Polar Biol (2007) 30:1417–1430
DOI 10.1007/s00300-007-0303-1

ORIGINAL PAPER

Patterns of gammaridean amphipod abundance and species composition associated with dominant subtidal macroalgae from the western Antarctic Peninsula

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Received: 6 March 2007 / Revised: 24 April 2007 / Accepted: 30 April 2007 / Published online: 7 June 2007

Abstract The communities of gammaridean amphipods associated with eight dominant macroalgal species were examined near Palmer Station, Western Antarctic Peninsula. A total of 78,415 individuals belonging to 32 amphipod taxa were identified with mean densities ranging up to 20 individuals/g algal wet wt. The most abundant amphipod taxon, *Metaleptamphopus pectinatus*, was found to associate predominately with the brown alga *Desmarestia menziesii*, while the second most common taxon, *Jassa* spp. occurred primarily on the red alga *Gigartina skottsbergii*. Non-metric multidimensional scaling analysis demonstrated that the population densities of each amphipod species and amphipod species composition were similar on the same algal species but dissimilar on different species of algae. Comparisons of amphipod communities associated with a given algal species but from different sampling sites indicated that although the structure of species-specific macroalgal-associated amphipod communities can vary across spatial scales of 3 km, 50% of the macroalgal species examined showed no significant inter-site differences in associated amphipod community structure. Spearman rank correlation analyses showed that higher abundances of amphipods occurred on the macroalgae with the highest number of branches. As many Antarctic amphipods are known consumers of macroalgae, their remarkable abundances are likely to play a significant role in mediating energy and nutrient transfer in nearshore Antarctic Peninsular macroalgal communities.

Keywords Macroalgae · Amphipod · Gammaridean · Antarctic Peninsula · Community Structure

Introduction

Both biological and physical factors regulate the distribution and abundance of mesograzers associated with marine plants (Hay and Fenical 1988; Hughes and Gliddon 1991; John et al. 1992; Jernakoff et al. 1996). These factors include epiphytic architecture and community composition (Hacker and Steneck 1990; Mukai and Iijima 1995; Pavia et al. 1999), chemical defenses (Stachowicz and Hay 1999), predation (Wooster 1998; Sparrevik and Leonardsson 1999), structural complexity and toughness (Lubchenco 1978; Parker et al. 2001), nutritional factors (Cruz-Rivera and Hay 2000, 2001), and hydrological parameters (Aikins and Kikuchi 2001; Duggins et al. 2001). While the vast majority of studies conducted to date have been in temperate and tropical marine systems, it is likely that mesograzers similarly associate with marine plants in polar marine environments and that these interactions are essential to understanding the dynamics of these communities (Richardson 1977; Iken et al. 1997; Lippert et al. 2001; Takeuchi and Watanabe 2002; Wessels et al. 2006).

Investigations of the ecology of nearshore antarctic benthic communities began in earnest in the late 1950s through the 1970s (Neushul 1965; Zaneveld 1966; Dayton

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et al. 1974; DeLaca and Lipps 1976; Moe and DeLaca 1976). Macroalgae are common along the Antarctic Peninsula where they often form dense undersea forests (Amsler et al. 1995). These macroalgal communities provide abundant food resources for a rich fauna of sympatric grazing gastropods, annelids, crustaceans, and fish (Iken et al. 1997; 1998). Such trophic relationships may be complex, and it is now evident that different antarctic macroalgal species are not necessarily consumed by grazers in proportion to their abundance (Huang et al. 2006). Such observations have facilitated recent studies examining whether chemical defenses mediate patterns of macroalgal grazing by a variety of sympatric meso- and macrograzer consumers, including amphipods, gastropods, sea urchins, sea stars, and fish (Iken et al. 1997, 1998; Amsler et al. 1998, 2005; Iken 1999; Fairhead et al. 2005). While the role of Antarctic macrograzers such as sea urchins and fish in mediating patterns of materials and energy flow in macroalgal food webs has received limited attention (Barrera-Oro and Casaux 1990; Iken et al. 1997, 1998, 1999; Amsler et al. 1998, 2005), surprisingly little is known about the prospective influence of mesograzers on the ecology of nearshore macrophytic communities in macroalgal rich regions such as the Antarctic Peninsula. To understand such relationships studies are first needed to determine the abundance and distribution patterns of the most common functional mesograzer groups such as the herbivorous gammaridean amphipods. If an abundant macroalgal-associated amphipod community exists, then understanding the degree to which macrophytes provide such mesograzers with structural or chemical refuge or direct or indirect sources of nutrition becomes important.

The main objectives of the present study were to determine the abundance and species composition patterns of gammaridean amphipods associated with dominant species of macroalgae along the western Antarctic Peninsula. By sampling amphipods from the same macroalgal species but from two different collection sites, we extended our analysis to allow for an evaluation of potential differences on a local spatial scale. In addition, for each of the algal species examined, we measured a suite of characters that define its three-dimensional morphology and examined whether patterns of amphipod abundance and species composition are related to the provision of structural refuge for crustacean mesograzers. Finally, we discuss how additional characteristics not measured in the present study including macroalgal palatability (Huang et al. 2006), and chemical defenses (Amsler et al. 2005; Fairhead et al. 2005) may play a role in mediating patterns of gammaridean amphipod abundance and species composition in nearshore macroalgal communities of the Antarctic Peninsula.

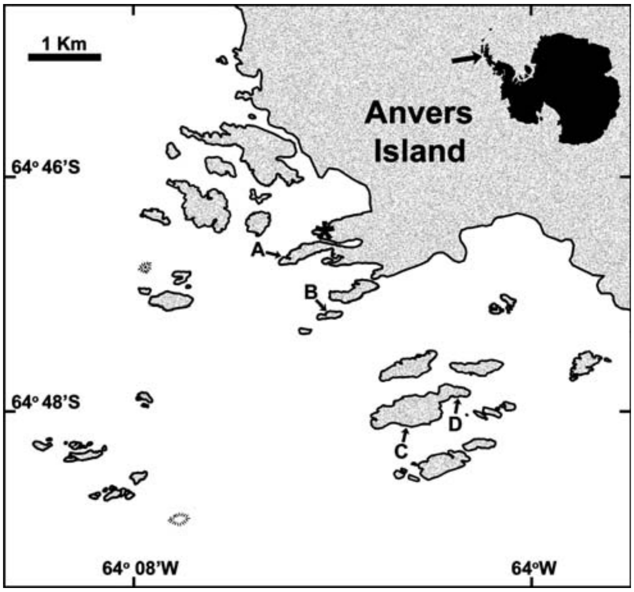

Fig. 1 Sampling locations of subtidal macroalgae and associated amphipods off Anvers Island, Antarctica. Palmer Station (*), Bonaparte Point **A**, Eichorst Island **B**, South Hermit Island (Hermit Wall; **C**), and Southeast Hermit Island (Hermit Cove; **D**). The silhouette at the upper right corner indicates the Antarctic continent and the arrow points to the location of Anvers Island

Materials and methods

Study site

Field collections of macroalgae and their associated epifauna were conducted in near-shore subtidal habitats near Palmer Station, Anvers Island, on the western Antarctic Peninsula (64°46'S, 64°04'W; Fig. 1). All samples were collected using SCUBA between February and April 2003. Four different subtidal sampling sites were selected including a site on northeast Bonaparte Point (64°46.7'S, 64°04'W), a site on the northern portion of Eichorst Island (64°47.2'S, 64°03.2'W), and southern (64°48.1'S, 64°01.4'W, herein referred to as Hermit Wall) and southeastern (64°47.9'S, 64°00.4'W, herein referred to as Hermit Cove) sites on Hermit Island (Fig. 1). These sites were chosen because they were home to more than one of the targeted species, thereby allowing all eight species to be collected in two different of the four sites. In terms of exposure to the open ocean and resultant wave energy and currents, the Eichorst Island site is slightly but noticeably more protected than the Bonaparte Point site. The Hermit Cove is the most protected site (by a fair amount) and the Hermit wall site is the most exposed. Sea water temperatures and salinities in the vicinity of Palmer Station, Antarctica were approximately 0 ± 1°C and 28–32‰, respectively.

Field survey and sample collection

A suite of dominant macroalgal species that occur along the western Antarctic Peninsula was targeted for this study. This suite included three common species of brown macroalgae (Desmarestiaceae: *Desmarestia menziesii* J Agardh, *Desmarestia anceps* Montagne, and *Desmarestia antarctica* Moe and Silva) and five common species of red macroalgae (Gigartinaceae: *Gigartina skottsbergii* Setchell and Gardner, *Iridaea cordata* (Turner) Bor; Delesseriaceae: *Myriogramme mangini* (Gain) Skottsberg; Palmariaceae: *Palmaria decipiens* (Reinsch) Ricker; Plocamiaceae: *Plocamium cartilagineum* (Linnaeus) P F Dixon) (DeLaca and Lipps 1976; Amsler et al. 1995). Using SCUBA, each algal thallus was gently dislodged from the attached substrate and, quickly but carefully enclosed along with its associated epifauna, within a mesh-collecting bag (mesh size < 0.5 mm). The collecting bags were made of fine soft fabric and the mouth of each bag remained wide-open underwater for collecting purposes but could be readily closed tightly. Immediately following collection, algal samples were returned to the laboratory. Ten individual thalli of each macroalgal species were sampled to allow a quantitative and statistical analysis of all associated marine invertebrate fauna (epifaunal communities were comprised primarily of crustacean mesograzers). Individual samples of each of the macroalgal species were collected from two different locations ($n = 5$ samples from each location) at similar depths for a comparison of site-specific variations over a scale of 1–3 km (see Table 4 for sampling depth of each algal species). The *D. menziesii*, *G. skottsbergii*, and *P. decipiens* were collected from both Hermit Cove and Bonaparte Point; *I. cordata* and *M. mangini* were collected from both Eichorst Island and Bonaparte Point; *D. antarctica* was collected from Hermit Cove and Eichorst Island; *D. anceps* was collected from Bonaparte Point and Hermit Wall; and *P. cartilagineum* was collected from Eichorst Island and Hermit Wall. Collecting depths ranged from 6 to 16 m.

The abundance and distribution of gammaridean amphipods

Macroalgal-associated epifauna were separated from each alga by mixing and shaking each alga in a series of buckets (5–6) filled with seawater. Each alga was then visually examined further to confirm that all mobile fauna had been removed. The epifaunal invertebrates retained on a 0.5-mm mesh sieve were fixed immediately in a solution of 5% formalin in seawater for later enumeration and identification. Gammaridean amphipod samples were sorted using a dissecting microscope according to Thurston (1972, 1973). To analyze the structure of gammaridean amphipod community assemblages the following variables were calculated: total abundance of individuals (N), total number of species (S), species richness (d), and Shannon-Wiener diversity (H') (Clarke and Warwick 2001), and densities of epifaunal species were determined (see below) and expressed in terms of individuals per g algal wet wt.

Morphological attributes of macroalgae

After epifaunal removal, each macroalga was whirled by hand in a mesh bag to remove surface water and then weighed to determine fresh weight (FW). In addition, each alga was submerged in a large graduated cylinder in order to determine total thallus volume. To facilitate measurements necessary to estimate the spatial components of algal architecture we employed the techniques given in Hacker and Steneck (1990). Briefly, each alga was submerged completely in a seawater tank to allow it to assume a normal vertically suspended configuration. The total spaces between fronds and branches were calculated for each of the ten individuals of each species and expressed in terms of volumetric displacement of water (ml). Measurements included: (1) canopy volume (CV), the product of the length, width and height (cm) of the cuboid formed by a plant when completely expanded in the seawater tank (the holdfast is excluded), (2) thallus volume (TV), the volume occupied by an algal thallus, and (3) interstitial volume (IV), the volume of the spaces between fronds as determined by subtracting the thallus volume from the canopy volume.

For structural component determinations the following attributes were evaluated for ten individual thalli of each species: (1) degree of branching (DB), counted from the distal branch to the stem. The final branches were considered first order, and wherever two branches of the same order join, the order of the resultant branch was increased by one (Chemello and Milazzo 2002) and (2) number of branches (NB). The numbers of branches were estimated (ten replicates for each algal species) for three morphologically complex species (*D. menziesii*, *D. anceps*, and *P. cartilagineum*) and for other algal species all branches were actually counted. To measure the NB for the three largest brown algal species (*D. menziesii*, *D. anceps*, and *D. antarctica*), each individual alga collected was cut evenly into three sections along the main axis. The branches of each section were trimmed off the main and secondary axes then counted. The total NB was the summation of the top (NB1), the middle (NB2), and the bottom (NB3) section. The shape and arrangement of interstitial spaces and branches was not measured.

Statistical analyses

Quantitative statistical comparisons of total abundance, species richness and species diversity indices of amphipod communities associated with all eight species of common brown and red macroalgae were conducted using a one-way ANOVA test followed by Tukey's Honestly Significant Difference (HSD) tests using SAS statistical software (SAS Institute, Cary, North Carolina). To investigate relationships between the community composition of the associated gammaridean amphipods and characteristics of algal morphology, multivariate analyses (ordination and classification) were undertaken using PRIMER (Plymouth Marine Laboratory, Plymouth, UK; Clarke and Gorley, 2001). Densities and species composition data matrices of the amphipod species were $\log(x + 1)$ transformed so that the succeeding ordination and hierarchical categorization were not determined only by the most dominant species (Clarke and Warwick 2001). To determine the similarity of the amphipod communities associated with the different macroalgal species a Bray-Curtis similarity coefficient was calculated. This test was based on amphipod species distributions and their relative population densities (number of amphipods per gram wet wt algal tissue). In addition, an MDS analysis (non-metric multidimensional scaling) was performed on the matrix of amphipod species composition and population densities. This technique has been found to be the most robust for the analysis of community data (McCune and Grace 2002). To test the ordination, the stress coefficient of Kruskal was used (McCune and Grace 2002). The descriptive algal morphometrics data matrices collected for each target macroalgal species were $\log(x + 1)$ transformed to decrease the influence of outliers and then examined using cluster analysis (Romesburg 1984; McGarigal et al. 2000). Analysis of similarity (ANOSIM) was employed to facilitate a statistical comparison of overall similarities of amphipod species compositions among different species of macroalgae and algal morphology. For further testing matched similarity matrices derived from algal morphology data and amphipod abundance and species composition data, a RELATE significance test was conducted (Clarke and Warwick 2001). Spearman rank correlation analysis was conducted to determine the correlation between amphipod abundance and algal morphological parameters.

As each targeted macroalgal species was collected from two of the four separate field sites (five individuals from each of the two sites) we performed an analysis of similarity (ANOSIM) to evaluate whether significant differences occurred in amphipod community structure (analysis of similarity based on standardized amphipod density) associated with each macroalga collected from different locations.

Results

Total abundance, species number and diversity of algal-associated amphipod communities

A total of 78,415 individuals representing 32 gammaridean amphipod taxa were collected among the eight target macroalgal species (see Table 1 for amphipod species list and density of each amphipod species on each of the eight macroalgal species). As it was not possible to identify all amphipods to the species level, four amphipod taxa were designated at either the genus or family level: *Jassa* spp., *Oradarea* spp., Lysianassoidea, and Eophliantidae. When considered in terms of amphipod density per unit algal mass (wet wt), more than 64% of the total amphipods collected were found in association with *D. menziesii*. Additionally, more than 72% of the total amphipods collected were associated with the brown algae in general. Thus, a relatively minor percentage of the total amphipods per unit wet mass (28%) were collected in association with red algal species. The most numerically dominant amphipod taxa (calculated as a function of amphipod abundance per unit wet algal mass) were *Metaleptamphopus pectinatus* (59%), *Jassa* spp. (14%), *Oradarea* spp. (9%), *Probolisca ovata* (5%), *Gondogeneia antarctica* (4%) and *Prostebbingia gracilis* (2%). Except for *P. gracilis,* which was not found on either *M. mangini* or *I. cordata*, each of remaining amphipod species was collected from at least seven of the eight macroalgal species. Total amphipod densities associated with each of the eight target macroalgae were significantly different from one another (ANOVA; $F_{7,72} = 48.7$, $p < 0.001$) (Fig. 2a). Total amphipod density was greatest for *D. menziesii* (20.1 ± 3.8 amphipods per g wet algal weight, $\bar{x} \pm 1$ SE) followed by *P. cartilagineum* (5.9 ± 1.1 amphipods per g algal wet wt, $\bar{x} \pm 1$ SE), and lowest for *I. cordata* (0.1 ± 0.03 amphipods per g algal wet wt, $\bar{x} \pm 1$ SE). Both the numbers of species and diversity indices for each of the eight algal-associated amphipod communities differed significantly (ANOVA; $F_{7,72} = 15.6$ and 5.3, respectively, $p < 0.001$) from one another (Fig. 2b,c). Greatest numbers of amphipod species were detected in association with *D. menziesii*, *D. anceps*, and *G. skottsbergii* (Fig 2b). In contrast, smaller numbers of amphipod species were found in association with *I. cordata* and *P. decipiens* (Fig 2b). Significantly higher species diversity indices were detected in association with *D. anceps*, *P. cartilagineum*, and *G. skottsbergii* (ANOVA; $F_{7,72} = 5.3$, $p < 0.001$) (Fig. 2c). Although the numbers of amphipod species were highest in association with *D. menziesii*, the species diversity index was relatively low.

Table 1 Species assemblages and mean density (individuals per 100 g algal wet wt) of gammaridean amphipods associated with eight subtidal antarctic macroalgae (10 individuals of each algal species were collected)

Species	DME	DAN	ANT	PAL	GIG	MYR	PLO	IRI	Total
Ampeliscidae									
Ampelisca bouvieri Chevreux	0	0	0	0	0.09	0	0	0	0.09
Amphilochidae									
Gitanopsis squamosa (Thomson)	1.5	1.5	0.3	0	3.1	0.1	2.0	0	8.5
Colomastigidae									
Colomastix sp. *(fissilingua)* Schellenberg	1.3	0.06	0.06	0	0.2	0.1	0	0	1.7
Dexaminidae									
Paradexamine fissicauda Chevreux	0.04	0.2	0.06	0	0.6	0.1	66.8	0.5	68.3
Eophliantidae	7.2	0.02	0.05	0	0.6	1.7	1.2	0	10.8
Eusiridae									
Atyloella magellanica (Stebbing)	0.02	0.03	0	0	0	0	4.3	0	4.3
Atylopsis sp. Stebbing	0.03	0	0	0	0	0	0	0	0.03
Bovallia gigantea Pfeffer	1.7	4.3	0	0	0.3	1	4.6	0	11.9
Djerboa furcipes Chevreux	0.1	0	0	0	0.8	0	0	0	0.9
Eurymera monticulosa Pfeffer	0.07	0	0	0	0.1	0.2	0	0	3.6
Metaleptamphopus pectinatus Chevreux	1736.4	14.7	18.3	5.8	1.5	0.5	72.5	4.4	1854
Oradarea spp. Walker	174.3	41.8	1.6	2.3	19.7	4.8	47.9	0	292.6
Paramoera sp. Miers	0	0	0	0	0.07	0	0	0	0.07
Pontogeneia sp. Boeck	0.07	0	0	0	0.07	0	0	0	0.1
Prostebbingia brevicornis (Chevreux)	0	0.06	0	0	0.09	0	0.2	0	0.3
Prostebbingia gracilis (Chevreux)	41.4	5	0.4	0.7	2.5	0	28	0	77.9
Schraderia dubia Thurston	0.2	5.8	0.09	0	1.8	0.1	24.5	0.2	32.6
Schraderia gracilis Pfeffer	0.06	0.6	0	0	1.9	0	0.1	0	2.7
Schraderia sp. Pfeffer	0	0.2	0	0	0.2	0	0.4	0	0.8
Gammarellidae									
Gondogeneia antarctica (Chevreux)	10.8	17.3	0.4	5.9	12.2	32.3	28.3	2.1	109.4
Gondogeneia redfearni (Thurston)	0.5	15.3	0.3	1.8	0.1	0.3	4.9	0	23.3
Iphimediidae									
Gnathiphimedia barnardi Thurston	0	0	0	0	0	0	0.3	0	0.3
Gnathiphimedia fuchsi Thurston	0.09	0.08	0	0	0	0.09	0	0	0.3
Pariphimedia integricauda Chevreux	0.1	1.3	0	0	0.4	1.7	1.4	0	4.9
Ischyroceridae									
Jassa spp. Leach	5.7	87.3	0.9	5.4	85	55.5	202.2	2.9	445
Leucothoidae									
Leucothoe spinicarpa (Abildgaard)	0.01	0	0	0	0	0	0	0	0.01

Table 1 continued

Species	DME	DAN	ANT	PAL	GIG	MYR	PLO	IRI	Total
Lysianassoidea	0.8	0.08	0	0.7	0	0	0	0	1.6
Allogaussia sp. Schellenberg	0	0	0	0	0	0	1	0	1
Sebidae									
Seba sp. Bate	0	0.04	0	0	0	0	0	0	0.04
Stenothoidae									
Probolisca ovata (Stebbing)	20.3	15.7	1.5	3.3	16.7	7.4	99	0.4	164.2
Prothaumatelson nasutum (Chevreux)	2.3	2.9	0.5	0.4	1.3	0.02	1.1	0	8.5
Thaumatelsonidae									
Thaumatelson herdmani Walker	0.09	0.4	0.04	0	0	0	0	0	0.5
Total number of individuals	2005.2 (64.1%)	214.6 (6.9%)	24.5 (0.8%)	26.3 (0.8%)	149.1 (4.8%)	106.1 (3.4%)	590.7 (18.9%)	10.4 (0.3%)	3127
Total number of species/taxa	12 ± 1.2	12 ± 1.1	6 ± 0.5	3 ± 0.6	10 ± 1.4	6 ± 1.0	8 ± 1.4	2 ± 0.4	
Species richness (d)	1.3 ± 0.1	1.8 ± 0.1	1.3 ± 0.1	0.9 ± 0.2	1.5 ± 0.2	1.1 ± 0.1	1.3 ± 0.2	0.7 ± 0.1	
Species diversity (H')	0.6 ± 0.1	1.5 ± 0.1	1.0 ± 0.1	0.9 ± 0.2	1.1 ± 0.2	1.0 ± 0.1	1.3 ± 0.2	0.7 ± 0.1	

Distribution of dominant amphipod species within and across algal species

The composition of the amphipod community in association with algal species illustrated that the most abundant amphipod, *M. pectinatus*, numerically dominated three different algal species: *D. menziesii* (87%), *D. antarctica* (75%), and *I. cordata* (42%). The second most abundant amphipod taxon, *Jassa* spp., were found in abundance in association with *G. skottsbergii* (57%), *M. mangini* (52.3%), and *D. anceps* (41%). Amphipods belonging to *Oradarea* spp. were found commonly among seven of the eight target macroalgae (range 5–20%). No individuals of *Oradarea* spp. were collected from *I. cordata*. *G. antarctica* was found most commonly associated with the red alga *M. mangini* (31%) and *P. decipiens* (23%).

In terms of amphipod density (abundance per unit algal wet mass), *M. pectinatus* and *Oradarea* spp. were predominately found associated with the brown alga *D. menziesii* (Fig. 3a, c), while *Jassa* spp. was found primarily in association with the red alga *Plocamium cartilagineum* (Fig. 3b). Individuals were particularly abundant on *Plocamium cartilaginieum* (45%) but were also found in equal, but lower abundances on *G. skottsbergii* (19%) and *D. anceps* (20%). The majority of *Oradarea* spp. individuals, 74% of the total algal-mass standardized amphipod density, were found in association with *Desmarestia* spp. (*D. menziesii* 60% and *D. anceps* 14%).

Species composition of amphipod communities associated with macroalgal species

Amphipod taxa (listed in Table 1) were considered as independent units for ANOSIM analysis. Significant differences in amphipod densities and species composition were determined across the algal species (ANOSIM global test: $R = 0.65$, $p < 0.05$). Employing non-metric two-dimensional scaling (MDS) based on the species numbers and the standardized density of each amphipod species (abundance per g algal wet wt), we analyzed species composition patterns in association with the algal species examined (Fig. 4). In most cases the differences of amphipod species composition associated with different algal species were highly significant. However, amphipod species composition patterns associated with *Palmaria decipiens* and *I. cordata* did not differ significantly (ANOSIM pair-wise test: $R = 0.03$, $p = 0.3$). The amphipod species compositions associated with *D. anceps* and *G. skottsbergii* were barely separable (ANOSIM pair-wise test: $R = 0.12$, $p = 0.06$) (Table 2). Cluster analysis indicated that amphipod communities collected from all *D. menziesii* replicates fell into a mono-group (similarity > 65%). In addition, amphipod communities sampled

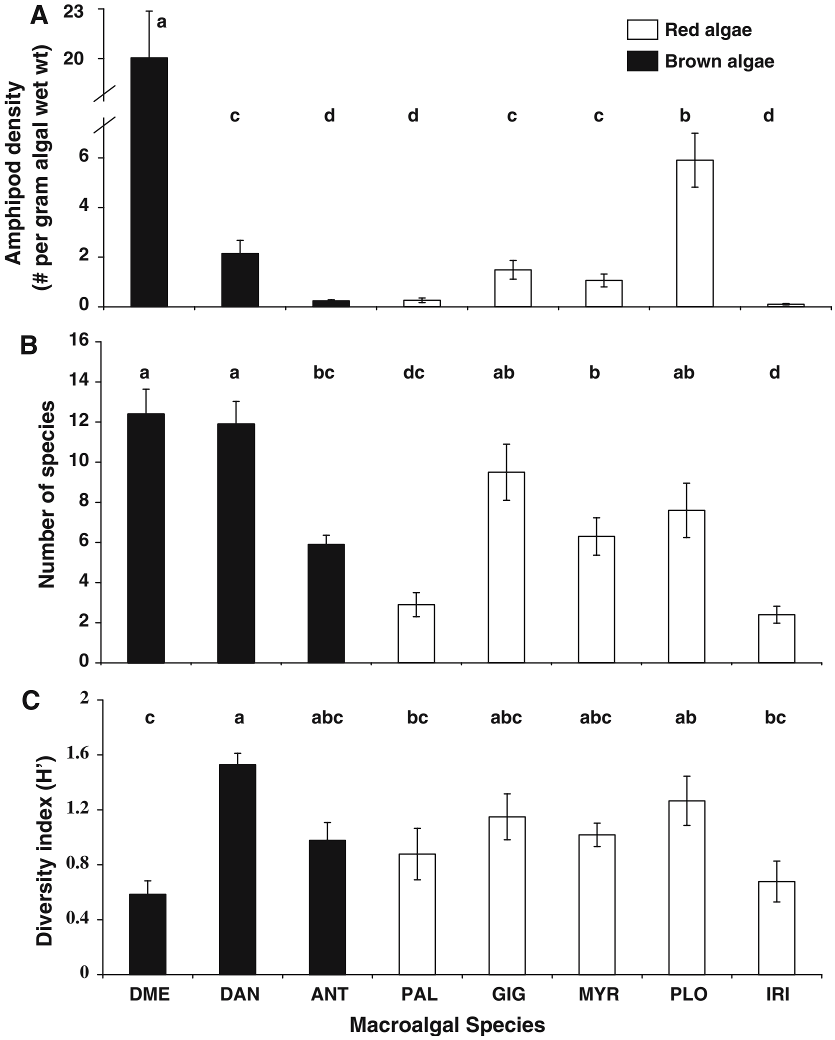

Fig. 2 Total abundances, numbers of species and diversity indices of amphipods associated with the eight target macroalgae. **A** Total amphipod abundances (number of amphipod per g algal wet wt) associated with the eight target macroalgae. Data were log(x + 1) transformed and presented as means ± SE; $n = 10$ (ANOVA; $F_{7,72} = 48.7$, $p < 0.01$). **B** Number of species. **C** Diversity index (H') of amphipod communities associated with eight target macroalgae. Data are means ± SE; $n = 10$ (ANOVA; $F_{7,72} = 15.6$ and 5.3, respectively, $p < 0.01$). Different letters indicate statistical differences. DME = *Desmarestia menziesii*; DAN = *Desmarestia anceps*; ANT = *Desmarestia antarctica*; PAL = *Palmaria decipiens*; GIG = *Gigartina skottsbergii*; MYR = *Myriogramme mangini*; PLO = *Plocamium cartilagineum*; IRI = *Iridaea cordata*

across eight of the ten *D. antarctica* replicates formed a group with similarity greater than 59%, while the other two replicates were in close proximity to the *D. antarctica* group. The distributional patterns of amphipod communities across the remaining algal species showed no clear patterns (Fig. 5).

Distributions of amphipods among different sampling sites

In order to determine whether amphipod abundance and composition patterns differ by collection site we examined algal samples from two different sites for each algal species ($n = 5$ replicates per site) (Fig. 5 and Table 3). The results of ANOSIM revealed that amphipod communities associated with *D. antarctica*, *G. skottsbergii*, *M. mangini*, and *I. cordata* collected from two sites that included Hermit Cove, Eichorst Island, or Bonaparte Point were not significantly dissimilar ($p > 0.05$). The amphipod abundance and composition patterns associated with *D. menziesii* and *P. decipiens* collected from Hermit Cove and Bonaparte Point were dissimilar ($p < 0.05$). The amphipod communities associated with *D. anceps* and *P. cartilagineum* collected from Hermit Wall and Bonaparte Point and Hermit Wall and Eichorst Island, respectively, were also dissimilar ($p < 0.05$).

Morphological traits of macroalgae

The morphological attributes of eight ecologically important macroalgae selected for this study are presented in Table 4. According to the global test of the analysis of similarity (ANOSIM), all species are significantly distinct in their morphology ($R = 0.9$, $p < 0.05$). In terms of the morphological parameters measured, these eight macroalgal species can be categorized into two groups: branched and bladed macroalgae. The branched algal species, including *D. menziesii*, *D. anceps*, and *P. cartilagineum* have higher numbers of branches per g algal wet wt than other algal species. *D. antarctica* with ligulate branches has

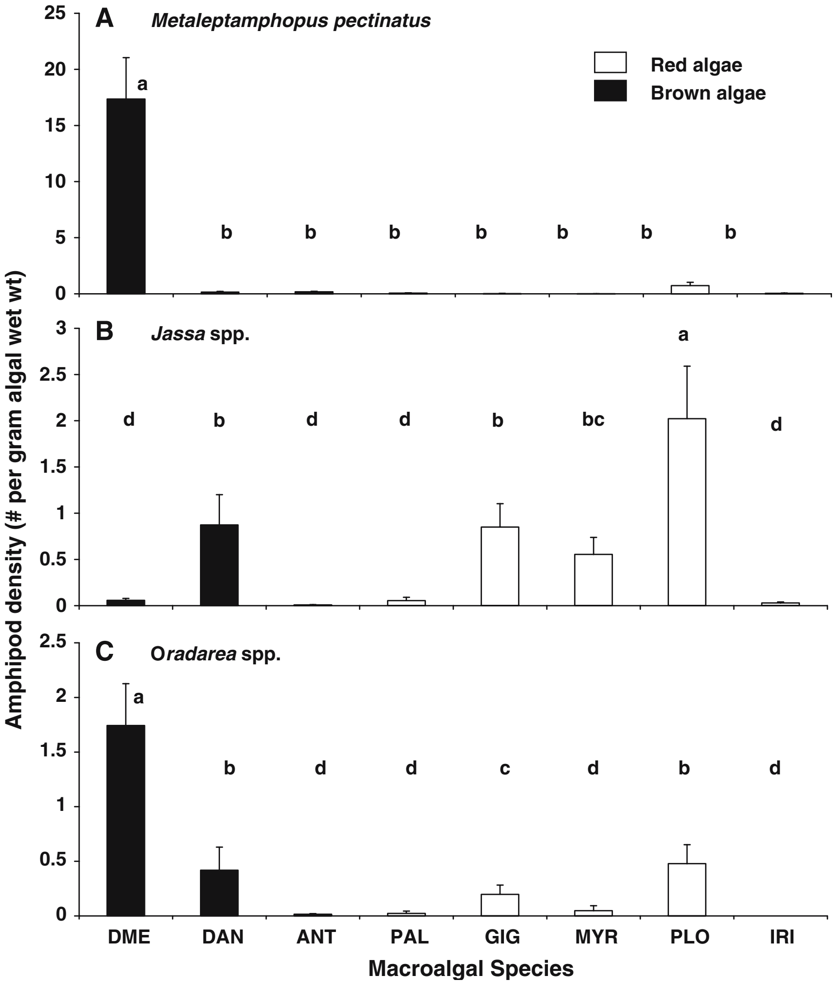

Fig. 3 Densities of the three most abundant amphipod species associated with the eight target macroalgae. Data are mean ± SE; n = 10 (ANOVA; $F_{7,\,72}$ = 24.1, 38.2, and 13, respectively, $p < 0.01$). Different letters indicate statistical differences. (Abbreviations given in Fig. 2)

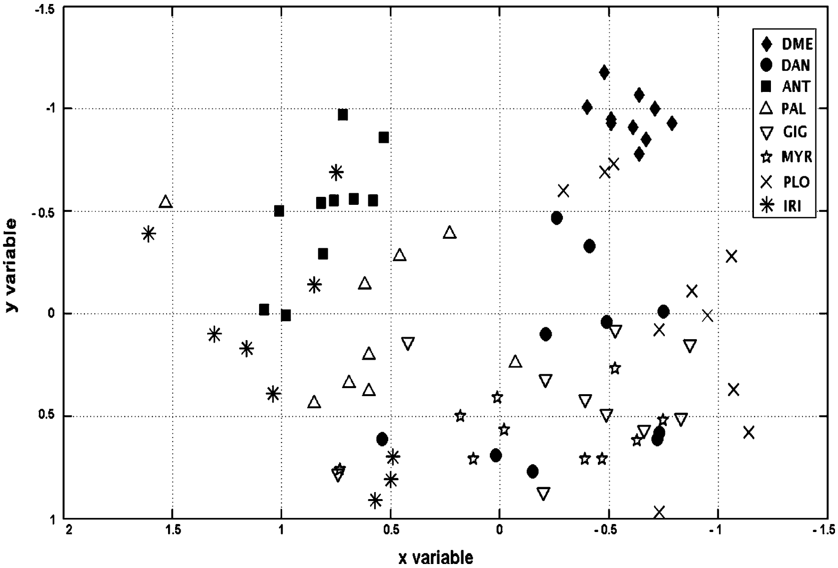

Fig. 4 MDS ordination analysis of ten replicates of each of the eight target macroalgae based on both the associated species abundance and compositions of 32 amphipod taxa. The MDS analysis was conducted using standardized (numbers of amphipods per g algal wet wt) and log(x + 1) transformed amphipod data and presented as a two-dimensional scatter graph using x and y variables. (stress = 0.15) (Abbreviations given in Fig. 2)

medium number of branches. The high degree of branching in these four algal species also contributes to an increase in complexity of alga morphology. In contrast, the bladed algal species, *G. skottsbergii*, *I. cordata*, *M. mangini*, and *P. decipiens* have an obviously simpler morphology with both a low number of branches per g algal wet wt and a low

Table 2 The pair-wise *R* values of analysis of similarity (ANOSIM) based on the amphipod densities and community compositions associated with eight macroalgae. *p* values are shown in parentheses. Significance levels greater than 0.05 are shown in bold. Algal abbreviations are given in Fig. 2

Algal species	DAN	ANT	PAL	GIG	MYR	PLO	IRI
DME	0.8 (0.001)	1 (0.001)	0.8 (0.001)	0.9 (0.002)	1 (0.001)	0.7 (0.001)	0.9 (0.001)
DAN		0.9 (0.001)	0.4 (0.001)	**0.1 (0.06)**	0.4 (0.001)	0.3 (0.01)	0.7 (0.001)
ANT			0.4 (0.002)	0.9 (0.001)	1 (0.001)	0.9 (0.001)	0.4 (0.001)
PAL				0.4 (0.001)	0.4 (0.001)	0.7 (0.001)	**0.03 (0.3)**
GIG					0.2 (0.009)	0.3 (0.001)	0.6 (0.001)
MYR						0.6 (0.001)	0.7 (0.001)
PLO							0.9 (0.001)

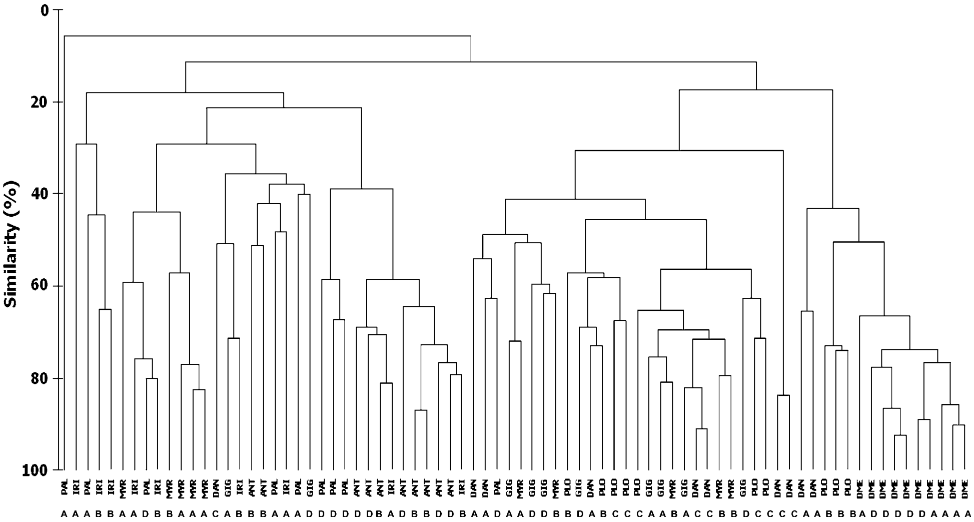

Fig. 5 Bray-Curtis cluster analysis dendrogram generated on the basis of the standardized abundances of amphipod species distributions and their relative population densities (number of amphipods per g algal wet wt). Shown is the percent similarity between 10 replicate samples of each of the eight target macroalgae. Sampling sites are indicated in capital letters as in Fig. 1. (Abbreviations given in Fig. 2)

Table 3 Analysis of similarity (ANOSIM) between two different sampling sites based on the amphipod community structure associated with the alga collected. NA indicates not available. *p* values are shown in parentheses. Significance levels greater than 0.05 are shown in bold. Algal abbreviations are given in Fig. 2

	Hermit Wall	Eichorst Is.	Bonaparte Pt.
Hermit Cove	NA	**ANT (0.159)**	**GIG (0.135)** DME (0.008) PAL (0.008)
Bonaparte Pt.	DAN (0.008)	**IRI (0.905) MYR (0.071)**	–
Eichorst Is.	PLO (0.016)	–	–

degree of branching. The dendrogram generated from the average values of morphological attributes demonstrated that the intraspecific morphology of each species is similar (Fig. 6). The morphology of *D. menziesii* and *D. anceps* were similar (ANOSIM pair-wise test: $R = 0.066$, $p = 0.13$). In contrast, while the shapes of their blades share a common form, the overall morphology of *I. cordata* and *P. decipiens* was statistically dissimilar (ANOSIM pair-wise test: $R = 0.233$, $p = 0.01$) when based on the broad suite of morphometrics presented in Table 1.

To compare the relationship of algal morphology and amphipod abundance and species composition, a RELATE significance test showed that there is no relation between the two similarity matrices derived from the amphipod abundance and population density data and algal morphology data ($\rho = 0.2$). This analysis indicated the patterns of amphipod abundance and species composition were not significantly similar with the morphological metrics of the respective alga from which they were collected. Results of the Spearman rank correlation analysis between algal morphological metrics (wet weight, canopy volume, interstitial volume, thallus volume, degree of branching order, and number of branches) and total amphipod abundances yielded a significant correlation between amphipod abundances and numbers of branches (branches per g wet wt algae; $p < 0.001$).

Table 4 Morphological attributes of eight dominant subtidal Antarctic macroalgae. Means ± 1 SE for 10 individuals of each algal species

Morphological attributes	Algal species							
	DME	DAN	ANT	PAL	GIG	MYR	PLO	IRI
Wet weight (g)	388 ± 91	307 ± 43	230 ± 28	40 ± 5	267 ± 47	162 ± 54	30 ± 10	83 ± 15
Width (cm)	39 ± 4	33 ± 3	39 ± 2	16 ± 1	61 ± 5	35 ± 3	19 ± 2	24 ± 1
Depth (cm)	31 ± 3	23 ± 2	26 ± 3	11 ± 1	50 ± 5	25 ± 2	15 ± 2	17 ± 2
Height (cm)	111 ± 10	136 ± 11	144 ± 10	65 ± 5	10 ± 1	43 ± 3	20 ± 2	55 ± 6
Canopy volume (ml)	152299 ± 31831	113311 ± 21145	142111 ± 20750	11958 ± 1870	34395 ± 6708	43664 ± 11077	7550 ± 2713	21236 ± 2643
Thallus volume (ml)	354 ± 101	288 ± 40	202 ± 29	38 ± 5	247 ± 42	146 ± 50	27 ± 9	87 ± 15
Interstitial volume (ml)	151944 ± 31752	113023 ± 21108	141909 ± 20729	11920 ± 1866	34147 ± 6668	43519 ± 11030	7523 ± 2705	21149 ± 2634
Degree of branch	5.2 ± 0.4	4.7 ± 0.2	3.1 ± 0.1	1.3 ± 0.2	1 ± 0	3.6 ± 0.2	7.2 ± 0.3	1.4 ± 0.2
Number of branches 1	1738 ± 312	4291 ± 1208	82 ± 14	–	–	–	–	–
Number of branches 2	9241 ± 1698	16561 ± 3723	403 ± 132	–	–	–	–	–
Number of branches 3	29519 ± 4132	31188 ± 4555	546 ± 121	–	–	–	–	–
Total number of branches	40497 ± 4958	52040 ± 7529	1020 ± 197	1.5 ± 0.3	1 ± 0	168 ± 112	36817 ± 11612	1.4 ± 0.2
Number of branches/g w.w.	260 ± 127	192 ± 33	4.5 ± 0.8	0.047 ± 0.013	0.006 ± 0.002	0.7 ± 0.3	1365 ± 114	0.019 ± 0.002
Sampling depth (m)	10.6 ± 0.6	12.3 ± 0.4	10.7 ± 0.8	7.0 ± 0.1	8.1 ± 0.7	7.3 ± 0.2	13.1 ± 0.7	10.1 ± 0.7

Discussion

Most studies investigating epifauna associated with antarctic hard bottom or macroalgal communities have employed either trawl or grab sampling techniques (Dhargalkar et al. 1988; Jaźdźewski et al. 1991a, b). As a consequence of these gross sampling techniques, it is not possible to distinguish whether sampled individuals are associated with a specific living or inert substrate. Moreover, this sampling approach obscures microhabitat-specific quantitative or qualitative evaluations of most mobile epifauna, as many likely escape such disruptive collection techniques. More recent studies in Antarctica have emphasized the analysis of algal-associated epifauna and in some cases have employed underwater sampling techniques (Gambi et al. 1994; Iken et al. 1997, 2000; Takeuchi and Watanabe 2002). In the present study, scuba-based net collections were likely to facilitate effective capture and minimal loss of mesograzers associated with macroalgae.

Total density, species number and diversity of algal-associated amphipod communities

The highest total densities occurred among amphipod communities in association with the most highly branched algal species; *D. menziesii* and *P. cartilagineum* followed by *D. anceps*. The complexity of algal morphology is an important factor in determining habitat preference of amphipods (Hacker and Steneck 1990; Holmlund et al. 1990). Total numbers of amphipod species were moderately high in the highly branched *P. cartilagineum* and the single-bladed alga *G. skottsbergii*. Although *G. skottsbergii* is not a morphologically complex branched algal species (Wiencke and Clayton 2002), and lacks chemical defenses against omnivorous predatory fish (Amsler et al. 2005), its suitability for associated amphipods is unique when compared with other single bladed macroalgae we examined. Specifically, as a result of its multiple haptera, the large flattened blades rest against the benthic substrate, in contrast to remaining upright in the water column as seen in other single-bladed macroalgae. The resultant space between the substrate and ventral blade surface forms a protective retreat for amphipods. In addition, numerous papillae on the surface of *G. skottsbergii* might provide suitable substrate for amphipod clinging.

The lowest numbers of amphipod species were associated with the single-bladed macroalgae *P. decipiens* and *I. cordata*, each harboring only two species. Patterns of species diversity indices for amphipods associated with the eight macroalgae were similar to those seen for amphipod species numbers except for amphipods associated with *D. menziesii*. Here, in striking contrast to its high species number, species diversity was the lowest recorded for any

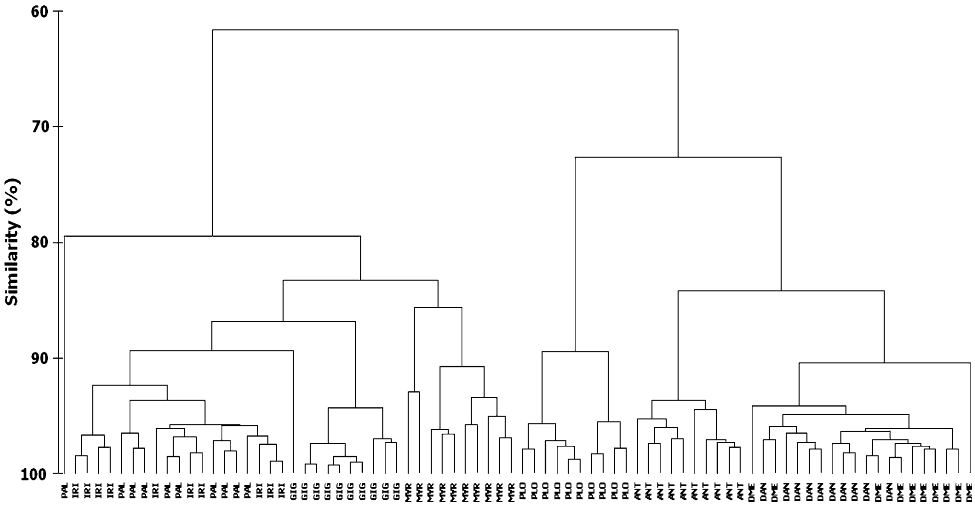

Fig. 6 Bray-Curtis cluster analysis dendrogram generated on the basis of morphometrics of macroalgae. Shown is the percent similarity between ten replicate samples of each of the eight target macroalgae. (Abbreviations given in Fig. 2)

of the targeted macroalgae. This discrepancy is the result of the disproportionate numerical dominance of the amphipod *M. pectinatus* that comprised 87% of those amphipods found in association with this macroalga.

Patterns of amphipod species composition associated with macroalgae

The most abundant amphipod, *M. pectinatus*, occurred on all eight macroalgal species examined but was primarily found on *D. menziesii* where it comprised 94% of total algal-mass standardized amphipod abundance. Moreover, even when small numbers of amphipods occurred in association with other targeted macroalgae, *M. pectinatus* still comprised the greatest fraction. The tight association between *D. menziesii* and *M. pectinatus* would suggest that this alga serves loosely as a host species. Thurston (1972) similarly observed that *M. pectinatus* occurred primarily in association with *Desmarestia* spp., where it likely inhabited tufts of epiphytes on holdfasts. In laboratory feeding bioassays, we found that *M. pectinatus* does not consume measurable amounts of any of the macroalgae with which they are associated in the field including *D. menziesii* (Huang et al. 2006). Microscopic examination of the guts of several *M. pectinatus* revealed fragments of diatom frustules (authors' pers. obs.) suggesting that in the absence of macroalgal grazing, epiphytic diatoms may be an important component of the diet. *D. menziesii* likely serves different functions than food provision. Two factors could explain this association. First, *D. menziesii* has a comparatively complex morphology that includes a high degree of branching that may provide amphipods a physical refuge from predation. Second, Amsler et al. (2005) recently found that *D. menziesii* is chemically defended against the common sympatric omnivorous fish *Notothenia coriiceps*, a species known to include amphipods in its diet (Iken et al. 1997) and by far the most common fish in the study area (authors' pers. obs.). Thus, as has been demonstrated for amphipods associated with macroalgae in tropical and temperate latitudes (Duffy and Hay 1994; Hay 1996, 1997; Sotka et al. 1999), *M. pectinatus* may be exploiting chemically defended macroalgae to avoid fish predation.

The second-most abundant amphipod taxon, *Jassa* spp., occurred on all eight species of macroalgae. In contrast to other herbivorous gammaridean amphipods, *Jassa* spp. are usually considered to be suspension-feeders (Dixon and Moore 1997). While *Jassa* spp. do not appear to have a primary host alga, its comparatively common association with *P. cartilagineum* could be related to the highly branched morphology of this alga (most highly branched of all eight algal species examined) that may provide both a physical and chemical refuge from predation.

The third-most abundant amphipod taxon, *Oradarea* spp., was collected from all the macroalgal species examined except for the red alga *I. cordata*. Gammaridean amphipods of the genus *Oradarea* are characterized by having slender, elongated legs with hooked distal tips (Thurston 1972). These adaptations may facilitate clinging on the fine, highly branched, terete (cylindrical) branches that characterize *D. anceps* and *D.menziesii*, especially the latter (Wiencke and Clayton 2002). Previous gut content analyses suggest that diet may be important in this association as Graeve et al. (2001) found small pieces of *Desmarestia* spp. in gut contents of the herbivorous *Oradarea edentata*.

While the gammaridean *Paradexamine fissicauda* occurred in very low abundance overall, more than 83% of the total 246 individuals collected occurred exclusively on *P. cartilagineum*, a clumpy red alga characterized by unilateral branches. One potential explanation for this close association is that *P. fissicauda* possesses several characteristics that may facilitate its crypticity against visual predators. These include a reddish pigmentation similar to the coloration of *P. cartilagineum*. In addition, the highly spinate pleomeres mimic the morphology of the fine, unilateral branches. This cryptic nature became evident during collections as individuals were difficult to locate amongst the branches of *P. cartilagineum* (Huang, pers.obs.). Similar to *M. pectinatus* possibly associating with its chemically defended host alga, *D. menziesii*, *P. cartilagineum* is chemically defended against a sympatric omnivorous fish (Amsler et al. 2005) and thus may provide *P. fissicauda* a chemical refuge from predation (Duffy and Hay 1994; Hay 1996, 1997). To date it is unknown whether *P. fissicauda* grazes on the tissues of its host alga, *P. cartilagineum*. We were unable to collect sufficient numbers of amphipods to provide adequate replication for feeding bioassays.

In a previous study (Huang et al. 2006), we found that the Antarctic gammaridean amphipods *G. antarctica* and *P. gracilis* generally did not consume macroalgae with which they primarily associate (present study), but did consume other species of sympatric macroalgae. This suggests that structural complexity or algal chemical defenses are more important than dietary preferences in determining patterns of amphipods associated with macroalgae. Total numbers of amphipod species associated with *D. menziesii* and *D. anceps* were the highest recorded for any of the eight macroalgal species examined. As discussed earlier, these two macroalgal species are large, have high numbers of branches per unit wet mass as well as a high degree of branching that renders them complex in their morphology. These traits collectively contribute to a comparatively large volume of interstitial space that likely provides attractive microhabitat for a broad suite of amphipod species. This, coupled with the numerous fine, terete branches provide amphipods a suitable substrate for efficient clinging (Hacker and Steneck 1990), and the chemical feeding deterrent properties of *Desmarestia* spp. against omnivorous fish (Amsler et al. 2005) could contribute to making these macroalgae particularly attractive habitats.

Site-specific patterns of amphipod abundance and species composition

In an effort to evaluate the potential for spatial variability in community structure of macroalgal-associated amphipods, targeted macroalgae and their associated gammaridean amphipods communities were collected from four different locations, each 1–3 km from one another and all within a 3 km radius of Palmer Station. While all eight species of macroalgae were not present at each of the four sampling sites, for each alga it was possible to compare its associated amphipod community with one alternate site. In general, macroalgal-associated amphipod communities were relatively similar at the Hermit Cove, Eichorst Island and Bonaparte Point sites. The dissimilarity values for amphipod communities associated with *P. decipiens* from two collecting sites are likely related to the small sample sizes of amphipods that we found in association with this alga. Amphipod communities associated with *D. anceps* and *P. cartilagineum* were dissimilar across sites (Hermit Wall and Bonaparte Point and Hermit Wall and Eichorst Island, respectively), with lower numbers of amphipods consistently found at the Hermit Wall site. It is possible that these observed dissimilarities are the result of different hydrological conditions that could be expected at Hermit Wall, a site that is exposed to high wave energy and tidal currents (Huang pers. obs.). While we have no direct evidence, it is possible that the ability of gammaridean amphipods to cling to these respective macroalgae is compromised by increased water turbulence. Alternatively, highly turbulent environments may simply be avoided by certain species of amphipods. Finally, we also found that amphipod communities associated with *D. menziesii* were dissimilar at its two collecting sites (Hermit Cove and Bonaparte Point). Here it appears that there were large differences in the relative abundances of amphipods at each of these sites, with higher abundances occurring consistently at Hermit Cove. Macroalgal-associated amphipod species diversity values were not dissimilar between either site.

In summary, our findings indicate that while the structure of species- specific macroalgal-associated amphipod communities can vary across spatial scales of only 3 km (seen in four of 8 macroalgae examined) such differences appear to be species-specific among macroalgae. Thus for select macroalgal species, extrapolating the community dynamics of their associated amphipods from one region to another, even across spatial scales as small as 3 km, is inappropriate. For those 50% of the macroalgal species that had no between-site dissimilarities in their associated amphipod communities, we would argue that macroalgal-specific factors are likely to be mediating the dynamics of their associated amphipod communities.

Relationship between patterns of amphipod communities and algal morphology

The influence of algal morphology on the abundance of amphipod mesograzers has been investigated in several studies (Edgar 1983; Buschmann 1990; Hacker and Steneck 1990; Holmlund et al. 1990; Martin-Smith 1993). The results of our study are similar to those of Hacker and Steneck (1990). Both amphipod abundance and total numbers of species were significantly higher on the most physically complex macroalgal species. Although the cluster analysis dendrograms of amphipod species distributions on individual algal species and the morphometrics of the algal species were not significantly similar, the results of our Spearman Rank Correlation analysis did detect a significant positive correlation between overall amphipod abundances and numbers of algal branches. Amphipods collected from the target macroalgae prefer to inhabit branched algae compared to bladed algae. The contrasting findings of our study and that of Holmlund et al. (1990) may be in part the result of how one defines the ''morphological complexity of algae''. Measures of the complexity of algal morphology are typically linked to the numbers of branches as a function of algal tissue mass. However, this approach is not consistently applicable to different morphotypes of macroalgae. While Holmlund et al. (1990) reported that *Hypnea* spp. had high numbers of branches, the degree of branching is low and the distance from distal branches to the main stipe is small. Consequently, the effective structural complexity that would facilitate mesograzer cover from predators is compromised. In contrast, in the present study *D. menziesii*, *D. anceps*, and *P. cartilagineum* not only have higher numbers of branches per unit mass then *Hypnea* spp. but also have branches with a higher degree of branching. This is particularly evident in both *Desmarestia* species, where the length of the secondary branches and the distance from distal branches to the main stem are great and provide significant interstitial cover from prospective fish predators.

Acknowledgements We thank Anne Fairhead and Kevin Peters for assistance in the field. Assistance with amphipod taxonomy from Kathy Conlan and Ed Hendrycks is very much appreciated. We thank Huichien Kuo for assistance with graphics and SAS programming and five anonymous reviewers for constructive advice on an earlier version of the manuscript. We wish to also thank those individuals employed by Raytheon Polar Services for providing valuable logistical support in Antarctica. This research was facilitated by the generous support of the Office of Polar Programs of the National Science Foundation to C. D. A. and J. B. M. (OPP-0125181) and to B. J. B. (OPP-0125152). Support from an Endowed University Professorship in Polar and Marine Biology to J. B. M. is also acknowledged.

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