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Abundance and diversity of gastropods associated with dominant subtidal macroalgae from the western Antarctic Peninsula

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Abstract Gastropod assemblages associated with eight common macroalgae from the hard-bottom subtidal communities near Palmer Station, western Antarctic Peninsula, were investigated in order to establish a species inventory and determine abundance, distribution, and diversity. Four different sites within the area were sampled. Using SCUBA, selected algae were gently removed from the substrate and enclosed in a fine mesh bag. Shortly thereafter, all epibionts were removed and preserved. Twenty-one different gastropod taxa were identified, two of which not to species level. A total of 3486 individuals were quantified with *Skenella umbilicata* the numerically dominant, followed by *Laevilacunaria antarctica* and *Eatoniella calignosa*. Most individuals (86 %) were <0.5-mm shell length; the largest specimens did not exceed 20-mm shell length. No difference in gastropod species abundance or species diversity was observed between the algal species. Mean densities of a given species of gastropod associated with a given algal species ranged from 0 to 38 individuals per 100 g wet wt of sampled alga with no discernable pattern of algal host preference. Additionally, no consistent pattern of gastropod community composition with either associated macroalgal species or collection site was demonstrated with a non-metric multidimensional scaling analysis. Gastropods may, however, work in concert with other epibionts, in particular amphipod assemblages, to in some way benefit the host alga. Specifically, gastropods may contribute to enhancing the photosynthetic capacity of the host alga by grazing upon fouling epiphytic microalgae and emerging endophytic filaments.

Keywords Gastropod · Macroalga · Antarctic Peninsula · Community structure · Benthic

Introduction

Mollusks, gastropods in particular, are known to be important macroalgal grazers in many worldwide communities (e.g., Underwood 1980; Johnson and Mann 1986; Williams 1993). Yet other than a few limited investigations (Richardson 1977; Iken 1996), little is known of the ecological relationship between Antarctic macroalgae and mollusks. Antarctic and subantarctic benthic mollusks have been collected during oceanographic expeditions dating back to HMS challenger in the 1870s leading to volumes of taxonomic publications (for review see Engl 2012). Recently, over 12000 records of specimens from such expeditions have been incorporated into the Southern Ocean Mollusc Database (SOMBASE) as an effort to advance the understanding of Antarctic malacological biodiversity and biogeography (Griffiths et al. 2003; Linse et al. 2006; Clarke et al. 2007). The majority of SOMBASE records are of specimens collected by bottom dredges or grabs representing primarily deepwater communities from surveys of the Ross and Weddell Seas (e.g., Dell 1964; 1990; Arnaud and Hain 1992). There are relatively fewer records on mollusks from

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shallow water near-shore habitats, particularly those along the western Antarctic Peninsula (WAP).

Perhaps, the most extensive survey of mollusks in near-shore Antarctic marine benthic communities has been done at Signy Island (60°42′S, 54°40′W), at the very northern end of the islands along the WAP (Picken 1980). Each month for a calendar year quadrats of algal-covered benthos was sampled by SCUBA diver-controlled suctioning. Retrieved biomass was sorted by algal and mollusk species and analyzed for seasonal changes in taxon composition and biomass. Due to the indiscriminate sampling technique, it was not possible to determine whether the many mollusks were either in or on the sediment or associated with a particular species of the numerous algal species collected. The collections do, however, serve to identify dominant gastropod members of the Signy Island benthic community.

By comparison, using more refined SCUBA-based sampling, another study at Signy Island quantified mollusk species on a single macroalgal species, the brown alga *Desmarestia anceps* (Richardson 1977). WAP macroalgae are diverse with at least 124 recognized species (Wiencke et al. 2014) and often reach 5–10 wet kg m^{-2} biomass, which is comparable to temperate kelp forests (Wiencke and Amsler 2012). Yet, to our knowledge, no other quantitative survey exists coupling mollusks associated with other species of WAP macroalgae.

Antarctic algae are unique in several respects compared to algal flora of other world ocean regions. Many of the more abundant and common macroalgae of the WAP are chemically defended, an adaptation to prevent herbivory (Amsler et al. 2008, 2009). Nonetheless, these algae may host a wide array of fauna (e.g., fish, crustaceans, and mollusks) (Iken et al. 1997, 1999; Huang et al. 2007), which in other regions of the world ocean can be major grazers on non-defended algae (Schiel and Foster 1986). Another feature of the Antarctic algal flora that is unusual compared to more temperate flora is the general lack of small filamentous macroalgae such as epiphytes (Peters 2003; Amsler et al. 2009). In reality, the filamentous algae are not absent but rather exist as endophytes within macroalgal thalli, probably to escape grazing pressure from abundant grazers such as amphipods (Amsler et al. 2014).

Amphipods, like gastropods, are important macroalgal grazers in many aquatic and marine worldwide communities (Arrontes 1999; Duffy and Hay 2000). Early investigations on the relationship between amphipods and macroalgae in Antarctica were limited in scope; i.e., one amphipod species: one algal species (Richardson 1977) and one amphipod species: a few algal species (Iken 1999). In order to establish a more community-wide understanding of the interactions between amphipods and macroalgae, Huang et al. (2007) quantitatively sampled fauna associated with a suite of macroalgal species common in the subtidal off Anvers Island (64°46′S, 64°04′W), revealing an impressively diverse and abundant amphipod community, which in some cases were algal species dependent.

A number of recent studies have investigated aspects of the relationship between the generally unpalatable WAP macroalgae and associated fauna (reviewed by Amsler et al. 2014). One of the most intriguing aspects of Antarctic macroalgal amphipod dynamics, and also the most germane to the present study, is that the amphipods appear to have a mutualistic relationship with their host macroalgae. By nature of its defensive chemistry, the host macroalga serves the amphipod as a refuge from omnivorous fish predation. In turn, the amphipods benefit the alga by grazing on epiphytic microalgae and emergent endophytic algal filaments that would otherwise impair the host alga's photosynthetic capacity (Amsler et al. 2014).

The objective of the present study is to extend our knowledge of dominant groups of mesograzers associated with WAP macroalgae to include gastropods. The WAP macroalgal-associated epifaunal survey by Huang et al. (2007) encompassed quantitative collections of both associated amphipods and attached mollusks. Using the coincidentally sampled mollusks, we establish a taxonomic inventory of gastropods and evaluate patterns of their abundance, species number and diversity, and community composition across a suite of host macroalgae. Moreover, as macroalgae and their associated fauna were collected from two different local sites for each alga, differences in gastropod distribution and abundance are compared across a local spatial scale. This information facilitates an evaluation of whether gastropods, similar to amphipods, may reduce macroalgal epibionts while at the same time deriving some benefit by associating with chemically defended macroalgae. Our overall findings contribute to better defining the ecological role of gastropods in marine subtidal macroalgal communities of the WAP.

Materials and methods

Study area and sites

The gastropods examined in the present study were obtained as a component of the total macroalgal-associated fauna collected quantitatively in a study of amphipods (Huang et al. 2007). Samples of macroalgae and their associated mesograzers were collected from near-shore subtidal hard-bottom habitats near Palmer Station, Anvers Island, off the central western Antarctic Peninsula (64°46′S, 64°04′W; Fig. 1) in February through April 2003. Samples were collected using SCUBA within a 5 km radius from Palmer Station at four different sampling sites:

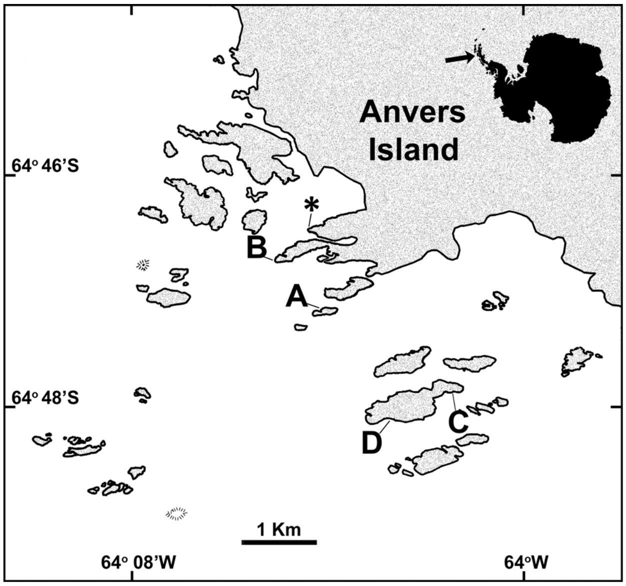

Fig. 1 Sampling locations of subtidal macroalgae and associated gastropods off Anvers Island, Antarctica. Palmer Station (*), Eichorst Island *A*, Bonaparte Point *B*, Hermit Island cove *C*, and Hermit Island wall *D*. The silhouette at the *upper right corner* indicates the Antarctic continent, and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

Eichorst Island (A), Bonaparte Point (B), and two sites off Hermit Island (C, D). Sites were chosen based on the availability of desired algal species and that allowed all eight algal species to be collected in two different of the four sites. Seawater temperatures measured by standard laboratory thermometer in the Palmer Station incoming seawater system were approximately 1 ± 1 °C which is typical of that time interval in other years (Schram et al. 2015). In terms of relative wave energy and currents, the Eichorst Island site is more protected than the Bonaparte Point site. Hermit Island C, in a cove, is the most protected site, while site D, a steep wall on Hermit Island, the most exposed.

Field survey and sample collection

Eight species of macroalgae documented to be common in a survey of subtidal communities of Palmer Station by Amsler et al. (1995) were selected for this study. The sampling included three representative species of brown macroalgae (Desmarestiaceae: *Desmarestia antarctica* Moe and Silva, *Desmarestia menziesii* J Agardh, and *D. anceps* Montagne) and five species of red algae (Plocamiaceae: *Plocamium cartilagineum* (Reinsch) Ricker; Gigartinaceae: *Gigartina skottsbergii* Setchell and Gardner, *Iridaea cordata* (Turner) Bory; Delesseriaceae: *Myriogramme mangini* (Gain) Skottsberg; Palmariaceae: *Palmaria decipiens* (Linnaeus) P F Dixon) (DeLaca and Lipps 1976; Amsler et al. 1995). Ten individual thalli of each of the species were collected from two different locations per site ($n = 5$ samples from each location) for a comparison of small-scale (1–3 km) site-specific variation. The *D. menziesii*, *G. skottsbergii*, and *P. decipiens* were collected from both Bonaparte Point (B) and Hermit Island cove (C); *D. antarctica* was collected from Eichorst Island (A) and Hermit Island cove (C); *D. anceps* was collected from Bonaparte Point (B) and Hermit Island wall (D); *I. chordata* and *M. mangini* were collected from Eichorst Island (A) and Bonaparte Point (B); *P. cartilagineum* was collected from Eichorst Island (A) and Hermit Island wall (D). Sampling depths at the two locations were as similar as possible, and overall sampling ranged from 6 to 16 m.

Biomass of the alga sampled varied between species in part due to morphology. All three of the brown macroalgal species selected are branched, overstory canopy-forming species. For ease of handling, small individual thalli of ~300 g wet wt were collected. Red algae of the WAP, generally more diminutive than the browns, may form a dense understory. Also, red algae are morphologically more diverse than browns, so typical thallus biomass plus morphology guided sampling criteria. *P. cartilagineum* is the most foliose and a representative thallus ~30 g wet wt. Three of the remaining four red algae (*M. mangini*, *I. cordata*, and *P. decipiens*) have a strappy blade-like morphology, and a typical individual collected was 40–150 g wet wt. *G. skottsbergii* is characterized by a thick and leathery sheet-like thallus, and representatives sampled were ~250 g wet wt (see Huang et al. 2007, Table 4 for detailed morphological measurements).

Individual algal thalli were carefully cut from the substrate and gently drifted into the water column with the ambient water motion to minimize dislodging the associated epibionts including particularly highly mobile amphipods. The freed thallus and all associated components were then quickly enclosed within a fine mesh bag (0.25 mm), and the bag opening sealed to prevent escape of epibionts. The algal sample bags were transported in buckets of ambient seawater for processing in the Palmer Station laboratory. All epibionts, including gastropods, were removed from the alga by a combination of thallus shaking, repeated seawater rinses, and hand picking. Dislodged epibionts from each alga were preserved in 5 % formalin, and gastropods were identified to the lowest possible taxon (per Engl 2012) and enumerated. To analyze the gastropod community assemblages, the following variables were calculated: total abundance of individuals, total number of species, and Shannon–Wiener diversity ($H' = -\Sigma_i\, p_i \log_e (p_i)$; p_i is the proportion of the total count). Densities of gastropods were calculated and expressed in terms of individuals per 100 g algal wet wt.

Statistical analyses

Quantitative statistical comparison of gastropod abundance, number of species, and species diversity among algal taxa was conducted with a Kruskal–Wallis test using SPSS software (SPSS Inc.) because the data could not be transformed to meet the assumptions of parametric tests. Post hoc analyses utilized pairwise Mann–Whitney tests (SPSS) corrected for type I error with the Sequential Dunn–Sidak Method (Sokal and Rohlf 1995). Because of the very large number of pairwise comparisons, alpha was set at 0.1 for the error correction. To determine relationships between gastropod communities associated with particular macroalgae, multivariate analyses were conducted using PRIMER-E (Plymouth Marie Laboratory, Plymouth, UK, Clarke and Gorley 2006). Zero data (*I. cordata*) and outlier (*P. decipiens*) were excluded in the following analyses. Since abundances of gastropod species differed by three orders of magnitude, densities and species composition data matrices 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 gastropod communities associated with the selected macroalgae, a Bray–Curtis similarity coefficient was calculated. In addition, a non-metric multidimensional scaling (MDS) analysis was performed on the matrix of gastropod species composition and population densities. To test the ordination, the stress coefficient of Kruskal was used (McCune et al. 2002). Analysis of similarity (ANOSIM) was employed to facilitate a statistical comparison of overall similarities of gastropod species among different macroalgal species. As each macroalgal species was collected from two of the four field sites (five individuals from each of the two sites), we performed ANOSIM to evaluate whether significant differences occurred in gastropod community structure associated with each macroalga collected from different locations.

Results

A total of 3486 individual gastropods were obtained from the eight macroalgal species. Approximately 3000 were <5 mm in shell length, and the remaining individuals were no >20 mm. One species of red alga sampled in the present study, *I. cordata*, was found to be completely devoid of any gastropods. A second red algal species, *P. decipiens*, had only a few *Skenella umbilicata* present and only on two out of the ten *P. decipiens* individuals sampled.

Twenty-one gastropod taxa were identified from the algal collections, and most were identified to the level of species (Table 1). Three individuals could not be identified beyond family Littorinidae despite their excellent condition. Another three individuals were damaged beyond recognition. The majority of the gastropods are herbivorous with the exception of two individuals identifiable only to the genus *Natica*, a taxa characterized by predatory, carnivorous feeding (Dell 1990). The numerically dominant gastropod species were *S. umbilicata* ($n = 2483$), *Laevilacunaria antarctica* ($n = 422$), and *Eatoniella calignosa* ($n = 306$). Mean densities of a given species of gastropod associated with a given algal species ranged from 0 to 38 individuals per 100 g wet wt of the sampled alga.

Total gastropod densities associated with the eight macroalgal species surveyed ranged from zero (*I. cordata*) to 98 (*P. cartilagineum*) individuals/100 g alga (Table 1) and were significantly different from one another ($U_7 = 39.374$; $p < 0.0005$) (Fig. 2a). The high degree of variability observed precluded any definitive intraspecific comparisons. For example, *P. cartilagineum* had the greatest density of gastropods (mean of 89 individuals/100 g wet alga ± 41) but also a high level of variation and as such was not significantly different from any alga except *I. cordata*, which had no gastropods whatsoever.

Both the number of gastropod species and the Shannon Diversity Index (H') associated with each of the eight algal species were significantly different from each other ($U_7 = 49.472$; $p < 0.0005$ and $U_7 = 35.426$; $p < 0.0005$, resp.) (Fig. 2b, c, respectively). The alga *G. skottsbergii* had the highest number of gastropod species (5.6 ± 0.95), followed by *D. anceps* and *D. menziesii* both with approximately 4.5 species. *D. antarctica*, *M. mangini*, and *P. cartilagineum* ranged between 1.3 and 1.9 species. Both *P. decipiens* and *I. cordata* were close to (0.2 ± 0.13) or at zero (Fig. 2b). A similar trend was evident in the Diversity Index (H') with *D. anceps* determined to be the most diverse (0.99 ± 0.85), followed by *G. skottsbergii* (0.84 ± 0.13) and *D. menziesii* (0.71 ± 0.13). *D. antarctica* and *P. cartilagineum* had approximately the same index (0.40), followed by *M. mangini* (0.26 ± 0.11) and last with an index of 0 were both *I. cordata* and *P. decipiens* (Fig. 2c).

Two of the gastropod species identified, *Laevilacunaria bennetti* and *Eatoniella kergulensis regularis*, were found only on the brown algae *D. anceps* and *D. menziesii* (Table 1). Otherwise, no consistent pattern of gastropod species with associated macroalga (algae with no gastropods (zero data) excluded) was apparent as evidenced on a 2D MDS ordination (Fig. 3a). However, significant differences in gastropod densities and species composition were determined across the algal species (ANOSIM global test: $R = 0.31$, $p = 0.001$), and in most cases (11 of 15 ANOSIM pairwise tests; all $p < 0.05$), the differences of gastropod species composition associated with different

Table 1 Species assemblages, number of individuals counted, and mean density (individuals per 100 g algal wet wt) of gastropods associated with eight subtidal Antarctic macroalgae (ten individuals of each algal species sampled)

Gastropod	No. of counted	*Desmarestia antarctica*	*Desmarestia anceps*	*Desmarestia menziesii*	*Gigartina skottsbergii*	*Myriogramme mangini*	*Plocamium cartilagineum*	*Iridaea cordata*	*Palmaria decipiens*
Cingulopsidae									
Skenella umbilicata (Ponder, 1983)	2483	4.36	1.14	28.06	41.11	0.42	36.92	0	1.98
Calliostomatidae									
Margarella antarctica (Lamy, 1905)	34	0	0.13	0.02	1.09	0	0	0	0
Colloniidae									
Leptocollonia innocens	2	0	0	0	0.07	0	0	0	0
Cyclostrematidae									
Cyclostrema meridionale (Melvill & Standen, 1912)	52	1.08	0.02	0.67	0	0	0	0	0
Diaphanidae									
Toledonia palmeri (Dell, 1990)	8	0	0.1	0	0.19	0	0	0	0
Eatoniellidae									
Eatoniella caliginosa (Smith, 1975)	306	0.25	0.78	1	4.76	0.53	38.79	0	0
Eatoniella cana (Ponder, 1983)	9	0	0.2	0	0.11	0	0	0	0
Eatoniella kerguelensis regularis (Smith, 1915)	3	0	0.07	0.02	0	0	0	0	0
Littorinidae									
Laevilacunaria antarctica (v. Martens, 1885)	422	1.07	2.06	4.43	2.25	4.99	18.27	0	0
Laevilacunaria bennetti (Preston, 1916)	2	0	0.03	0.02	0	0	0	0	0
Laevilitorina caliginosa (Gould, 1848)	52	0	0.69	0.61	0.19	0	0.37	0	0
Laevilitorina umbilicata (v. Martens & Pfeffer, 1886)	46	0.1	0.1	0.51	0.52	0.21	1.49	0	0
Pellilitorina pellita (v. Martens, 1885)	7	0	0	0.02	0	0	2.24	0	0
Pellilitorina setosa (Smith, 1875)	29	0	0	0.02	1.05	0	0	0	0
Littorinidae sp. Naticidae	3	0.5	0	0.5	0	0	0	0	0
Natica sp.	2	0	0	0.02	0	0.11	0	0	0
Omalogyridae									
Omalogyra antarctica (Egorova, 1991)	6	0.05	0.07	0	0.11	0	0	0	0
Patellidae									
Nacella polaris (Hombron & Jacquinot, 1841)	5	0.05	0.03	0	0.11	0	0	0	0
Rissoellidae									
Onoba grisea (v. Martens, 1885)	3	0	0	0	0.7	0	0.37	0	0
Onoba kergueleni (Smith, 1875)	7	0	0.7	0	0.19	0	0	0	0
Rissoella powelli (Ponder, 1983)	2	0	0	0	0.07	0	0	0	0
Damaged	3								
Total counted	3486								
Total # individuals/100 g alga		6.38	7.18	34.8	53.19	6.26	98.45	0	1.98

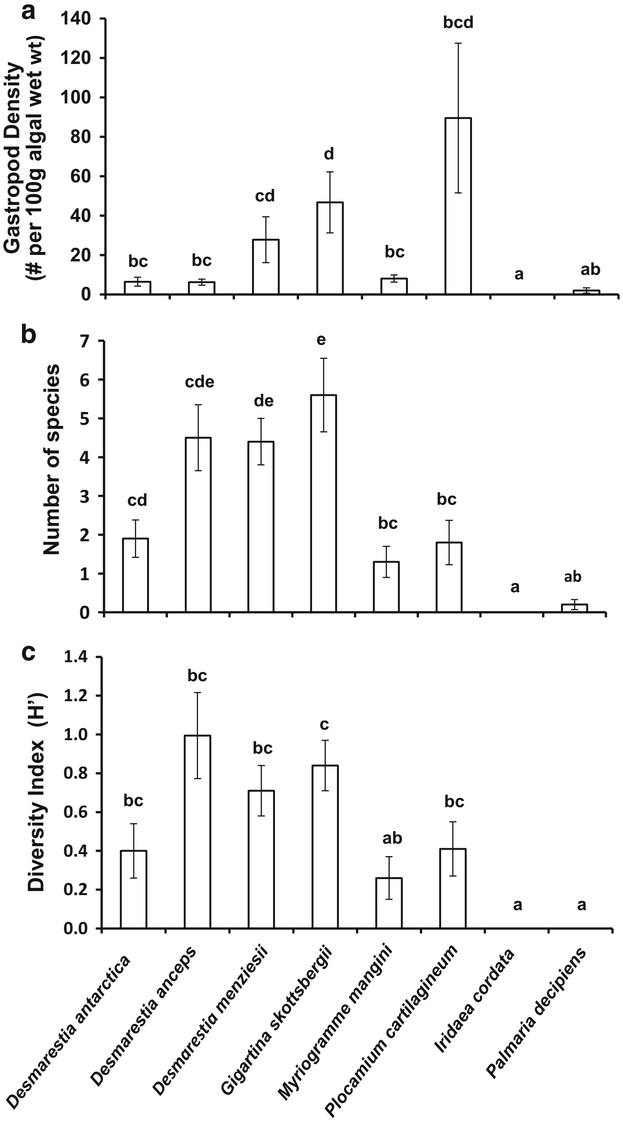

Fig. 2 Total abundances, numbers of species, and diversity indices of gastropods associated with dominant macroalgal species. **a** Total gastropod abundances (individuals per 100 g algal wet wt) associated with eight macroalgal species. Data presented as mean ± SE; $n = 10$. **b** Number of gastropod species (mean ± SE) per alga. Data are mean ± SE; $n = 10$. *Different letters* indicate statistical differences. **c** Diversity index (H') of gastropod assemblages associated with sampled algae. Data are mean ± SE, $n = 10$. *Different letters* indicate statistical differences

algal species were highly significant. Nonetheless, patterns of gastropod species associated with *D. menziesii* and *D. antarctica*, *D. anceps* and *M. mangini*, *D. menziesii* and *G. skottsbergii,* and finally *D. anceps and D. antarctica* did not differ significantly between pairs ($p = 0.367$, 0.139, 0.122, 0.052, respectively). Matching Bray–Curtis cluster analysis dendrogram reinforced the lack of significant pattern observed in MDS ordination analysis (Fig. 3b). An arbitrary cutoff of 50 % on the cluster analysis dendrogram resulted in ten separated groups in which patterns of gastropod species composition associated with algal species remained diversified (Fig. 3b).

In order to determine whether gastropod abundance (individuals per gram wet wt) and composition patterns differ by collection site, we examined algal samples from two different sites for each algal species (n varies due to the exclusion of zero data) (Fig. 3b; Table 2). The results of ANOSIM revealed that gastropod communities associated with *D. menziesii*, *D. anceps*, *G. skottsbergii*, *M. mangini*, and *P. cartilagineum* collected from two sites that included Hermit Island cove, Bonaparte Point, Hermit Island wall, or Eichorst Island were not significantly different ($p > 0.05$). The gastropod abundance and composition patterns associated with *D. antarctica* collected from Hermit Island and Eichorst Island were different ($R = 0.528$, $p = 0.036$). Noteworthy, the sensitivity to heterogeneity and test power to detect important changes in ecological communities will decrease as the differences of unequal sample size comparison increase (Anderson and Walsh 2013). A MDS ordination analysis plot and Bray–Curtis cluster analysis dendrogram based on gastropod abundance and species composition associated with pooled algal species collected from the four sites revealed no consistent visual pattern of community composition (Fig. 2c, 3a); however, significant differences in gastropod densities and species composition were determined across the sampling sites (ANOSIM global test: $R = 0.221$, $p = 0.001$). Abundance and species composition of gastropod communities collected from Bonaparte Point and Eichorst Island are not significantly different (ANOSIM pairwise test: $R = 0.103$, $p = 0.073$).

Discussion

Prior to the present study, three Antarctic macroalgal-associated gastropod taxonomic surveys were available. One of the two studies conducted at Signy Island surveyed a single brown algal species, *D. anceps* (Richardson 1977), on which 29 gastropod species were reported but only the 13 most abundant are detailed. The other survey of gastropods at Signy Island documented 31 species among as many as ten macroalgae collected via indiscriminant suction sampling (Picken 1980). Additionally, a WAP survey in the subtidal of King George Island (62°42′S, 59°36′W) quantified epibionts, including mollusks, on six locally common macroalgae, but only the most abundant species was identified, the remaining gastropods grouped simply as "others" (Iken 1996). In the present WAP-based survey of near-shore subtidal macroalgal communities in the vicinity of Palmer Station, 21 gastropod taxa were identified to occur in association with eight different species of locally common macroalgae. This represents the most extensive

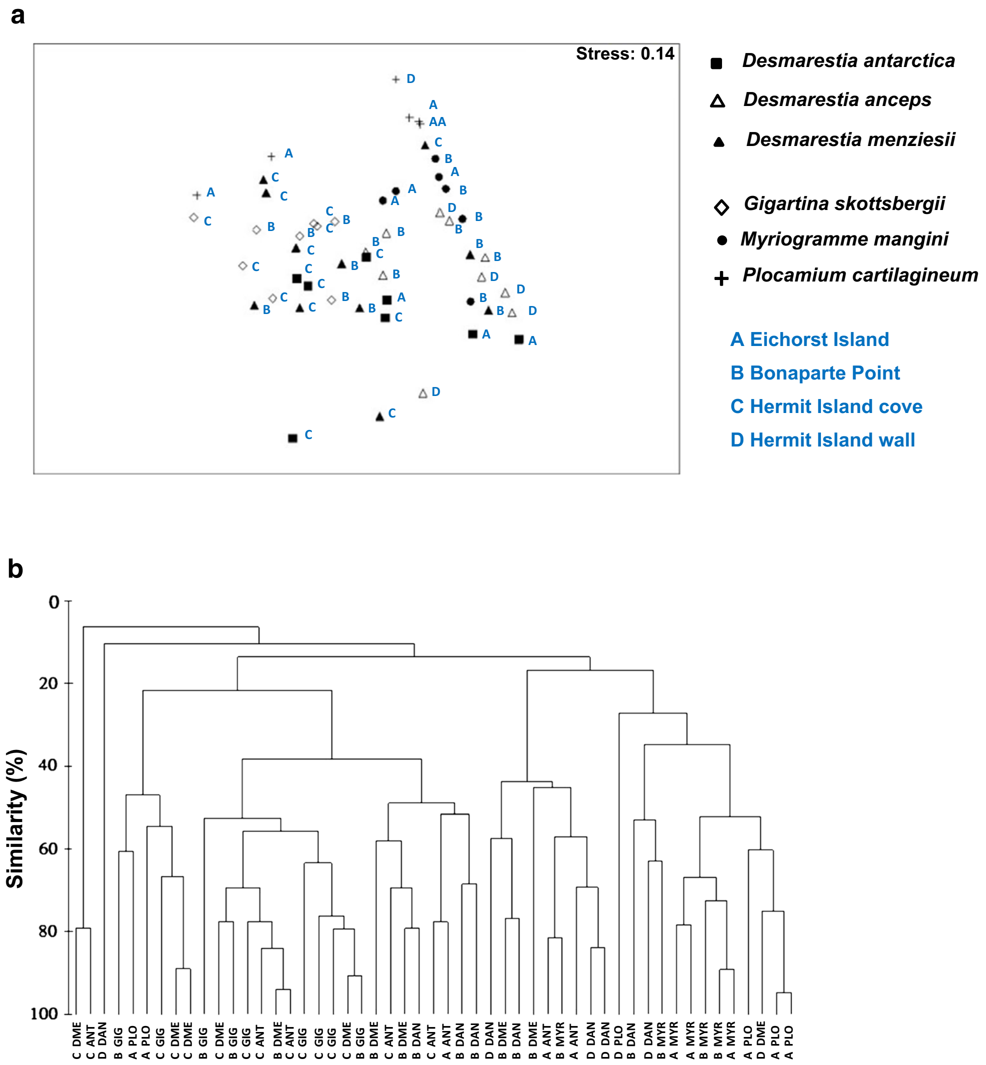

Fig. 3 **a** Multidimensional scaling (MDS) ordination analysis of replicates of each of six macroalgal samples based on both the associated species abundances and compositions of 21 gastropod taxa. The MDS analysis was conducted using standardized and log $(x + 1)$-transformed numbers of gastropods (100 g^{-1} algal wet wt) in association with macroalga and sampling site. The combined data are presented as a two-dimensional scatter graph using x and y variables. Zero data were excluded (stress = 0.14). **b** Bray–Curtis cluster analysis dendrogram generated on the basis of standardized abundances of gastropod species distribution and their relative population densities (individuals 100 g^{-1} wet weight algal tissue). Shown is the percent similarity between replicate samples of each of the seven macroalgae combined with sampling site. Zero data were excluded. ANT = *Desmarestia antarctica*; DAN = *Desmarestia anceps*; DME = *Desmarestia menziesii*; GIG = *Gigartina skottsbergii*; MYR = *Myriogramme mangini*; PLO = *Plocamium cartilagineum*; PAL = *Palmaria decipiens*

quantitative survey of WAP macroalgal-associated gastropods to date. Abundances of gastropods in the vicinity of Palmer Station are considerably lower, both on an individual alga basis and a community-wide level, than that documented in the subtidal of Signy Island during the same months but of different years. When the macroalgal community at Signy Island was indiscriminately sampled, total abundances of gastropods calculated ranged from 1230 to 10,025 individuals/100 wet g macroalga (Picken 1980). These values are six to fifty times greater than the 200 individual/100 wet g value measured in the present study for eight macroalgal species along the central WAP (For comparative purposes, data from both Signy Island investigations were recalculated to standardize units with the present study.) Similarly, on a per alga basis, total gastropod abundance ranged from 119 to 255 individuals/100 wet g *D. anceps* at Signy Island (Richardson 1977). Comparative values in the present study are an order of magnitude lower (1–13 gastropods/100 wet g *D. anceps*). At another WAP site, King George Island, 200 km north of Palmer Station, a similar magnitude and density were reported (20 gastropods/100 wet g *D. anceps* Jan data

Table 2 Analysis of similarity (ANOSIM) between two different sampling sites based on the gastropod community structure associated with the alga sampled

	Hermit Wall	Eichorst Is.	Bonaparte Pt.
Hermit Cove	NA	ANT (0.036)	**DME (0.344) GIG (0.262)**
Bonaparte Pt.	**DAN (0.127)**	**MYR (0.257)**	–
Eichorst Is.	**PLO (0.500)**	–	–

p values are shown in parentheses. Significance levels >0.05 are shown in bold

NA not available

ANT = *Desmarestia antarctica* (5,3); DAN = *Desmarestia anceps* (5,5); DME = *Desmarestia menziesii* (5,5); MYR = *Myriogramme mangini* (4,3); PLO = *Plocamium cartilagineum* (5,1). Zero data excluded sample sizes shown in parentheses (column site, row site)

recalculated, Iken 1996). It must be noted that decades as well as distance separate these WAP and Signy Island studies and perhaps time is a contributing factor in the regional differences. Yet clearly, the subtidal macroalgal community in the near vicinity of Palmer Station and at least one other location on the central WAP do not support the abundance of gastropods seen in the subtidal during the summer months at Signy Island.

The order of magnitude(s) difference gastropod abundance observed in Antarctic subtidal communities is surprising in the light of parallel studies addressing amphipod macroalgal associations, wherein abundance on *D. anceps* at Signy Island ranged from 69 to 435 amphipods/100 g alga (Richardson 1977) compared to an equally variable but at least similar magnitude of 8–269 individuals/100 g *D. anceps* in the Palmer Station subtidal (Huang et al. 2007). This suggests that within Antarctic subtidal communities some components of epibiont populations maintain a steady density across relatively broad geographic regions, as demonstrated here with macroalgal-associated amphipods, whereas other epibionts, gastropods in this scenario, exhibit dramatic latitudinal differences. Perhaps, this indicates that a gastropod latitudinal gradient exists in Antarctic subtidal communities and gastropods are not as influential community drivers as is postulated for amphipods (e.g., Gambi et al. 1994). Additionally, the relatively similar numbers of highly mobile amphipods collected by the comparable sampling methods used by Richardson (1977) and Huang et al. (2007) infer confidence that the observed differences in gastropod numbers between the two surveys are not a function of sampling technique, yet does not rule out shortcomings in sampling design, which apparently suitable for amphipods may not have been optimal for gastropods.

Although gastropod abundances in Antarctic macroalgal communities can differ greatly, the overall rank of gastropod species associated with the brown macroalga *D. anceps* is consistent with *L. antarctica* ranking as the dominant gastropod in the present study as well as in the communities of Signy and King George Islands. In decreasing order, the second most abundant gastropod on Signy Island *D. anceps* was *Eatoniella* spp., followed by *Onoba* spp. and finally *Cyclostrema meridionalis* (Richardson 1977). Comparatively, on *D. anceps* collected in the present study at Palmer Station the second most abundant gastropod species was *S. umbilicata* followed by *C. meridionalis* and *Eatoniella* spp. The non-dominant gastropods in the King George Island study were not listed (Iken 1996). Thus, despite notable differences in patterns of gastropod abundance between Signy Island and Palmer Station on the WAP, at least with regard to the brown macroalga *D. anceps*, the incidence of dominant gastropod taxa is similar. Accordingly, geographically distinct communities may exhibit quantitative differences in gastropod abundances yet retain qualitative similarities in gastropod assemblages.

Numerous studies in temperate and tropical systems demonstrate that macroalgal shape and architecture can influence epibiont assemblages, including gastropods (see Williams and Seed 1992). For instance, in the Mediterranean, gastropod abundance and diversity on six macroalgal species varied significantly correlating with algal metrics including the degree of branching (Chemello and Milazzo 2002). Despite morphological variations among the eight algal species investigated, our results indicate no such algal associational patterns evidenced by a lack of statistical variation in both gastropod species diversity and species abundances on the eight common and morphologically different macroalgae. Interestingly, studies conducted in Terra Nova Bay (Ross Sea, Antarctica) found significant differences in the diversity of epiphytic diatom species on three different species of red macroalgae including bladed *I. cordata* and highly branched *P. cartilagineum* (Majewska et al. 2013a, b). Yet in the present study, gastropods were absent on all replicates of *I. cordata* and extremely variable on *P. cartilagineum.* The majority of the gastropod species in the present study are herbivorous, bearing a taenioglossan radula characterized by chitinous teeth and musculature unsuitable for cutting, but better for scraping diatoms and filamentous material than for cutting into surfaces (Steneck and Watling 1982). Although the present study did not encompass measures of food preference such as direct feeding observations or gut content analyses, the data in the present study suggest that the epiphytic diatom and filamentous algal assemblages associated with a given macroalga, rather than the macroalga's shape or architecture, could influence the composition of the gastropod assemblage. Investigations of gastropod food preferences are necessary to evaluate this possibility.

Collections of the chemically defended red alga *P. cartilagineum* at King George Island (Iken 1996) documented a wide range of algal-associated gastropods and amphipods similar to that determined in the present study and that reported in Huang et al. (2007). The recalculated density of gastropods associated with *P. cartilagineum* at King George Island ranged from 191 to 577 gastropods/100 wet g alga. The dominant gastropod species, *L. antarctica*, ranged from 18 to 143 individuals/100 wet g alga. These densities are one to three times higher than the present study (0–257 gastropods/100 wet g and 0–40 *L. antarctica*/100 wet g *P. cartilagineum*). An even greater magnitude difference in mesograzer density was noted in terms of amphipods, with 125–897 amphipods/100 wet g at King George (Iken 1996) and 0–700 amphipods/100 wet g at Palmer Station (Huang et al. 2007) found in association with the red alga *P. cartilagineum*. The high variability in both gastropods and amphipods densities between these studies could be explained by either the quantity or quality of secondary metabolites of individual *P. cartilagineum*. Recently, Young et al. (2013) found that individuals of *P. cartilagineum* have unique secondary metabolite signatures and can be grouped into distinct chemotypes. It is possible that in addition to influencing observed variations in amphipod herbivory (Amsler et al. 2013), defensive secondary metabolite chemogroups may also influence microhabitat selection in associated amphipods and gastropods. Furthermore, mobility differences between amphipods and gastropods likely influence their macroalgal association. Some amphipod species exhibit active habitat choice in the presence of a sympatric predator significantly choosing a chemically defended alga over a non-defended species (Zamzow et al. 2010). In contrast, gastropods are less mobile and their movement between "algal islands" is not as common as that of amphipods. Hence, the patterns of gastropod distribution in association with macroalgae may in large part be due to passive dispersal and driven by local hydrological features (Gutow et al. 2009; Tuya et al. 2009).

Out of the 3486 gastropods enumerated in the present study, the majority of individuals had shell lengths smaller than 0.5 mm. This finding supports predictions and observations that species assemblages of mollusks at high latitudes have a greater percentage of smaller-sized species than those at lower latitudes (Schiaparelli and Linse 2014). While in other animal groups gigantism is observed at higher latitudes (e.g., Chapelle and Peck 1999) conceivable factors driving selection for smaller body size at higher latitude have included the possibility of an increased cost of incorporating calcium carbonate into the production of shells at low temperature (Nicol 1978; Picken 1980), the lack of a need for a refuge in size given the absence of crushing predators in the Antarctic benthos (Aronson et al. 2007), or decreased growth, development, or metabolic rates with lower temperatures (cf. Watson et al. 2012).

Regarding the role of gastropods in community dynamics in near-shore subtidal macroalgal communities of the WAP, the present study suggests gastropods may play a less important role than that of amphipods. Studies on mesograzer–macroalgal interactions have highlighted the critical role that amphipods play in the maintenance of algal thalli by grazing epiphytic microalgae and emergent endophyte filaments (Amsler et al. 2014). Macroalgal-associated gastropods, due to their small size, comparatively low abundance, and absence of cutting mouthparts, are unlikely direct consumers of their chemically defended macroalgal hosts. A more probable scenario is that gastropods augment amphipods as grazers of epiphytic microalgae and emergent endophytic filaments. These concerted grazing activities counteract biofouling and enhance the photosynthetic capacity of ecologically dominant macroalgae.

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