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RESEARCH/REVIEW ARTICLE

Sponge richness on algae-dominated rocky reefs in the western Antarctic Peninsula and the Magellan Strait

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Abstract

Sponges are important components of high-latitude benthic communities, but their diversity and abundance in algal-dominated rocky reefs has been underestimated because of the difficulty of in situ identification. Further, the influence of canopy-forming algae on sponge richness has been poorly studied in southern high-latitude rocky reefs compared to other latitudes. Here, we quantified taxon richness of sponges in algae-dominated rocky reefs at three sites in the western Antarctic Peninsula (62–64° S) and two sites in the Magellan region (53° S). We found higher sponge richness at sites in Antarctica (15) than in Magallanes (8), with Antarctic sponge richness higher than that reported for Arctic algal beds and similar to that reported for temperate regions. Estimated sponge richness at our Antarctic sites highlights diverse sponge assemblages (16–26 taxa) between 5 and 20 m that are typically dominated by macroalgae. Our results suggest that sponge assemblages associated with canopy-forming macroalgae on southern high-latitude reefs are more diverse than previously thought.

Despite the abundance and diversity of sponges generally being considered to be negatively correlated with macroalgae (Bell & Barnes 2000; Cárdenas et al. 2012), some studies have reported positive associations between canopy-forming algae and sponges (Wright et al. 1997; Ávila et al. 2010; Cárdenas et al. 2016). This suggests that some sponge species might benefit from the presence of canopy-forming algae that provide sponges with protection within their holdfasts or alter the abiotic and biotic environment in ways that favour sponges, for example, by reducing ambient light and/or competition (Cárdenas et al. 2016). However, the associations between canopy-forming algae and sponge richness and diversity, and how these relationships change across latitudinal gradients are not well understood.

Shallow-water rocky reefs in the western Antarctic Peninsula are characterized by the presence of algae-dominated benthic communities (Zamorano 1983; Amsler

et al. 1995; Valdivia et al. 2015). In general, macroalgae dominate the substrate from 5 to 25 m depth, with sponges and other filter-feeding organisms dominating diversity and abundance at depths greater than ca. 25 m (Zamorano 1983; Barnes 1995a, b). Despite sponges being important members of Antarctic benthic communities (McClintock et al. 2005; Janussen & Downey 2014), the diversity and abundance of sponges are likely to have been underestimated in many surveys and studies of shallow-water benthic communities as they are considered taxonomically challenging and are hard to identify in the field (Bell & Barnes 2001; Ávila et al. 2015). This has led to a general view that sponges are depauperate on Antarctic Peninsular algae-dominated reefs in shallow water (<25 m) since they have not been recorded in most studies or have been treated as one species/group (e.g., Sakurai et al. 1996; Valdivia et al. 2015). Therefore, only limited information is available on

the diversity and abundance of subcanopy sponges, and data is only available for a few sites in King George Island (South Shetland Islands) and Wilkes Land in East Antarctica (Clark et al. 2011; Newcombe & Cárdenas 2011). The sub-Antarctic part of the Magellan region hosts dense beds of brown algae (*Macrocystis pyrifera* and *Lessonia* spp.); however, these communities are arguably less well studied than their Antarctic equivalents.

The impacts of climate change have the potential to have dramatic effects on shallow-water benthic communities, as significant changes in light regimes associated with sea-ice cover may produce shifts from algae- to invertebrate-dominated communities or vice versa (Clark et al. 2013; Clark et al. 2015). Determining the consequences of stable-state shifts from algal to invertebrate-dominated communities on sponge diversity and abundance requires an understanding of current spatial and temporal patterns in shallow-water sponge assemblages and their relationship with canopy-forming algae. These insights may be further strengthened by contrasting the relationship between canopy-forming algae and sponges between areas with different abiotic conditions (e.g., along latitudinal gradients).

The aim of this study was to quantify the taxon richness of sponges associated with canopy-forming algae in King George Island and Doumer Island, Antarctic Peninsula and the Magellan Strait. We also aimed to compare observed and estimated sponge richness from southern high-latitude algal beds with those reported from other latitudes.

Materials and methods

Algae-dominated rocky reefs were opportunistically sampled at three sites on the Antarctic Peninsula—Collins and Fildes bays (South Shetland Islands) and South Bay (Doumer Island)—and two sites in the Magellan region—Fuerte Bulnes and Puerto del Hambre (see Table 1 for descriptions of dominant macroalgal types). At each site, a

series of 0.5 m² quadrats were haphazardly placed and photographed. In Antarctica, photoquadrats were sampled from 10 to 20 m depth, whereas in the Magellan region, photoquadrats in *Lessonia* beds were taken at 1 m depth, and photoquadrats in *Macrocystis pyrifera* beds were taken at 5 m depth. Sponges were either identified to the lowest possible taxonomic level from photoquadrats, using the image analysis software CPCe version 3.5 (Kohler & Gill 2006) or tissue samples, following the procedure described by Hajdu et al. (2011). We also used photoquadrats to quantify the direct (i.e., those using holdfasts as substratum) and indirect (i.e., those attached to the rock surface) associations of sponges with canopy-forming algae.

We estimated taxon richness and occurrence of sponges for each site, with occurrence calculated as the percentage of the total number of quadrats sampled at each site in which a taxon was found. Variation in taxon richness between sites was calculated using the non-parametric estimator $Chao2 = S_{obs} + (Q_1)^2/2(Q_2)$, where S_{obs} is the number of species observed in the total data set, Q_1 is number of species found at only one sample and Q_2 species found in two samples. $Chao2$ was calculated using EstimateS version 9.1 (Colwell 2013) and provides robust estimates of true species richness even for a low number of samples (Gotelli & Colwell 2010).

We also collected 10–15 holdfasts of *Himantothallus grandifolius* and *Desmarestia* spp. in Antarctica, and *Lessonia* spp. and *M. pyrifera* in the Magellan region. We used Spearman's rank correlations to test for correlations between holdfast volume (determined by water displacement) and the number of epithetic sponge individuals.

Results and discussion

We recorded a total of 42 Demospongiae and 1 Calcarea taxa (Table 2). In Antarctica, observed taxon richness ranged between 15 taxa in Collins Bay and 10 taxa in Fildes and South bays (Fig. 1a). In the Magellan region, the

Table 1 The location of each of our study sites on the western Antarctic Peninsula and the Magellan Strait and the dominant canopy-forming algae present.

Region	Site	Coordinates	Dominant macroalgae
Antarctica	Nebles Point, Collins Bay	62° 11' 02" S; 58° 51' 14" W	<i>Desmarestia menziesii</i> and <i>D. anceps</i>
	Albatross Islet, Fildes Bay	62° 12' 17" S; 58° 56' 47" W	<i>Himantothallus grandifolius</i> (Newcombe & Cárdenas 2011)
	South Bay, Doumer Island, Palmer Archipelago	64° 52' 32" S; 63° 35' 02" W	<i>Himantothallus grandifolius</i> (Zamorano 1983)
Magellan Strait	Fuerte Bulnes	53° 37' 34" S; 70° 55' 32" W	<i>Lessonia</i> spp. in the shallows (1–2 m)
	Puerto del Hambre	53° 36' 57" S; 70° 55' 43" W	<i>Macrocystis pyrifera</i> form dense beds from 3 to 12 m depth, being gradually replaced by <i>Lessonia</i> spp. in deeper waters (10–15 m) (Newcombe & Cárdenas 2011)

Table 2 Sponges associated with canopy-forming algae at sites in Antarctica and Magallanes. Asterisks indicate direct associations between sponge taxa and algal holdfasts. Operational taxonomic unit is abbreviated to OTU.

Site (no. of quadrats sampled)	Algae	Sponge taxa	Occurrence (%)
Antarctica			
Collins (14)			
	<i>Desmarestia</i> spp.	<i>Cribochalina</i> sp.	21
		* <i>Haliclona</i> (<i>Gellius</i>) sp. 1	14
		<i>Haliclona</i> (<i>Gellius</i>) sp. 2	7
		* <i>Clathria</i> (<i>Thalysias</i>) sp.	7
		<i>Dendrilla antarctica</i>	14
		<i>Dendrilla</i> sp.	7
		<i>Iophon</i> sp. 1	14
		<i>Iophon</i> sp. 2	7
		cf. <i>Myxilla</i> sp.	7
		<i>Artemisia</i> cf. <i>jovis</i>	14
		<i>Megaciella</i> sp.	7
		<i>Hemigellius</i> sp.	7
		<i>Phorbas</i> sp.	14
		Haplosclerida unidentified (OTU1)	7
		Demospongiae unidentified (OTU2)	7
Fildes (8)			
	<i>H. grandifolius</i>	<i>Dendrilla antarctica</i>	25
		<i>Haliclona</i> (<i>Gellius</i>) cf. <i>cucurbitiformis</i>	13
		<i>Sphaerotylus antarcticus</i>	13
		<i>Polymastia invaginata</i>	13
		<i>Iophon</i> cf. <i>unicorne</i>	13
		Demospongiae unidentified (OTU3)	13
		Demospongiae unidentified (OTU4)	13
		Demospongiae unidentified (OTU5)	13
		Demospongiae unidentified (OTU6)	13
		Demospongiae unidentified (OTU7)	13
Doumer (20)			
	<i>H. grandifolius</i>	<i>Mycale</i> (<i>Oxymycale</i>) <i>acerata</i>	35
		<i>Kirkpatrickia variolosa</i>	5
		<i>Dendrilla antarctica</i>	15
		<i>Hemigellius</i> sp.	15
		<i>Haliclona</i> (<i>Rhizoniera</i>) sp.	15
		<i>Clathria</i> sp. 1	5
		cf. <i>Myxilla</i> sp.	10
		<i>Dragmacidon</i> sp.	15
		<i>Haliclona</i> (<i>Gellius</i>) sp. 2	5
		<i>Sphaerotylus antarcticus</i>	5
Magallanes			
Bulnes (15)			
	<i>M. pyrifera</i>	<i>Suberites</i> sp.	7
		* <i>Haliclona</i> cf. <i>porcelana</i>	7
		<i>Mycale</i> (<i>Aegogropila</i>) <i>magellanica</i>	13
		<i>Phorbas</i> cf. <i>shackeltoni</i>	13
		* <i>Amphimedon</i> cf. <i>maresi</i>	7
		<i>Halichondria</i> (<i>Eumastia</i>) <i>atenuata</i>	7
		<i>Tedania</i> sp.	13
		Haplosclerida unidentified (OTU9)	7
Hambre (5)			
	<i>M. pyrifera</i>	* <i>Clathrina</i> sp.	20
		<i>Halichondria</i> unidentified (OTU10)	20

Table 2 (Continued)

Site (no. of quadrats sampled)	Algae	Sponge taxa	Occurrence (%)
Bulnes (14)			
	<i>Lessonia</i> spp.	* <i>Haliclona</i> cf. <i>porcelana</i>	14
		* <i>Halisarca</i> sp.	14
		<i>Scopalina</i> sp.	50
Hambre (15)			
	<i>Lessonia</i> spp.	* <i>Scopalina</i> sp.	80
		<i>Clathria</i> sp. 2	40
		<i>Halichondria</i> unidentified (OTU10)	20
		Demospongia unidentified (OTU11)	20

observed taxon richness ranged between two taxa in *Macrocystis pyrifera* beds at Puerto del Hambre and eight taxa in *Lessonia* and *M. pyrifera* beds at Bulnes (Fig. 1a). Lower sponge richness within *M. pyrifera* beds at Puerto del Hambre may be explained by the substrate being mainly unstable boulders (Newcombe & Cárdenas 2011), whereas lower taxon richness within shallow *Lessonia* beds may be due to increased wave action and ultraviolet radiation, both of which can be detrimental for many sponge species (Wilkinson & Vacelet 1979; Roberts et al. 2006).

The *Chao2* index estimated higher sponge richness for Antarctic than Magellan sites (Fig. 1b). Although the accumulation curves suggest Antarctic sponge richness was highest at Fildes Bay (26 taxa), sponge richness at Collins Bay (21 taxa) and Doumer Island (16 taxa) did not reach an asymptote, suggesting substantial undiscovered sponge biodiversity at these locations (Fig. 1b). Magellan sites had estimated taxon richness of 10 and three taxa in *M. pyrifera* beds at Fuerte Bulnes and Puerto del Hambre, respectively (Fig. 1b), and four and three taxa were in *Lessonia* beds in Hambre and Bulnes, respectively.

The sponges *Dendrilla antarctica* and *Cribochalina* sp. were the most frequent taxa in Collins and Fildes Bays, whereas *Mycale* (*Oxymycale*) *acerata* was the most common species at Doumer Island (Table 2). In Magallanes, the encrusting species *Scopalina* sp. was the most common species in shallow-water *Lessonia* beds. Massive sponges such as *Mycale* (*Aegogropila*) *magellanica*, *Tedania* sp. and the encrusting *Phorbas* cf. *shackeltoni* were the most common species in *M. pyrifera* beds at Fuerte Bulnes (Table 2).

Of the 43 sponge taxa recorded, only two were directly associated with holdfasts in Antarctica, compared to five in Magallanes (Table 2); however, none of these taxa exclusively associated with holdfasts and they were more commonly found on rock surfaces underneath the canopy. In Antarctica, the number of sponge individuals was positively correlated with the volume of *Desmarestia*

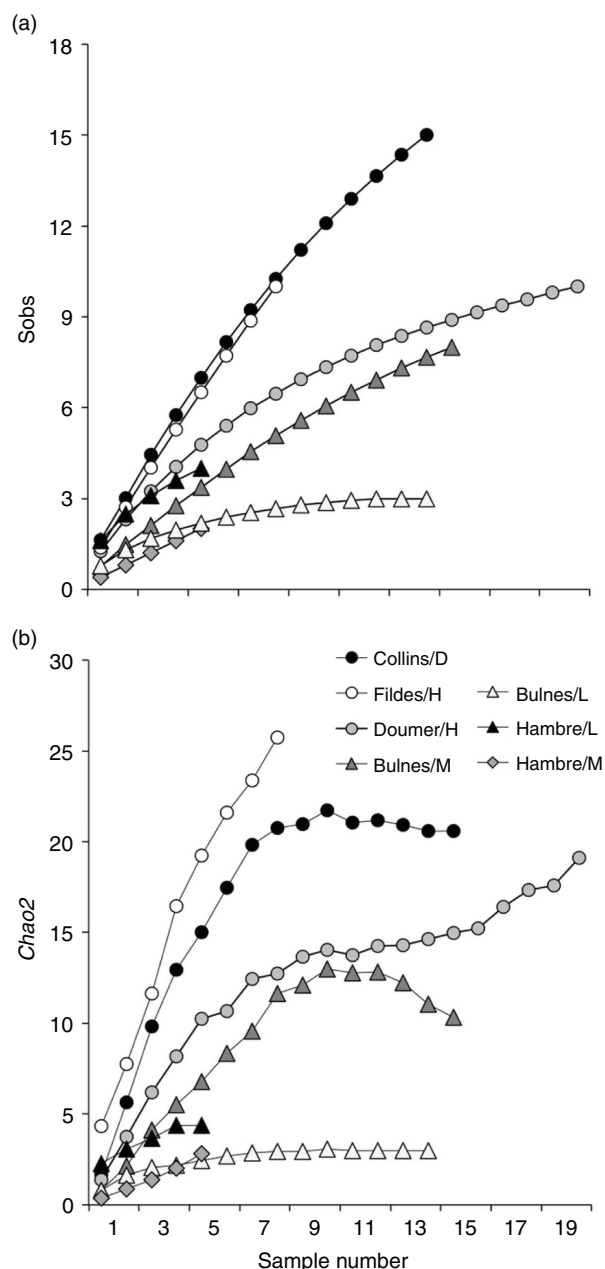


Fig. 1 The taxon richness of sponges associated with canopy-forming algae as a function of the number of quadrats sampled at sites in Antarctica (circles) and Magallanes (triangles). (a) Observed sponge richness and (b) estimated sponge richness by using *Chao2* estimate. Plotted values of *Chao2* are based on 100 randomizations of sample order. Note that the scale on the Y axis differs between panels.

spp. holdfasts, with sponges typically colonizing large holdfasts, 200–900 cm³ in size (Spearman rank = 0.805, $P = 0.015$). Sponges were associated with *Desmarestia* in 28.6% of the holdfast analysed (Table 2). Conversely, sponges were not epithetic on *Himantothallus grandifolius* holdfasts, which may be explained by the small volume

and morphology of holdfasts or by chemical defences, as it has been previously demonstrated (Amsler et al. 2005). In the Magellan Strait, sponges were positively correlated with *Lessonia* spp. holdfast in the shallows (Spearman rank = 0.809, $P = 0.009$). However, there was only a low correlation with holdfasts of *M. pyrifera* and no relationship with holdfast volume (Spearman rank = 0.174, $P = 0.607$).

With a few exceptions (e.g., Wright et al. 1997; Cárdenas et al. 2016), most studies from other latitudes have focused on sponges directly associated with holdfasts (e.g., Smith et al. 1996). Further, previous research on *Lessonia* spp. and *M. pyrifera* in northern and central Chile (21 sites from 20° to 40° S) has either not reported sponges (Ojeda & Santelices 1984; Villouta & Santelices 1984) or has reported them as a group (Vásquez & Santelices 1984), although López-Gappa et al. (1982) did report sponges in very low abundance on the Atlantic coast of Patagonia (47° S). Our results begin to address this existing knowledge gap by demonstrating that in high-latitude algal beds sponges form not only direct associations with holdfasts, but also indirect associations. Our results also suggest the existence of richer sponge assemblages than previously described for Antarctic and sub-Antarctic latitudes (see Dayton et al. 1974; Zamorano 1983; Ojeda & Santelices 1984; Barnes & Brockington 2003; Bowden 2005; McClintock et al. 2005; Clark et al. 2011). We observed sponge richness in the western Antarctic Peninsula to be higher than that previously reported in: (i) East Antarctica (seven taxa) by Clark et al. (2011), (ii) Arctic macroalgal beds (two–three taxa) by Lippert et al. (2001) and Włodarska-Kowalczyk et al. (2009) and (iii) mixed kelp beds of *Ecklonia radiata* and *M. pyrifera* (7 taxa) on the south coast of Wellington, New Zealand, by Cárdenas (unpubl. data). Sponge richness reported by our study is comparable or higher than temperate kelp beds of *Sargassum* spp. (12 taxa) in Baja California, Mexico (Ávila et al. 2010).

Results from our study suggest that canopy-forming macroalgae may play an important role in structuring sponge assemblages on Antarctic shallow rocky reefs. It is possible that canopy-formers may help maintain sponge richness in highly disturbed areas in the western Antarctic Peninsula. Further manipulative studies, however, may provide more information that will clarify if canopy plays a positive effect on sponge species. In contrast, the role of canopy-formers may play a different role as the impact of fast ice or ice-scour is absent in the study area (Cárdenas & Montiel 2015). Instead, protection from waves and high irradiance may be more relevant, especially for sponges in the shallows.

In recent years, there has been a growing amount of research examining impacts of global climate change and ocean acidification on sponges and their relationship with canopy-forming algae (e.g., Bell et al. 2015; Cárdenas et al. 2016); however, little is known about potential impacts of predicted changes in water temperature, pH and turbidity on sponges and their relationships with macroalgae (but see Duckworth & Peterson 2012; Schoenrock et al. 2015). Baseline information, such as that presented here, combined with experimental research will further our understanding of the drivers of current diversity patterns and potential impacts of climate change and ocean acidification on high-latitude sponges and their relationships with other members of shallow-water benthic communities.

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