet with hydrophilic extract than the control pellet (Fig. 3).

Discussion

Our findings indicate that finely branched red algae from the western Antarctic Peninsula are chemically defended against mesograzer herbivory. Fresh thallus pieces from all species tested, *Cystoclonium obtusangulum*, *Picconiella plumosa*, *Plocamium cartilagineum*, and *Pantoneura plocamioides*, were grazed by neither *Gondogeneia antarctica* nor *Prostebbingia gracilis* in no-choice experiments. Furthermore, artificial alginate control pellets were consumed significantly more by both amphipod mesograzers than similar pellets containing natural concentrations of either lipophilic or hydrophilic algal extracts. This indicates that secondary metabolites produced by these algae have anti-mesograzer properties, and that the ecological relationship between these common amphipods and algae is, at least in part, chemically mediated.

Several previous studies have investigated the importance of natural products in rhodophytes, the richest division of algae in terms of secondary metabolite diversity and abundance (Munro & Blunt 2005). To date, over 1,500 different compounds have been found in red algae, along with representatives in all major classes of natural products except the phlorotannins (Maschek & Baker 2008). Terpenes, mainly isoprenoid and acetogenin derivatives, are recognized as the primary class of defensive metabolites in red algae (Harper et al. 2001). A majority of these defensive compounds (~60%) come from the family Rhodomelaceae (Maschek & Baker 2008), whose only member represented in the present study was *Picconiella plumosa*. Additionally, rhodophytes produce an impressive array of halogenated compounds, which have in some instances been shown to possess anti-herbivory properties (e.g. Ankisetty et al. 2004), anti-fouling activity (e.g. Steinberg et al. 2002), or function as intracellular signal antagonists (e.g. Rasmussen et al. 2000). However, definitive proof of the ecological roles of such compounds is still in question (e.g. Sudatti et al. 2008). Algal families known to produce halogenated compounds include Plocamiaceae and Delesseriaceae (Bates et al. 1979), which include *Plocamium cartilagineum* and *Pantoneura plocamioides*, respectively. Ankisetty *et al.* (2004) found that *P. cartilagineum* from the western Antarctic Peninsula produced halogenated monoterpenes which deterred amphipod feeding. However, bioassay-guided isolations are needed to differentiate the identity of the secondary metabolites that function as chemical deterrents against various herbivores.

Most lipophilic and hydrophilic extracts of filamentous red algae in the present study demonstrated significant anti-grazing effects, although it appears that these algae depend more on lipophilic rather than hydrophilic secondary metabolites for chemical defenses against mesoherbivory. With respect to the mesograzer *Prostebbingia gracilis*, the mean difference between consumption of the control versus the pellets containing lipophilic extracts was 64% greater than the respective difference between hydrophilic extract pellets and their controls. This difference increases to 68% in corresponding experiments using *Gondogeneia antarctica*. Hydrophilic extracts of two of the macroalgae tested, *Plocamium cartilagineum* and *Pantoneura plocamioides*, did not deter grazing by *P. gracilis*. Additionally, *P. gracilis* consumption of alginate pellets was <10 mg. when pellets contained lipophilic extracts of *P. cartilagineum*, *Picconiella plumosa*, or *Cystoclonium obtusangulum.* These were much lower than consumption rates on any of the hydrophilic extract pellets combined, regardless of macroalgal or amphipod grazer.

Amsler *et al.* (2005a) found that 45% of the ecologically relevant macroalgal species along the western Antarctic Peninsula were unpalatable to macrograzers (sea stars and fish) due to their chemical defenses. Many of these species, including *Plocamium cartilagineum* and *Picconiella plumosa*, were also found to be chemically defended against the mesograzer amphipod *Gondogeneia antarctica* (Amsler et al. 2005a). The present study reinforces those findings and broadens the list of mesoherbivores shown to be chemically deterred to include *Prostebbingia gracilis*, an amphipod more often associated with finely branched red algae (Huang et al. 2007). The broadening array of consumers, both macro- and mesograzers, chemically deterred by these algae suggests more of a generalist defensive strategy than one in which natural products are grazer-specific. This defensive strategy has regularly been considered to be most favorable in marine communities with a diverse assortment of generalized herbivores (Hay & Fenical 1988, Hay et al. 1990).

One filamentous macroalgal species that did not coincide with previously reported results was *Pantoneura plocamioides*. Amsler *et al.* (2005a) reported that *P. plocamioides* thallus was rejected by *Notothenia coriiceps*, an omnivorous fish, but did not deter feeding in the omnivorous sea star *Odontaster validus*. Additionally, extracts from *P. plocamioides* were accepted by *N. coriiceps* and the amphipod *Gondogeneia antarctica*. Although no work was done with macrograzers in the present study, our results suggest that some lipophilic secondary metabolite(s) produced in *P. plocamioides* may provide chemical defenses against both the amphipods *G. antarctica* and *Prostebbingia gracilis*. Moreover, secondary metabolites in the hydrophilic extract of *P. plocamioides* were also an effective grazing deterrent against *G. antarctica*. The reason for this discrepancy is unclear. Amsler *et al.* (2005a) reported that volumetric extract yields in *P. plocamioides* were 40.6 and 14.0 mg dry extract per ml wet thallus for lipophilic and hydrophilic extracts, respectively. These numbers are very similar to the volumetric extract yields for lipophilic (45.0 mg dry extract per ml wet thallus) and hydrophilic (17.1 mg dry extract per ml wet thallus) found in this study. Individual specimen health and extract disparity along with annual variation in secondary metabolite production may have contributed to the difference in these results.

The finely branched brown alga *Halopteris obovata* and bladed red alga *Palmaria decipiens* yielded unique results. Thalli from *P. decipiens* were readily consumed by the amphipod *Gondogeneia antarctica*, and feeding rates were comparable to previous studies (0.125 mg hr^{-1} ind^{-1}; Huang *et al.*, 2006), although Huang *et al.* (2006) reported that "amphipod species exhibited significantly different consumption rates of algae on different days". Conversely, Huang *et al.* (2006) reported similarly high consumption rates by *Prostebbingia gracilis* on *P. decipiens* thallus, while our results indicate little to no grazing by *P. gracilis* on *P. decipiens*. Separate individual amphipod no-choice grazing experiments conducted in spring 2007-2008 showed reduced *P. gracilis* grazing rates on thallus from *P. decipiens* as well (Amsler et al. 2009c). In all studies, however, there has been a clear lack of chemical defense in *P. decipiens* (Huang et al. 2006), as there was no significant difference in amphipod consumption of control pellets versus those containing extracts of *P. decipiens*.

Halopteris obovata, a finely branched brown algae, was also not eaten by either amphipod in fresh thallus bioassays, but does not appear to be chemically defended based on results from the pellet bioassays. Amsler *et al.* (2005a) reported similar results, that although fresh thallus was rejected by the fish *Notothenia corriceps*, its extract did not deter grazing by *Gondogeneia antarctica*. There are several other types of algal defenses that may deter feeding. Structural defenses (Van Alstyne & Paul 1992, Van Alstyne et al. 1992, Steneck & Dethier 1994), nutritional content (Duffy & Paul 1992, Hay et al. 1994), and associations with protective hosts (McQuaid & Froneman 1993, Littler et al. 1995, Hay 1996, Stachowicz & Hay 1996) have all been proven effective at deterring marine herbivores. Relatively low thallus protein levels found in early season specimens of *H.*

obovata, compared to other brown algae, suggest that it may be a poor nutritional choice for herbivores (Peters et al. 2005). Toughness measurements (penetrometry) indicate that *H. obovata* thallus requires more force to puncture than any of the other alga in the present study with the one exception of *Cystoclonium obtusangulum*, which was not tested (Amsler et al. 2005a). These physical and chemical attributes may be the reason *H. obovata* is protected from mesoherbivory while lacking chemical deterrents. It is also possible that grazing deterrent compounds were degraded during the extraction process and/or became inactive from splitting the active compounds into two different extracts.

Overall, our collective observations that finely branched rhodophytes are chemically defended against two prominent mesograzers along the western Antarctic Peninsula suggest that filamentous material found in amphipod guts are not these algae despite their documented association with rhodophytes (Huang et al. 2007). Possibly, these unknown algal filaments are remnants of epiphytes or emergent filaments of endophytes, continually grazed by the extensive mesograzer community (as predicted by Peters 2003) and therefore rarely observed. Further research employing isotopic signatures and/or molecular techniques may identify this unknown algal material. If paraphytic in nature, it is possible that mesograzers occur in mutualism with their macroalgae hosts; living within the protective confines of chemically defended algae while continually grazing on epiphytes potentially harmful to the host alga (Amsler et al. 2009a, Amsler et al. 2009c). It is also possible that amphipods are merely grazing on the reproductive filaments emanating from endophytes within their macroalgal hosts. Several studies, including one recent survey, have indicated the prevalence of several species of endophytes scattered throughout western Antarctic Peninsular macrophytes

(Peters 2003, Amsler et al. 2009a). Many complex inter-relationships between mesograzers, macroalgae, and microalgae along the western Antarctic Peninsula are apparent. Future studies are necessary to clarify the nature of these relationships.

Acknowledgements

We are appreciative of Gil Koplovitz, Maggie Amsler, Philip Bucolo, Alan Mascheck, Dr. Jill Zamzow and the rest of our 2007 and 2008 Antarctic field team colleagues for their laboratory and field assistance. We would also like to thank Dr. Robert Angus for his statistical assistance. This project would not have been possible without the hard work and outstanding logistical support in Antarctica from the employees and sub-contractors of Raytheon Polar Services Company. This work was supported by National Science Foundation awards OPP-0442769 (CDA, JBM) and OPP-0442857 (BJB).

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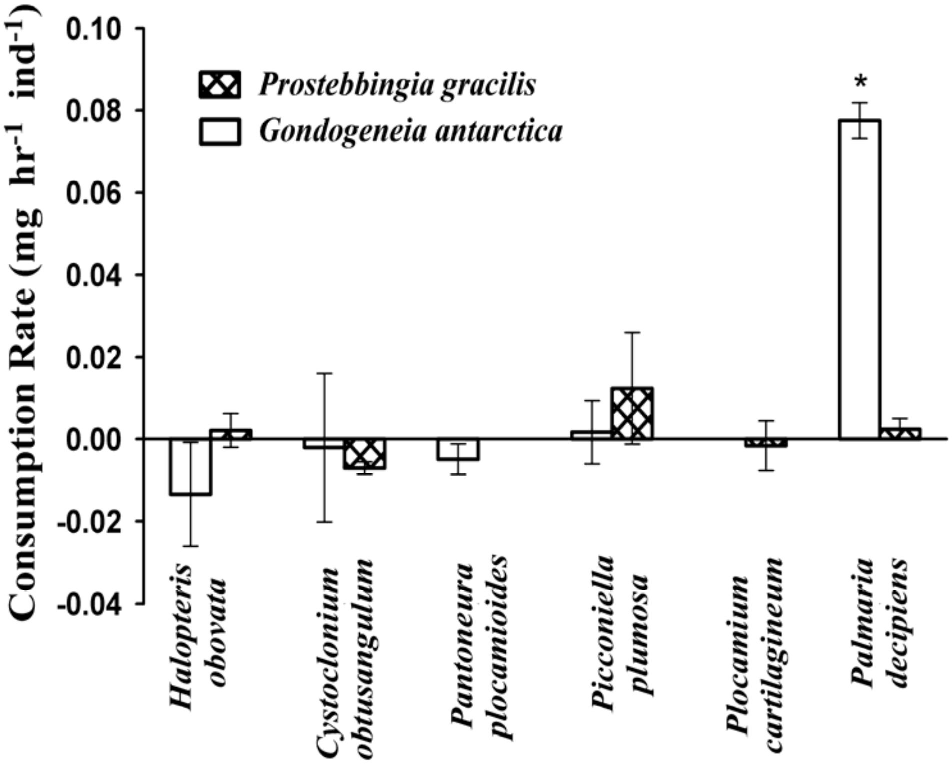

Figure 1: Consumption rate (mg h^{-1} ind^{-1}) of fresh thallus tissue by the endemic Antarctic amphipods *Gondogeneia antarctica* and *Prostebbingia gracilis*. Means ± standard error. Asterisk indicates significance (analysis of variance) between consumption rates ($p \leq 0.05$).

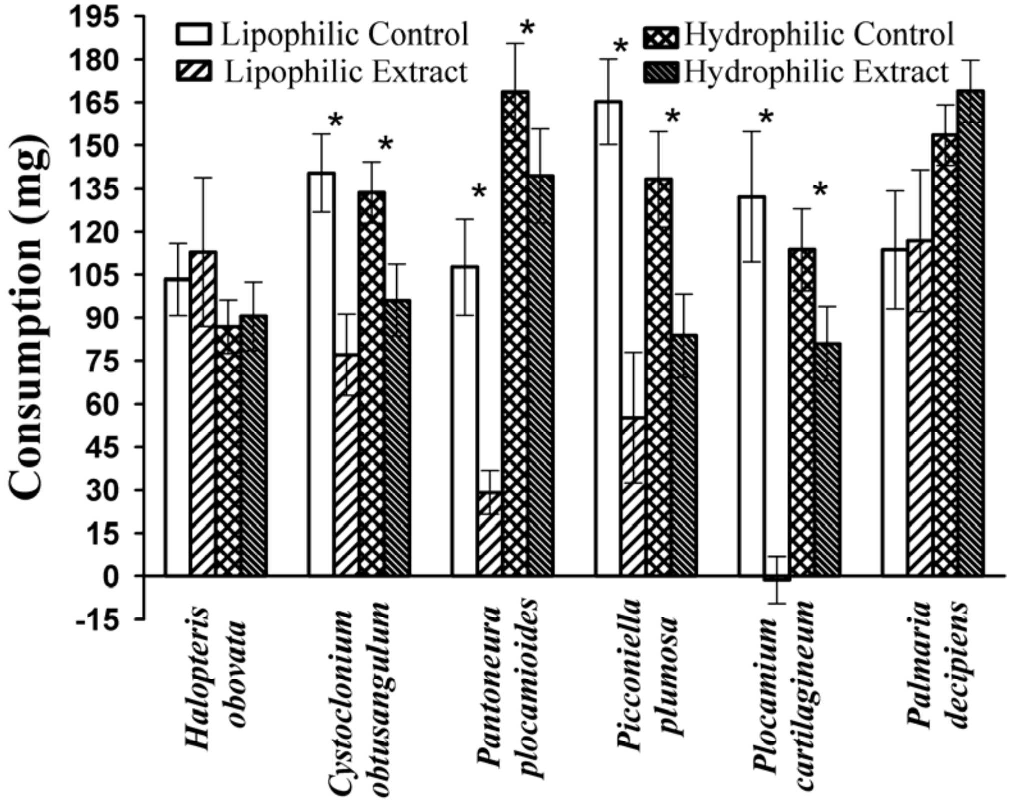

Figure 2: Results of bioassays offering artificial foods containing lipophilic or hydrophilic algae extracts to the endemic Antarctic amphipod *Gondogeneia antarctica* as a measure of total consumption (mg). Means ± standard error. Asterisks indicate significant difference between extract and control pellets (Wilcoxon signed ranks test; $p \leq 0.05$).

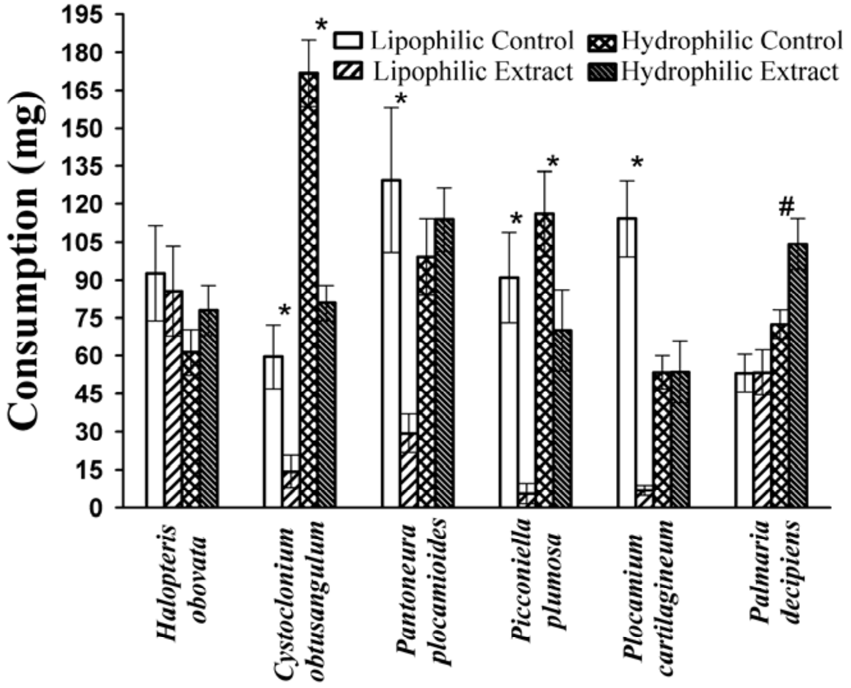

Figure 3: Results of bioassays offering artificial foods containing lipophilic or hydrophilic algal extracts to the endemic Antarctic amphipod *Prostebbingia gracilis* as a measure of total consumption (mg). Means ± standard error. Asterisks indicate significantly greater consumption on control pellets than extract pellets while # indicates significantly greater consumption on extract pellet than control pellet (Wilcoxon signed ranks test; $p \leq 0.05$).

CHANGES IN AMPHIPOD DENSITIES AMONG MACROALGAL HABITATS IN DAY VERSUS NIGHT COLLECTIONS ALONG THE WESTERN ANTARCTIC PENINSULA

by

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Submitted to:
Marine Ecology Progress Series

Submission No. 6948
October, 13, 2010

Format adapted for dissertation

ABSTRACT:

It is hypothesized that amphipods in the Western Antarctic Peninsula are able to limit predation by taking refuge among chemically defended macroalgae. Previous studies have reported significantly greater numbers, and densities, of amphipods among macroalgal species that are unpalatable to higher order predators while palatable macroalgae were less inhabited. However, nothing is known about amphipod activity at night in this community. If foraging on non-chemically defended macroalgae regularly occurs, then nocturnal lifestyle seems beneficial since larger vision based-predators, like the omnivorous fish *Notothenia coriiceps*, are disadvantaged. To test this hypothesis, we collected replicates of three different species of common macroalgae, and affiliated mesograzers, approximately three hours before and after sunset. All associated mesofauna were counted and densities calculated based on their respective numbers and corresponding macroalgal weights. Results indicated that amphipod densities are significantly decreased during the night on the chemically defended phaeophyte *Desmarestia menziesii* while significantly increased on the rhodophyte *Iridaea cordata* which is palatable to fish. Additionally, the amphipod *Gondogeneia antarctica* was found in significantly higher densities at night on the non-defended rhodophyte *Palmaria decipiens*, a species that has been shown to be readily eaten by *G. antarctica*. We believe that chemically defended macroalgae act as a refuge for many of mesograzers during the day, while more widespread foraging occurs at night. The macroalgae likely benefit from this relationship since the extensive amphipod assemblage, whose diet includes an array of diatoms and other fouling microalgae, is able to routinely clean their hosts of potentially harmful epiphytic organisms.

INTRODUCTION

Benthic communities along the Western Antarctic Peninsula possess several unique qualities which make them ideal for studying macroalgal-herbivore interactions. The area is dominated both in biomass and benthic coverage by large stands of perennial brown macroalgae, primarily in the order Desmarestiales, as well as scattered red macrophytes that together can average between 1.64 to 6.34 kg wet mass m^{-2} and cover ~ 85% of benthic substratum (Amsler et al. 1995). In comparison to other macroalgal dominated areas, these numbers are comparable to temperate kelp communities. Additionally, the Western Antarctic Peninsular communities are home to exceptionally dense mesograzer populations, primarily comprised by gammarid amphipods whose densities have been estimated to be as high as 300,000 individuals m^{-2} benthos (Amsler et al. 2008). Despite the exceedingly high density of mesoherbivores, there is little evidence that direct feeding on the dominant macroalgae has any substantial community affects. All the ecologically dominant phaeophytes and most of the contiguous rhodophytes are unpalatable to a suite of herbivores, including the two abundant amphipod species, *Gondogeneia antarctica* and *Prostebbingia gracilis* (Amsler et al. 2005a, Amsler et al. 2009b, Aumack et al. 2010).

Although some amphipods in the community associate with sessile invertebrates (Amsler et al. 2009d), most appear to live in association with the dominant macroalgae. However, there is a strong inverse relationship between amphipod abundance and feeding preference. Huang et al. (2007) showed that the phaeophyte *Desmarestia menziesii* and rhodophyte *Plocamium cartilagineum* had amphipod densities averaging 20.05 and 5.91 individuals g^{-1} algae wwt respectively, despite being two of the more chemically defended macroalgal species. In contrast, two palatable species of red algae, *Palmaria decipiens* and *Iridaea cordata*, had associated amphipod densities of only 0.26 and 0.10 individuals g^{-1} algae wwt respectively. This preference is probably the result of a combination of several factors. For example, the omnivorous fish *Notothenia coriiceps* is a primary amphipod predator which readily grazes on both *P. decipiens* and *I. cordata* (Iken et al. 1997, Iken et al. 1999) but finds *D. menziesii* unpalatable (Amsler et al. 2005a). Amphipod preference toward *D. menziesii* may be an ecological strategy to avoid predation by living in the protective confines of chemically defended species, while avoiding palatable species which may raise mortality via increased prey attractiveness or shared doom (Wahl & Hay 1995, Hay 1996). Macroalgal structural complexity may also affect amphipod host choice. Zamzow et al. (2010) reported that, given a choice, *P. gracilis*, preferred to affiliate with *D. menziesii* and a similar, highly-branched plastic analog over the bladed *P. decipiens* and other simple-structured plastic models. Regardless, it is evident that amphipod distribution is not random throughout the benthos and that structurally complex, chemically defended macroalgae are preferred hosts.

All of these studies, including the initial density counts by Huang et al. (2007), were either conducted during the daylight hours or indoors using illuminated aquaria. Nighttime amphipod distributions have never been investigated along the Western Antarctic Peninsula, an Antarctic region with continuous day and night cycles, and nocturnal activity is not uncommon in a variety of amphipod species. Several studies have shown that various amphipod species from temperate regions are more active at night (Brawley 1992, Grabe 1996, Ide et al. 2006, Forward et al. 2007). Buschmann (1990) showed that amphipod densities in Central Chile increased on *Mazzaella* *laminaroides*, a preferred food source, at night while amphipod densities on other macroalgae remained unchanged. If macroalgal host preference is a partial result of predator avoidance, nighttime distributions, when visual predators like *Notothenia coriiceps* are less successful, may be different from the daytime (Donatti & Fanta 2002). The objective of this study was to look for differences between both day and nighttime mesograzer density distributions on several macroalgal species. We hypothesized substantial increases in mesograzer association with palatable macroalgae species at night when foraging may entail less predation risk from sympatric fish populations.

MATERIALS AND METHODS

Collections: Four individuals from three different species of macroalgae were collected via SCUBA on each of four separate occasions in late April, 2008 (austral autumn) from Hero Inlet near Anvers Island, Antarctic Peninsula (64° 46.5' S, 64° 03.3' W; for map see Amsler 2005, 2009a). Hero Inlet is a relatively shallow site whose rocky benthos is distinguished by fine silt from glacial runoff. Two of the macroalgal species were rhodophytes, *Palmaria decipiens* (Reinsch) RW Ricker and *Iridaea cordata* (Turner) Bory, and the other was the phaeophyte *Desmarestia menziesii* J Agardh. These macroalgae were chosen based on their differences in daytime amphipod densities and also their abundances in Hero Inlet, whose close proximity to Palmer Station allowed logistically safer nighttime SCUBA operations. Two individuals from each species were collected at depths ranging from 3-4 m. three hours before darkness (~14:30 local Palmer time). Each collected individual's thallus was carefully detached from the substrate and gently floated into a mesh collecting bag (<0.5 mm) to minimize loss of associated epifauna (Huang et al. 2007).

After daytime collections, six new macroalgae (two individuals per species) were tagged for nighttime collections and a lighted buoy attached to a bottom weight was deployed to mark the exact macroalgal beds sampled for comparison between day and night sampling. That same evening about three hours after darkness (~21:00 local Palmer time), divers returned to the collection site and carefully removed the second set of pre-marked individuals using only small, dim dive lights with red light filters to minimize amphipod attraction/repulsion.

After both day and night collections, the algae were submerged in buckets of seawater and immediately transported back to Palmer Station for processing. At Palmer, the macroalgae were repeatedly 'dunked' in seawater followed by freshwater to remove all associated mesoherbivores. All algae were then weighed while their respective mesoherbivores were collected and preserved in 70% ethanol. For denser samples from *Desmarestia menziesii*, a plankton splitter was used to equally fractionate mesograzer collections. Each set of preserved mesoherbivores was subsequently sorted, identified to the lowest taxonomic level possible, and counted. Counts were reported in numbers per species per gram wet weight host alga.

Statistical Analysis: Density differences for several general taxa, including specific densities for several amphipod species, were determined using a series of Student's t-tests comparing the interspecific means for daytime versus nighttime collections ($\alpha < 0.05$; SigmaPlot 11.0, Systat Software Inc, San Jose, CA, USA).

RESULTS

Major taxa: Although many invertebrate taxa were collected in day and night collections, four were found throughout all samples in higher densities (copepods, ostracods, gastropods, and amphipods). Copepods, almost exclusively calanoid species, ranged between 2.4 – 26.1 individuals g^{-1} algal wwt with no discernable differences between day and nighttime densities on either *Palmaria decipiens* or *Desmarestia menziesii*. There were significantly greater densities of copepods associated with *Iridaea cordata* at night ($P < 0.05$, Figure 1). Interspecific species comparisons showed that were significant differences between the three algal species ($p = 0.005$), with nighttime *I. cordata* copepod densities being significantly greater than either day or night *D. menziesii* copepod densities (Figure 1A).

Ostracods, which were not differentiated to lower taxonomic levels, ranged between 1.5 – 10.9 individuals g^{-1} algal wwt and were not found to differ between daytime and nighttime densities in any macroalgal species ($P > 0.05$; Figure 1B). However, interspecific comparisons indicated that ostracods are found in significantly greater densities on *Desmarestia menziesii* than on *Palmaria decipiens* ($P < 0.001$; Figure 1B). There were no significant differences between gastropod distributions, on any macroalgal species or in day versus night comparisons ($P > 0.05$; Figure 1C). Although the majority of gastropods were likely *Cerithiopsilla* spp. and *Laevilacunaria antarctica*, no individual species specific counts were conducted.

Collectively, amphipods ranged from 4.8 – 22.2 individuals g^{-1} algal wwt throughout the three macroalgal species collected. Although there was no day versus night difference between amphipod densities on *Palmaria decipiens*, there were statistically significant differences on the other two algal species (Figure 1D). For *Desmarestia menziesii*, there was a significant average decrease in total amhipod density at night compared to day (P = 0.029). In contrast, amphipod densities on *Iridaea cordata* during the daytime increased significantly at night (P = 0.014). Interspecifically, amphipods were found in significantly greater densities on *D. menziesii* during the daytime (P < 0.001) while there were no significant density differences between nighttime distributions on *D. menziesii*, *I. cordata*, or *P. decipiens*.

Amphipods: Some individual amphipod species also demonstrated nocturnal habitat selection. Both amphipod species from the family Calliopiidae, *Metaleptamphopus pectinatus* and *Oradarea* spp., had densities that were significantly greater during daytime on *Desmarestia menziesii* than at night (p = 0.01 and p = 0.005, respectively; Figure 2). Additionally, both *M. pectinatus* and *Oradarea* spp. were found at significantly higher densities on *Iridaea cordata* at night than during the day (p = 0.049 and p = 0.026, respectively; Figure 2). *Prostebbingia gracilis* also had significantly higher densities on *D. menziesii* during the day than during the night (p = 0.025; Figure 2) but showed no differences between daytime and nighttime abundances on neither *I. cordata* nor *P. decipiens*.

Gondogeneia antarctica, an omnivorous amphipod from the family Gammarellidae, showed no significant density differences between day and nighttime inhabitation of *Desmarestia menziesii*. However, *G. antarctica* densities were significantly less in the daytime on *Palmaria decipiens* and *Iridaea cordata* than at night

(P = 0.008 and P = 0.025; Figure 2). *Gitanopsis squamosa*, a smaller amphipod from the family Amphilochidae, also had an average nighttime density on *I. cordata* that was significantly higher than its corresponding daytime density (P = 0.017; Figure 2). Two amphipod taxa, identified only to family, Ischyroceridae and Stenothoidae, did not show any significant density differences between night and day samples on any of the macroalgae species studied (Figure 2).

DISCUSSION

It is hypothesized that the immense amphipod assemblage in the Western Antarctic Peninsula is able to limit predation by taking refuge among chemically defended macroalgae (Amsler et al. 2005, 2008, 2009a, Huang et al. 2006, 2007, Aumack et al. 2010, 2011, Zamzow et al. 2010). Huang et al. (2007) showed that amphipods in this community reside in significantly higher densities among chemically defended species like *Desmarestia menziesii*, *Desmarestia anceps*, and *Plocamium cartilagineum* (Amsler et al. 2005a) than among palatable species. In support of this, we found that amphipods, collectively, were in the highest densities among *D. menziesii* during the daytime (Figure 1D) at levels (22.2 individuals g^{-1} algal wwt) very similar to those reported by Huang et al. in 2007 (20.1 individuals g^{-1} algal wwt). However, in direct contrast, amphipods densities among *D. menziesii* at night were not statistically different from amphipod densities on *Iridaea cordata*, a structurally simpler macroalga which is palatable to fish (Iken et al. 1997, Amsler et al. 2005a). It appears that many amphipod species may be using chemically defended macroalgae as shelter during the day, while migrating to more palatable species at night when there is less risk from visual predators.

Total daytime amphipod densities on the two reds were noticeably higher than those reported by Huang et al. (2007). Our daytime densities were 4.0 and 4.8 individuals g^{-1} algal wwt on *I. cordata* and *Palmaria decipiens*, respectively while Huang et al. (2007) reported densities of 0.1 and 0.3 individuals g^{-1} algal wwt on the same respective algae. This could have been a result of differences between collecting sites. Huang et al. (2007) collected algal-associated amphipods from several offshore island sites around Palmer Station whose shallow subtidal algal coverage is fairly continuous. However, the algal beds where we collected in Hero Inlet have a more patchy distribution, likely, creating an island affect for mobile amphipods.

Four different individual amphipod taxa (*Gitanopsis squamosa*, *Gondogeneia antarctica*, *Metaleptamphopus pectinatus*, and *Oradarea* spp.) were all found associated with *Iridaea cordata* at night in significantly higher concentrations than during the day. The two taxa from family Calliopiidae (*M. pectinatus* and *Oradarea* spp.) were also collected in significantly lower densities among *Desmarestia menziesii* at night (Figure 2). This suggests a direct foraging strategy, remaining in the protective confines of chemically defended *D. menziesii* during the day while migrating to more palatable *I. cordata* at night. Although gut content analyses (Aumack, unpublished) indicate that both these species are most often consuming epiphytic algae (particularly diatoms), this does not necessarily contradict the idea of nocturnal migration to non-defended macroalgae. Epiphytic food sources may be limited by continual grazing from the widespread amphipod assemblage that inhabits *Desmarestia menziesii* during the day. This may be exacerbated during the long periods of daylight that occur during austral summers on the Antarctic Peninsula. Additionally, certain macroalgal species may be more susceptible to biofouling than others. In a separate mesocosm study, it was shown that *Desmarestia anceps* maintained very little epiphytic fouling (< 7% surface area) even after a 7 week incubation period without mesograzers while other macroaglal species had ~50% epiphytic coverage after the same treatment (Aumack et al. 2011). Even though the similar *D. menziesii* was not used in that study, it is possible that it may exhibit the same anti-fouling potential, thereby substantially reducing available prey to amphipods.

Gondogeneia antarctica was also found in significantly higher densities at night than during the day on *Iridaea cordata* although there were no differences between day and night densities of *G. antarctica* on *Desmarestia menziesii* (Figure 2). *G. antarctica* was also the only species of amphipod that was found associated with *Palmaria decipiens* in significantly greater densities at night than during the day (Figure 2). This could be directly related to feeding preferences. Many studies have indicated that *P. decipiens* is not chemically defended (Amsler et al. 2005, 2009a, Huang et al. 2006, Aumack et al. 2010, P. Bucolo, unpublished) but it is not directly grazed in fresh thallus assays by *Prostebbingia gracilis* (Aumack et al. 2010, P. Bucolo, unpublished), *Oradarea bidentata*, *Metaleptamphopus pectinatus*, nor *Paraphimedia integricauda* (P. Bucolo, unpublished). Despite its lack of chemical defenses, the lack of direct grazing on *P. decipiens* by these amphipod species could explain the lack of any day versus nighttime differences in amphipod density. *G. antarctica*, however, was the lone amphipod species separately enumerated in this study which readily consumes fresh thallus material of *P. decipiens* (Amsler et al. 2009a, Aumack et al. 2010), a fact that could explain its significant increase in nighttime densities.

Two other amphipod species appear to have nocturnal foraging strategies as well. *Gitanopsis squamosa* was found among *Iridaea cordata* in significantly greater densities at night than during the day, but had no significant difference between day and night densities on *Desmarestia menziesii*. Oddly, overall *G. squamosa* densities on *D. menziesii* are substantially lower than all the other individual amphipods tabulated with exception to those in family Ischyroceridae (Figure 2). Although it appears that *G. squamosa* may migrate to *I. cordata* at night, its daytime residence remains a mystery. There is an opposite pattern with *Prostebbingia gracilis*. It is found in the greatest densities on *D. menziesii* during the day with a significant reduction at night (Figure 2). However, there is no corresponding nighttime increase in density from either of the two palatable macroalgae that were studied. Future night and daytime amphipod comparisons on other macroalgal species may provide further clarity into the foraging habits of these particular amphipod species.

Amphipods from families Stenothiodae and Ischyroceridae were the only amphipods enumerated that did not have any significant differences between their day and nighttime densities on any of the macroalgal species studied (Figure 2). Stenothiodae are micrograzers, much smaller than the other amphipod species counted. Consequently, they may be at less risk of predation by large macrofauna, like *Notothenia coriiceps*, than smaller omnivorous or predatory amphipod species. The risk of incidental consumption by fish while occupying palatable macroalgae is probably offset by the risks of inhabiting chemically defended macroalgae with larger abundances of omnivorous/predatory amphipods. In this case, unnecessary diel movement from one macroalga to another would be energetically unfavorable while food is in abundance. Since these micrograzers are typically characterized as detritovores, it seems reasonable that they are not resource limited in Hero Inlet, a site characterized by a silty bottom. This could explain their general lack of overall macroalgal species preference (Figure 2). A similar strategy could be used by amphipods of the family Ischyroceridae, many of which are *Jassa* spp. or *Parajassa* spp. (Richardson 1977). These amphipods are not foragers but, primarily, are suspension feeders and sedimentary tube dwellers (Franz & Mohamed 1989, Scinto et al. 2007). As such, there is probably no need to move between macroalgae. There were considerably higher Ischyroceridae densities found on both *Palmaria decipiens* and *Iridaea cordata* than on *Desmarestia menziesii*, an irregular trend considering the general amphipod assemblage's preference of the chemically defended, more structurally complex *D. menziesii*. Although we did not record amphipods by size, a particularly high percentage of Ischyroceridae were either juvenile or gravid females at the time of capture. Life-cycle studies of *Jassa* spp. in temperate regions showed that the greatest number of juveniles occurred in spring with the peak number of juveniles occurring in April (Nair & Anger 1980, Scinto et al. 2007). Possibly the greater densities of Ischyroceridae, especially juveniles, among the two palatable rhodophytes is an escape response from omnivorous or predatory amphipod species who preferentially use *D. menziesii* as a refuge from predation themselves.

In conclusion, we believe that chemically unpalatable macroalgae shelter a number of mesograzers from visual predators during the day, while more widespread foraging occurs at night when visually based fish predators are less likely to feed effectively. Although it is apparent that some amphipod species do not migrate between hosts, several exhibit nocturnal behavior, selecting specific macroalgal species to inhabit.

This behavior implies some degree of behavioral adaptation in these mesograzers influenced, in part, by the chemical deterrents elaborated in the surrounding macroalgae. Clearly beneficial to amphipods, we hypothesize that the macroalgal flora may actually be living in mutualism with the mesograzer assemblage since the extensive amphipod assemblage, whose diet includes an array of diatoms and other fouling microalgae, is able to routinely clean their hosts of potentially harmful epiphytic organisms.

Acknowledgements. We thank Maggie Amsler, Philip Bucolo, Alan Maschek, Dr. Jill Zamzow, and the rest of our 2007 and 2008 Antarctic field team colleagues for their field assistance. This project would not have been possible without the hard work and outstanding logistical support in Antarctica from the employees and sub-contractors of Raytheon Polar Services Company. This work was supported by National Science Foundation awards OPP-0442769 (CDA, JBM) and OPP-0442857 (BJB) from the Antarctic Ecosystems and Organisms program and by an Endowed Professorship in Polar and Marine Biology to JBM provided by the University of Alabama at Birmingham.

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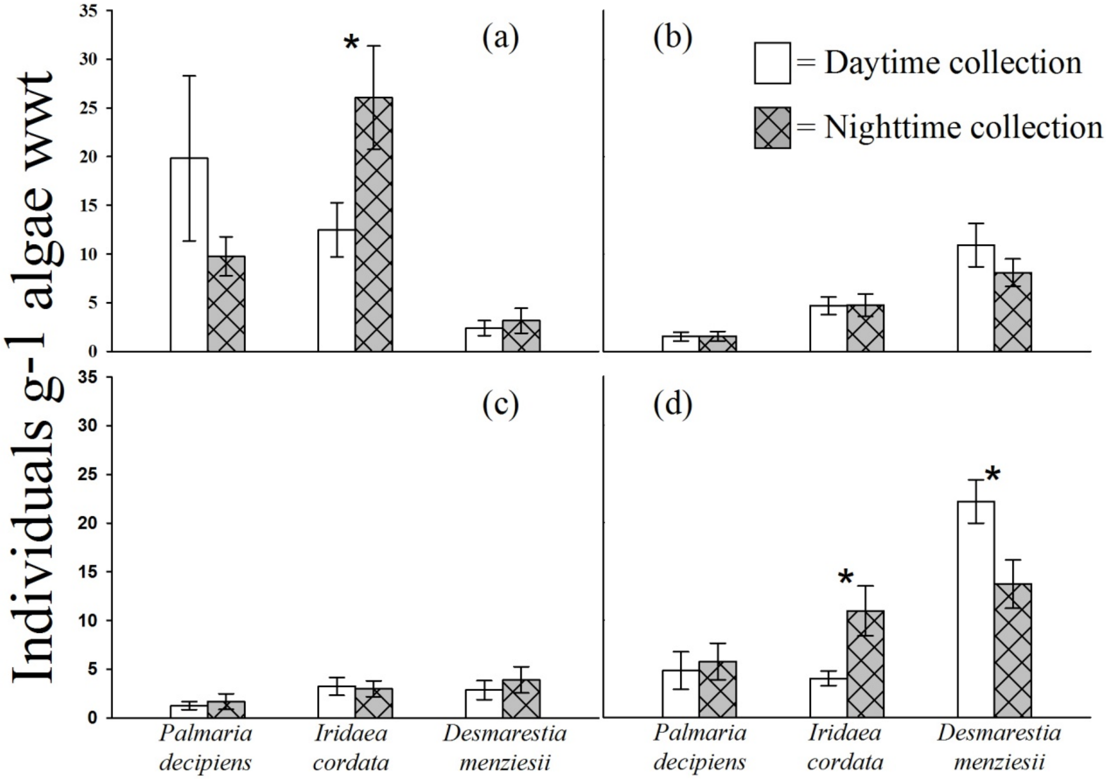

Figure 1: Day and nighttime densities (individuals g^{-1} algae wwt) of (a) copepods, (b) ostracods, (c) gastropods, (d) amphipods affiliated with *Palmaria decipiens*, *Iridaea cordata*, and *Desmarestia menziesii*. Means are ± standard error. Asterisks indicate significant difference (Student's t-test) between averages among species collected during the day versus night ($p<0.05$).

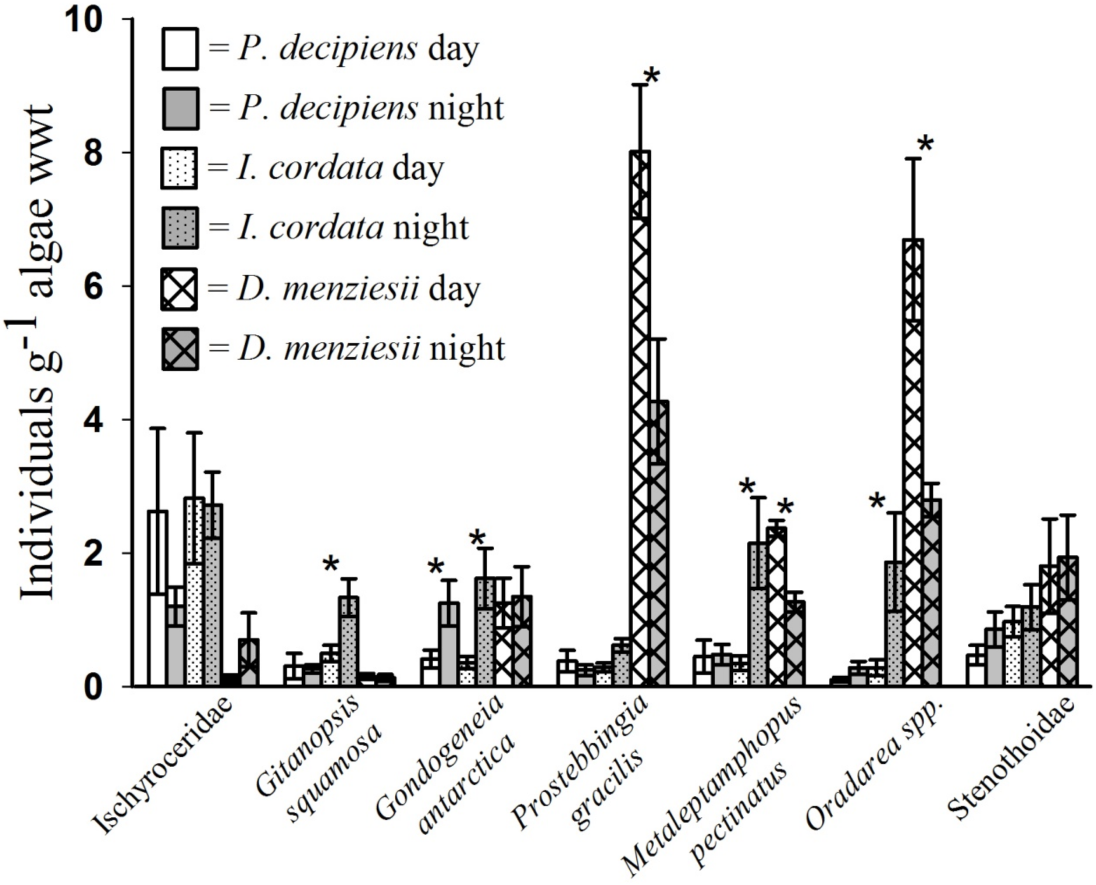

Figure 2: Day and nighttime densities (individuals g^{-1} algae wwt) of the individual amphipod species *Gitanopsis squamosa*, *Gondogeneia antarctica*, *Prostebbingia gracilis*, *Metaleptamphopus pectinatus*, *Oradarea* spp., and the amphipod families Ischyroceridae and Stenothoidae, affiliated with *Palmaria decipiens*, *Iridaea cordata*, and *Desmarestia menziesii*. Means are ± standard error. Asterisks indicate significant difference (Student's t-test) between average day and night densities ($p<0.05$).

IMPACTS OF MESOGRAZERS ON EPIPHYTE AND ENDOPHYTE GROWTH ASSOCIATED WITH CHEMICALLY DEFENDED MACROALGE FROM THE WESTERN ANTARCTIC PENINSULA: A MESOCOSM EXPERIMENT[1]

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Journal of Phycology, *in press*

Format adapted for dissertation

ABSTRACT

It has been hypothesized that the extensive mesograzer community along the western Antarctic Peninsula regulates epiphytic algae as well as emergent filaments from endophytic species. Should grazing limit growth of fouling or potentially pathogenic microphytes, then Antarctic macrophytes may actually benefit from the remarkably high densities of mesograzer amphipods that occur in these waters. Although initially counterintuitive, the negative impacts of epi/endophyte fouling may outweigh stresses caused by limited amphipod grazing on chemically defended macrophytes by reducing stress from endo/epiphyte biomass. If so, than alleviating mesograzing stress should result in significant increases in endo/epiphytic biomass. To test this hypothesis, a mesocosm experiment was conducted. Individuals representing four common species of Antarctic macroalgae were placed in flow-through seawater mesocosms. Amphipods were added to five mesocosms at simulated natural densities while the other five remained herbivore free. At the end of seven weeks, endo/epiphytic growth on individual macrophytes was quantified. Most species of macroalgae demonstrated noticeably higher instances of endophyte coverage, epiphytic diversity, and diatom colonization in consumer-free mesocosms than in the presence of amphipods. These data suggest that macroalgae along the western Antarctic Peninsula rely on grazers to control populations of potentially harmful epiphytes. We hypothesize that the chemically defended macroalgal flora lives in mutualism with high densities of mesograzers, providing amphipods with shelter from predation while continually being cleaned of potentially harmful endo/epiphytes.

INTRODUCTION

Shallow subtidal communities along the western Antarctic Peninsula provide a unique environment in which to study algal-herbivore interactions. The area is characterized by extensive macroalgal communities which can average between 1.64 to 6.34 kg wet mass m^{-2} (Amsler et al. 1995), comparable to temperate kelp dominated communities. However, in comparison to other macroalgal dominated regions, the macroalgae along the western Antarctic Peninsula are relatively free of fouling epiphytic macro- and microalgae (Peters 2003, Amsler et al. 2009a). Additionally, they are host to an unusually large and diverse array of mesograzers, primarily gammarid amphipods whose densities have been estimated as high as 300,000 individuals m^{-2} benthos (Huang et al. 2007, Amsler et al. 2008). Such high densities suggest there is only weak top-down control of mesograzers by predators.

What effects, collectively, do the immense mesograzer populations have on the macroalgal flora? In terms of direct grazing, there appears to be little evidence that amphipods have an important impact. All the dominant phaeophytes and most of the surrounding rhodophytes are chemically defended against an array of predators, including two of the most common grazing amphipods, *Gondogeneia antarctica* and *Prostebbingia gracilis* (Amsler et al. 2005a, Aumack et al. 2010*).* However, gut content analyses indicate that algal filaments make up a significant portion of both these amphipods' natural diets (C. Aumack, unpublished). The significant presence of filamentous algal material in amphipod guts is curious since there are almost no non-endophytic filamentous algae that occur in subtidal habitats of the western Antarctic Peninsula throughout most of the year (Peters 2003, Amsler et al. 2009a).

In contrast to this lack of uniseriate, filamentous macrophytes and epiphytes in the western Antarctic Peninsula, there is a wide array of filamentous endophytes throughout the community (Peters 2003, Amsler et al. 2009a). Amsler et al. (2009a) surveyed 13 common species of macroalgae and found that eight almost always had invasive filamentous endophytes growing within their tissues. Furthermore, Amsler et al. (2009a) demonstrated that, if left in culture under conditions that favored endophytic growth, erect filaments from endophytes would eventually protrude through the thalli of their macrophytic hosts. Peters (2003) hypothesized that the extensive mesograzer community affiliated with the western Antarctic Peninsula controlled epiphytic populations and evolutionary selected for an endophytic lifestyle. If this hypothesis is correct, then the elimination of mesograzer pressure should lead to an increase in fouling epiphytes that reduce macroalgal productivity (Brawley 1992). Although counterintuitive, the negative impacts of epi/endophyte fouling on macrophytic hosts (Sand-Jensen 1977, Duffy 1990, Short & Neckles 1999, Wear et al. 1999) may outweigh those caused by mesograzers. Hay and Fenical (1988) argued that most plant chemical defenses are directed against macrograzers, while the strategy against mesograzers, whose feeding activities cause significantly less structural damage, is that of tolerance. More recently, Toth and Pavia (2007) indicated that herbivory by small crustaceans and gastropods induced seaweed resistance and that the effects of induced responses were significantly greater after 11-20 days, a strategy combining tolerance with induced deterrents in response to continual grazing. However, amphipod feeding on epiphytic microalgae would cause significant structural damage to the microalgae, which may provide an inadvertent mechanism to defend macroalgae lacking chemical anti-fouling defenses, which otherwise would be highly susceptible to exterior epi/endophyte invasion.

The primary goal of the present study was to determine if the coverage of both epiphytes and endophytes growing on/within chemically defended macroalgae would significantly increase when released from mesograzer pressure. An additional goal was to determine if established endophytic colonies were more likely to produce erect filaments protruding from their associated macroalgal thalli if mesograzing pressure was removed.

MATERIALS AND METHODS

Collections: Thirty individuals each of four species of macroalgae were collected within 3.5 km of Palmer Station on Anvers Island, Antarctic Peninsula (64° 46.5' S, 64° 03.3'W; for map see Amsler 2005, 2009a). This included three pheophytes (*Desmarestia anceps* Montagne, *Desmarestia antarctica* RL Moe & PC Silva, and *Himantothallus grandifolius* [A&E Gepp] Zinova) and one rhodophyte (*Gymnogongrus turquetii* Hariot). The identification of *G. turquetii* was based on Wiencke and Clayton (2002) but it should be noted that Hommersand et al. (2009) have suggested that individuals of the morphology used here may in fact represent an undescribed species of *Hymenocladiopsis*. All individuals of each species were collected from the same locations. *D. antarctica, H. grandifolius,* and *G. turquetii* were chosen because a survey in the study area indicated nearly all individuals of each species had some endophytic colonies growing invasively within their tissues (Amsler et al. 2009a). In contrast, *D. anceps,* had only a few individuals with a low percentage of endophytes (Amsler et al. 2009a), and was used in the present study as a negative control. Macroalgae were collected by hand via SCUBA at depths ranging from 2 - 16 m in March 2008. After collection, the algae were submerged in buckets of seawater and immediately transported back to Palmer Station for processing. In the laboratory, macroalgal individuals were sorted by species and subsequently cleared of all mesograzers (primarily amphipods and gastropods) through agitation in repeated saltwater submersions. Detached herbivores were collectively enumerated and cleaned macroalgal individuals were temporarily held submerged in a flow-through seawater table equipped with ambient seawater pumped from the sea for pre-mesocosm processing.

Mesocosm Experiments: To examine the effects of grazing pressures on epiphytic growth, an outdoor mesocosm experiment was conducted at Palmer Station. Ten mesocosm tanks were constructed of heavy duty translucent plastic (76.2 x 76.2 x 61 cm. ~350 L each) and plumbed with continuous flow through, unfiltered seawater. Plankton mesh (63 μm) was fixed to the inflow pipes and to outflow valves of mesocosms to prevent incoming mesograzers as well as prevent their loss in those treatments seeded with mesograzers. Neutral density filter cloth was attached to the surface frame of each mesocosm to reduce surface irradiances to those measured at subtidal collection depths (~10% surface PAR).

At the start of the experiment, 30 individuals from each macroalgal species were randomly assigned to one of the ten mesocosm tanks (three individuals per species in each mesocosm). Macroalgae were either kept as sectioned laterals for larger species (*Desmarestia antarctica, Desmarestia anceps,* and *Gymnogongrus turquetii*), or were cut into similarly sized pieces (*Himantothallus grandifolius*) that contained no meristimatic tissue. All replicates contained at least one endophyte colony but macroscopic epiphytes and emergent endophytic filaments were absent in all individuals. Limited densities of epiphytic diatoms were present on the macroalgae. Each individual was inserted into braided rope on a frame at fixed, randomly determined positions. The rope frame was then affixed to a concrete substrate and loaded into one of the mesocosms. Among the ten mesocosms, five were randomly selected to include a full complement of mesograzers while the other five were maintained grazer-free. Mesograzer abundances were based on natural ranges of amphipod densities per unit algal wet weight associated with the macroalga *Desmarestia menziesii* J. Agardh as determined from field collections in the present study and those reported in previous studies (Amsler et al. 2005a, Huang et al. 2007). *D. menziesii* was chosen because the consistent abundance and diversity of amphipods associated this alga more regularly mirrors the collective macroalgal community. Mesograzer populations were collected from a wet weight of *D. menziesii* commensurate to that of the total wet weight of macroalgae placed into the collective five mesoherbivore-added mesocosms. Mesograzers were divided into five equal groups using a plankton splitter and each mesocosm provided with an equal compliment of mesograzers (primarily amphipods). According to Huang et al. 2007, there are no amphipod species found on any of the macroalgae used in the experiment that were not found associated with *D. menziesii* in comparable or larger concentrations. Three species (*G. turquetii*, *A. mirabilis*, and *H. grandifolius*) were not included in the study by Huang et al. However, when these macroalgal species were collected and subsequently had their mesograzers removed, none had any unique amphipods species associated with them that were not reported on *D. menziesii*. The same technique was used weekly to replenish any mesograzer loss attributable to mortality back to natural densities.

The mesocosms were maintained for a seven week period from mid-March to late May 2008, corresponding to the late Antarctic macroalgal growing season. Both pre- and post-individual macroalgal wet weights were measured using a portable top loading balance (Ohaus, Pine Brook, NJ, USA). The pre- and post-experiment percent coverage of both filamentous and microscopic epiphytes were quantified based on visual determination of 3-5 haphazardly located 10x visual fields of a dissecting microscope (Carl Zeiss Microimaging, Inc. Thornwood, NY, USA). Presence or absence of emerging filaments from invasive endophytic colonies was also recorded collectively among all specimens, regardless of species, following the seven week incubation period.

Statistical Analysis: Differences in wet mass gained, endophyte coverage, and epiphyte coverage were determined using a series of t-tests comparing the interspecific means for individuals held in mesocosms with and without mesograzers ($\alpha < 0.05$; SAS 9.2, SAS Institute Inc., Cary, NC, USA). Nominal comparisons between the total numbers of individuals possessing emergent filaments from endophytic colonies between the two treatments were made using a Chi-square goodness of fit ($P < 0.05$, k=2; SAS 9.2, SAS Institute Inc., Cary, NC, USA).

RESULTS

Weight Increase: The average initial weight of the individuals placed in mesocosms containing grazers was not significantly different from those kept free of grazing pressure (Figure 1). However, in three out of the four species, the average individual weight gain, based on percentage biomass, was significantly higher in mesocosms void of herbivores ($P < 0.05$; Figure 1). Laterals of both *Desmarestia antarctica* and *Gymnogongrus turquetii,* growing in mesocosms without herbivores, gained substantially more percent biomass (~12.5% and 5.0% respectively) than those growing in mesocosms with a full complement of mesograzers. *Himantothallus grandifolius* sections, growing among grazers, receded and lost ~5.5% biomass during the seven week incubation while similarly sized sections growing without grazers closely maintained their original biomass. There was no significant difference in weight gain between the two mesocosm treatments in *Desmarestia anceps* (Figure 1).

Endo/Epiphyte Coverage: Intraspecific specimens from all four species analyzed in this study did not contain any significant difference between the initial (pre-mesocosm) average percent of their tissues colonized by invasive endophytes (Figure 2). Although not shown, *Desmarestia anceps* laterals were chosen based on their containing at least one endophytic colony. However, all *D. anceps* laterals contained minute (<< 5%) amounts of endophytes that generally were almost indistinguishable.

At the end of the experiment, three species *(Desmarestia antarctica, Gymnogongrus turquetii,* and *Desmarestia anceps)* did not show any significant difference in endophyte percent coverage between mesocosms containing herbivores and those without (Figure 2). This includes *Desmarestia anceps,* in which all laterals post mesocosm incubation still contained endophytic colonies present in their tissues, albeit at quantities difficult to differentiate (<< 5%; <5% was the lowest category scored other than 0%). Additionally, there were no significant gains in endophytic growth throughout the course of the mesocosm incubation in these three species (Figure 2).

Himantothallus grandifolius, however, exhibited a significant increase in endophyte coverage through the course of the experiment both in mesocosms with and without mesograzers ($P < 0.05$; Figure 2). However, the average gain in individuals from mesocosms without grazers (41.0%) was significantly higher than in individuals from a grazer free environment (24.3%; Figure 2).

All individuals began the experiment with no macroscopic epiphytes and only limited amounts of fouling diatoms. After incubation, individuals of all species except *Desmarestia anceps* had significantly higher average percentages of their surface area covered by epiphytes when incubated without mesograzers than those incubated with mesograzers ($P < 0.05$, Figure 2). Epiphytes were mostly diatoms, but also included macroscopic filamentous phaeophytes, and some green algal epiphytes as well. Both *Desmarestia antarctica* and *Himantothallus grandifolius* displayed dramatic changes in epiphyte loads between the two treatments, with average coverage increasing ~50.0% in macroalgae from an herbivore free environment, mostly consisting of epiphytic diatoms. Although there were significant differences in average epiphyte coverage between the two treatments in *Gymnogongrus turquetii,* at ~15.0% difference the effects were not nearly as pronounced (Figure 2). With few exceptions, *Desmarestia anceps* surfaces all contained <7.0% coverage of epiphytes, including fouling diatoms, and were not statistically significant between the two treatments.

Emerging Filaments: No *Desmarestia anceps* individuals, regardless of mesocosm treatment, had any instances of emerging filaments growing out from endophyte colonies after the seven week incubation period. The other three species, however, had at least one occurrence. Of the 45 total individuals from the mesocosms with mesograzers, only four had emerging filaments from endophytic colonies protruding through their thallus. All four of these individuals were of the same species: *Desmarestia antarctica.* Of the 45 total individuals from mesocosms without consumers, a third contained at least one instance of emerging filaments from endophytic colonies. This included all species analyzed except *D. anceps.* Ten of the 15 *D. antarctica* individuals removed from the mesograzer free mesocosms contained emergent filaments. When emergent filaments from endophytic colonies have been observed in nature they are almost exclusively found early in the growing season on senescing second year *D. antarctica.*

DISCUSSION

Three out of the four species studied gained significant biomass when maintained free of herbivores while those kept with a full complement of grazers did not (Figure 1). Intuitively one would expect that the amphipods were consuming the macroalgae at rates that significantly reduce their growth compared to those protected from herbivores. However, all the species used in this study have been previously shown to be chemically defended against some of the most abundant macro- and mesograzers along the western Antarctic Peninsula (Amsler et al. 2005a, Amsler et al. 2009a). This fact, combined with the absence of bite marks or grazing patterns seen on the macroalgae themselves (personal observation) indicate that direct grazing cannot explain the reduced growth in algae maintained within mesocosms with herbivores. Rather, a substantial increase in epiphyte growth (mostly diatoms and some macroalgae) in individuals maintained in an herbivore-free environment accounted for the significant weight gain in those samples. The lone exception, *Desmarestia anceps,* is rarely seen fouled in the subtidal (authors' personal observation) and individuals rarely contain invasive endophytes (Amsler et al. 2009a). We had to search very hard to find individuals with even minimal endophyte growth for use in this study. It is possible that this alga elaborates secondary metabolites which deter endo/epiphytic colonization and/or growth even without the aid of grazers.

The low levels of weight gain observed in macroalgae maintained with mesograzers is almost certainly because the experiment was conducted at the end of the growing season.

Photo-efficiency measurements made using a PAM fluorometer at the end of the experiment suggested that all the species were light stressed by that time (Aumack, unpublished observation). Presumably, there was also little and likely even less growth in the macroalgae maintained without grazers but this could not be measured directly because of the heavy diatom fouling. Additionally, had the experiment been conducted at the height of the growing season, it is possible that the growth of epiphytic diatoms in the absence of mesograzers would have been even more pronounced as the shorter daylengths must certainly have constrained micoalgal growth as well.

Endophyte coverage throughout most species was relatively unaffected by the presence of amphipods. Only one species, *Himantothallus grandifolius,* showed significant differences in pre- and post endophyte coverage between replicates kept with grazers and those without (Figure 2). However, there was also a significant gain in endophyte coverage from pre-treatment levels in individuals kept in mesocosms with amphipods. *H. grandifolius* samples were sectioned into smaller pieces without meristematic tissues, making growth of new tissue impossible in the mesocosms. It is probable that stress resulting from sectioning large *H. grandifolius* individuals into smaller segments interfered with their natural ability to deter invasive endophytic growth, while their own comparative growth was prevented. Some studies have indicated that algae experiencing increased abiotic stresses are less likely to produce chemical deterrents (Renaud et al. 1990, Wiesemeier et al. 2008). Although these studies were examining chemical defenses as they applied to direct grazing, it stands to reason that the increased stress applied to recently sectioned *H. grandifolius* specimens hindered their resistance to endophyte expansion.

While endophyte coverage only increased significantly in one species, all species except *Desmarestia anceps* experienced a pronounced increase in algal epiphytes in replicates kept in a grazer free environment. Kept under more natural conditions with amphipods, *Desmarestia antarctica*, *Himantothallus grandifolius*, and *Gymnogongrus turquetii* all hosted relatively similar densities of epiphytes (8.1 - 13.0% coverage; Figure 2), almost exclusively diatoms. Without herbivores, both *D. antarctica* and *H. grandifolius* epiphyte coverage increased to 62 and 53% respectively, with the epiphyte population consisting of diatoms primarily, but filamentous phaeophytes, and some green algal epiphytes as well. Epiphyte coverage on G. *turquetii,* although significantly greater than coverage with grazers, only increased to 29% (Figure 2). The lower increase in algal epiphytes compared to the other two species may be the result of naturally produced anti-fouling metabolites produced within G. *turquetii.* Two *in vitro* studies of the effects of antifouling macroalgal extracts on the survival of sympatric diatoms (Amsler et al. 2005b, Sevak 2009) have reported that all four macroalgal species in the experiment have compounds that cause diatom mortality. Neither study, however, presented the extracted metabolites in an ecologically relevant manner. It is possible that *D. anceps* and, to a lesser extent, G. *turquetii* do indeed utilize such compounds as antifoulants in nature while *D. antarctica* and *H. grandifolius* do not. Further research needs to be conducted to discern whether or not anti-fouling compounds are presented by the macroalgae in an ecologically effective manner.

Several recent studies on various macrophytes have reported that epiphyte densities are negatively correlated with grazer abundances (Duffy 1990, Armitage et al. 2005, Heck & Valentine 2006, Jacobucci et al. 2009, McCall et al. 2009, Spivak et al. 2009). Many of these studies, however, have epiphyte biomass co-factored with abiotic factors such as light and nutrients. The standardized abiotic conditions in our experimental design reveal the independent importance of mesograzing pressures to control an otherwise significant epiphytic community. This was also observed in the frequency of filaments emerging from endophyte colonies throughout the host thallus. While no direct measurements of length or mass were taken, the significant difference in occurrence and diversity of species affected indicates the potential importance of mesograzers to controlling fouling populations.

Overall, our results suggest that the immense amphipod community may be crucial to the overall health of macroalgal beds along the western Antarctic Peninsula, continually grazing potentially harmful fouling diatoms/epiphytes that would otherwise be more widespread. Brawley (1992), Arrontes (1999), and Hay et al. (2004) have discussed the beneficial influence mesograzers can have to host macrophytes through consumption of algal epiphytes which may otherwise deter production via decreased light availability (Cebrian et al. 1999, Brush & Nixon 2002), interference with gas exchange (de Nys & Steinberg 1999), and competition for available nutrients (McRoy & Goering 1974, de Nys & Steinberg 1999). Both field and laboratory studies have examined mesograzers' roles in influencing community structure through elimination or alteration of epiphyte populations (Duffy & Hay 2000, Ruesink 2000, Duffy & Harvilicz 2001, Gacia et al. 2009). In the western Antarctic Peninsula, the dominant mesograzer and macroalgal populations may coexist in mutualism as the amphipods themselves are likely benefiting from the extensive chemically defended macroalgal community despite its unlikely use as a direct food source. Zamzow et al. (2010) reported that the common Antarctic amphipod species, *Prostebbingia gracilis,* was significantly more likely to escape predation from *Notothenia coriiceps,* an omnivorous Antarctic fish, while hiding in *Desmarestia menziesii,* a chemically defended alga, versus the palatable alga *Palmaria decipiens.* Although amphipod survivorship also increased based on macroalgal host morphology and complexity (Zamzow et al. 2010), other studies have shown that amphipod densities were greatest on more chemically defended macroalgae (Huang et al.

2007).

We hypothesize that the dominant, chemically defended macroalgae and extensive mesograzer fauna on the western Antarctic Peninsula exist in a mutualistic relationship. Likely, a vast majority of amphipods are taking refuge from predation in the protective confines of chemically defended macroalgae while continually consuming, and thereby cleaning their hosts of physiologically harmful epiphytes. Further evidence to support this mutualism hypothesis awaits additional experimental field research including more information on the impacts that endophytes and epiphytes have on the fitness of the larger, host macroalgae.

ACKNOWLEDGEMENTS

We are appreciative of Gil Koplovitz, Maggie Amsler, Philip Bucolo, Alan Maschek, Dr. Jill Zamzow and the rest of our 2007 and 2008 Antarctic field team colleagues for their field assistance. This project would not have been possible without the hard work and outstanding logistical support in Antarctica from the employees and sub-contractors of Raytheon Polar Services Company. This work was supported by National Science Foundation awards OPP-0442769 (CDA, JBM) and OPP-0442857 (BJB). JBM wishes to acknowledge the support provided by an Endowment in Polar and Marine Biology provided by the University of Alabama at Birmingham.

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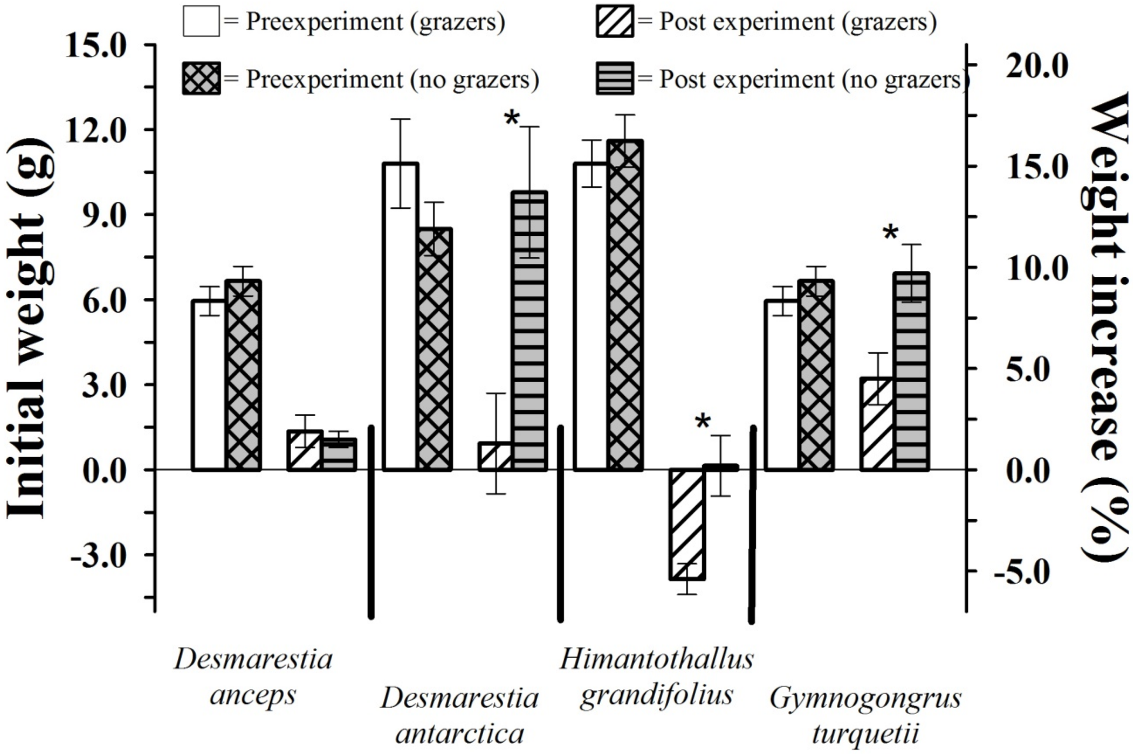

Figure 1: Initial weights (g) and the percent weight increased based on total biomass of *Desmarestia anceps, Desmarestia antarctica*, *Himantothallus grandifolius,* and *Gymnogongrus turquetii* contained in either predator free mesocosms or mesocosms with mesograzers present. Means are ± standard error. Asterisks indicate significant difference (student's t-test) between averages among species kept under different treatments ($p<0.05$).

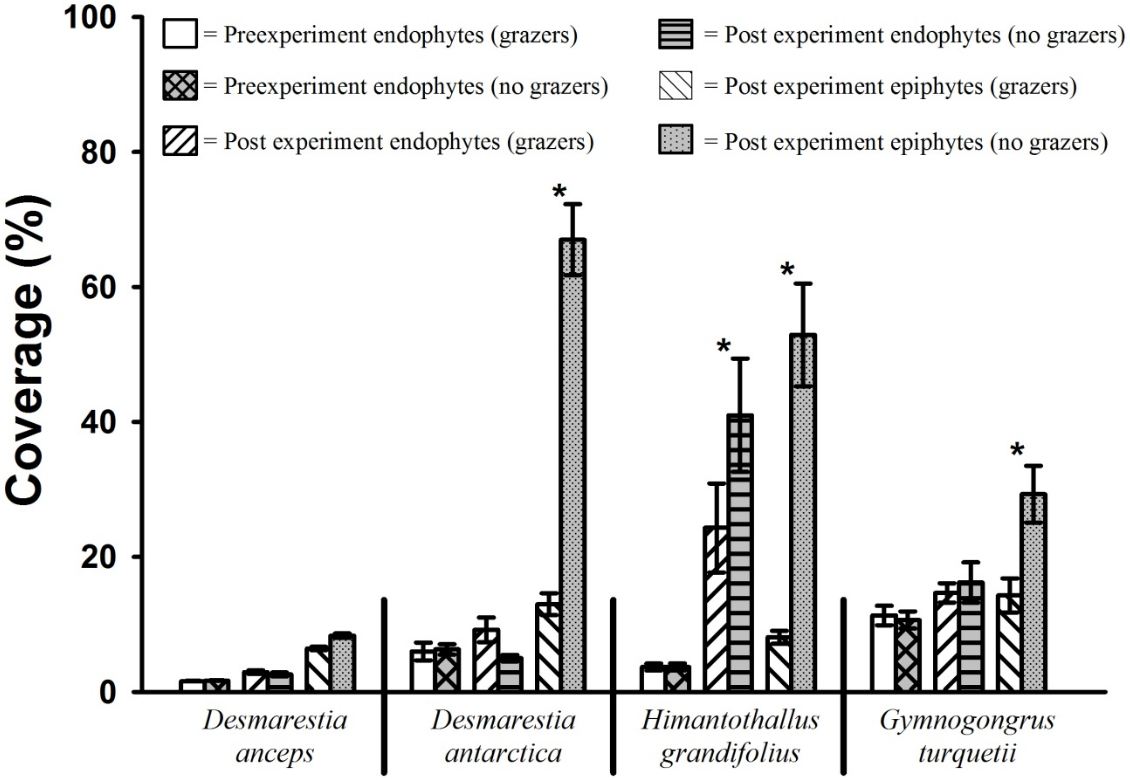

Figure 2: Pre- and post treatment coverage of both endophytes and epiphytes (% total thallus cover) on or in *Desmarestia anceps*, *Desmarestia antarctica, Himantothallus grandifolius,* and *Gymnogongrus turquetii* kept in either predator free mesocosms or mesocosms with mesograzers present. Means are ± standard error. Asterisks indicate significant difference (student's t-test) between averages among species kept under different treatments (p<0.05).

CONCLUSION

Throughout these studies I have determined that both epiphytic micro- and macroalgae are likely serving as a crucial food source for the large, endemic mesograzer assemblage in the western Antarctic Peninsula. Stable isotopic signatures from large perennial phaeophytic macrophytes, filamentous endo/epiphytes, as well as epiphytic diatoms all align with $\delta^{15}N$ and $\delta^{13}C$ values of several species of prominent amphipods, indicating primary consumption of these carbon sources. However, previous studies have demonstrated both the production of chemical feeding deterrents in all the large brown macrophytes as well as unhindered grazing by amphipods on cultured endophytic species. These previous findings, in addition to the significant relative importance of both diatoms and filamentous algae in amphipod guts suggest several amphipod species continually graze epiphytic diatoms and filamentous algae from their macrophytic hosts. The noticeable lack of sub-tidal filamentous algae and epiphytes along the western Antarctic Peninsula is likely the result of a considerable mesograzer population recurrently reducing their biomass beyond visible quantification.

The regular appearance of filamentous material throughout several amphipod species' guts is curious due to general lack of filamentous macroalgae growing sub-tidally. Although the likely explanation is emergent filaments from endophytic colonies growing invasively, it was not impossible that the filaments were the product of several species of finely branched rhodophytes, and one phaeophyte, growing throughout the area. However, our research demonstrated that fresh thallus material from each of these macroalgae were unpalatable to both *Gondogeneia antarctica* or *Prostebbingia gracilis*, two of the most abundant amphipods in the western Antarctic Peninsula. Artificial food experiments confirmed that all the finely branched red algal species elaborated either/both hydrophilic and/or lipophilic extracts facilitating their chemical defense against amphipod predation.

It has been shown that patterns of amphipod selection of host macroalgae is in direct contrast to their feeding preference, taking shelter in chemically defended macroalgae while avoiding more palatable species like *Iridaea cordata* and *Palmaria decipiens*. However, all previous amphipod density measurements had been conducted during daylight hours while any local amphipod nocturnal activity had been previously unreported. Our findings conclude that several amphipod species migrate from *Desmarestia menziesii*, a chemically defended brown, to *I. cordata* at night. *Gondogeneia antarctia*, which has been shown to readily consume *P. decipiens* in laboratory experiments, was also found on this alga in significantly higher numbers at night. Likely, amphipods have evolved their behavioral patterns to utilize the chemical deterrents elaborated in their would-be prey; seeking refuge from visual predators during the day on chemically defended, structurally complex macroalgae and foraging at night on more palatable species when threat of attack is decreased.

Finally, if epiphytic filamentous algae and diatoms are a continual dietary source for the amphipod assemblage in the western Antarctic Peninsula, then increased ephiphytic growth should be the natural byproduct of reduced grazing. We were able to demonstrate this fact using a mesocosm experiment. Three macroalgae species, growing without mesograzing amphipods, had significantly elevated epiphytic loads (mainly diatoms but some green and brown epiphytes as well) after a six week incubation period.

Additionally, substantially more individuals contained emergent filaments from endophytic colonies growing invasively within their tissues in the absence of predators. The physiological stress on macrophytes burdened with an abundance of endo/epiphytes has been well documented. We conclude that the enormous assemblage of mesograzers are living in mutualism with their macrophytic hosts, taking refuge from predation during the day in chemically defended macroalgae while continually cleaning them of potentially harmful fouling diatoms/epiphytes.

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