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RESEARCH/REVIEW ARTICLE

Sessile macro-epibiotic community of solitary ascidians, ecosystem engineers in soft substrates of Potter Cove, Antarctica

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Abstract

The muddy bottoms of inner Potter Cove, King George Island (Isla 25 de Mayo), South Shetlands, Antarctica, show a high density and richness of macrobenthic species, particularly ascidians. In other areas, ascidians have been reported to play the role of ecosystem engineers, as they support a significant number of epibionts, increasing benthic diversity. In this study, a total of 21 sessile macro-epibiotic taxa present on the ascidian species *Corella antarctica* Sluiter, 1905, *Cnemidocarpa verrucosa* (Lesson, 1830) and *Molgula pedunculata* Herdman, 1881 were identified, with Bryozoa being the most diverse. There were differences between the three ascidian species in terms of richness, percent cover and diversity of sessile macro-epibionts. The morphological characteristics of the tunic surface, the available area for colonization (and its relation with the age of the basibiont individuals) and the pH of the ascidian tunic seem to explain the observed differences. Recent environmental changes in the study area (increase of suspended particulate matter caused by glaciers retreat) have been related to observed shifts in the benthic community structure, negatively affecting the abundance and distribution of the studied ascidian species. Considering the diversity of sessile macro-epibionts found on these species, the impact of environmental shifts may be greater than that estimated so far.

In coastal marine environments, the availability of substrate is one of the main factors influencing the distribution and abundance of macrobenthic sessile organisms. Obtaining a suitable substrate for recruitment is an important event in the life cycle of any sessile benthic organism (Connell & Keough 1985; Wahl 1989). To optimize space, some species have developed the ability to establish themselves on secondary substrates consisting of other organisms, a phenomenon known as epibiosis (Harder 2008; Wahl 2009). This can contribute to generating complex three-dimensional structures and increased diversity in benthic assemblages (Gutt & Schickan 1998; Barnes 2001).

Various factors may influence the intensity of epibiosis, especially seasonality, latitude and depth (Wahl 1989; Barnes 1994; Vasconcelos et al. 2007). Other biological and physical processes, such as competitive interactions, predation or physical abrasion by water movement, can also determine the development of epibiotic communities (Ward & Thorpe 1991). However, epibiosis depends mostly on the epibiont/basibiont species interaction. A high degree of specialization in epibiotic communities has been detected related to the morphological and physicochemical features of the basibiont, that is, shape, surface area, texture (Sebens 1991; Harder 2008) and its antifouling substances (Nylund & Pavia 2005). In the particular case of ascidians, some chemical characteristics, such as vanadium concentration (Odate & Pawlik 2007; Koplovitz et al. 2009), production of secondary metabolites (McClintock et al. 2004) and acid pH (Stoecker 1978, 1980), may help to prevent epibiosis.

Ecosystem engineers are organisms that directly, or indirectly, control the availability of resources to other life forms by causing changes in physical states, that is,

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modifying or even increasing habitat heterogeneity (Jones et al. 1994; Wright & Jones 2006). Ascidians often act as ecosystem engineers and enhance local diversity by providing living habitat for some groups of epibionts, such as algae and sponges (Monteiro et al. 2002; Castilla et al. 2004; Voultsiadou et al. 2007).

In Potter Cove, the surrounding Fourcade Glacier has been significantly retreating over the last two decades (Rückamp et al. 2011). This has led to changes in hydrographical parameters, such as an increase in suspended particulate matter (Schloss et al. 2012). These may have caused the changes observed in macro-epibenthic community structure, including the decline of solitary ascidian populations and their replacement by other taxa, such as pennatulids (Sahade et al. 2008), which have greater capacity to cope with higher suspended particle concentrations (Torre et al. 2012), but which are not suitable substrata for epibionts.

Although it has been suggested that solitary ascidians are important as a substrate for sessile macro-epibionts in Potter Cove (Tatián et al. 1998), no studies have so far been performed to understand the composition of their sessile epibiotic communities.

The aim of this study is to describe and compare the diversity of sessile macrobenthic taxa living on the outer tunic of three of the most conspicuous solitary ascidian species inhabiting soft bottoms at Potter Cove. The results will make it possible to evaluate sessile macro-epibiotic community changes in the study area and in other nearby Antarctic coastal ecosystems, in a context of shifts mediated by the global change.

Materials and methods

Study area and sampling

Potter Cove, where the Argentine Carlini (formerly Jubany) Station and the Argentine–German Dallmann laboratory are situated, is an inlet of the larger Maxwell Bay, at King George Island (Isla 25 de Mayo), South Shetlands, Antarctica (62°14′S, 58°38′W). The cove is 4 km long and 2.5 km wide and has a maximum depth of 100 m (Schloss et al. 2012). The inner cove, characterized by soft bottoms, is dominated by suspension feeders, mainly solitary ascidians (Sahade et al. 1998).

Individuals of the most abundant solitary ascidian species were collected haphazardly during February 2004. These species, which can reach a large size, were: *Corella antarctica* (= *C. eumyota*: Alurralde et al. 2013), $n = 10$ (8 to 13 cm in length); *Cnemidocarpa verrucosa*, $n = 9$ (3.5 to 10 cm in length) and *Molgula pedunculata*, $n = 9$ (8–14.5 cm in length) (Fig. 1). Individuals were carefully taken by SCUBA diving from the muddy bottom of the inner cove at a depth of 30 m. Immediately after sampling, they were photographed and then fixed and stored in 2.5% formaldehyde in seawater for analysis. The tunic pH was determined on fresh individuals collected during January 2013 (see below). *Corella antarctica* has a flattened ovate body, with a cartilaginous tunic, and a smooth surface except in the dorsal area, where it can have some shallow grooves. Large individuals may reach 24 cm in length (Tatián et al. 1998). The species *C. verrucosa* is spherical or more or less cylindrical in shape. This ascidian has a resistant, rough tunic due to the presence of conical papillae ending in fine, transversely arranged spines, more abundant in the area of the siphons but less developed in very large specimens. Larger individuals can reach 18 cm in length (Kott 1969). *Molgula pedunculata* has an ovoid or rectangular erect body, supported by a peduncle of variable length, reaching a total length of 30 cm (Herdman 1882). The tunic is translucent and fairly flexible, naked or slightly downy, especially in the peduncle, with a smooth surface.

Identification of sessile macro-epibiotic taxa

Different taxa attached to the tunics of individuals (basibionts) of the three ascidian species were carefully observed under a CZM4 trinocular microscope (Labomed, Los Angeles, CA, USA) and identified (Häussermann & Försterra 2009). Vouchers of the examined material are stored at the Museo de Zoología, Universidad Nacional de Córdoba.

Estimation of percent cover of sessile macro-epibionts and data analyses

For every basibiont, richness was estimated as the number of different sessile macro-epibiont taxa. Percent cover was assessed after Sahade et al. (1998) using a grid of 100 uniformly distributed points, superimposed on a picture corresponding to an ascidian individual. Each point of the grid was considered as 1% cover. Taxa present, but that were not underlying any point, were considered a 0.5% cover. Differences in the richness and percent cover of different taxa of sessile macro-epibionts on the three ascidian species were assessed by one-way analyses of variance (ANOVA) at a significance level of 5% with a post-hoc Bonferroni test. Data normality and variance homogeneity were tested by Shapiro-Wilk and Cochran's C tests, respectively.

The relative abundance of higher sessile epibiotic taxa (phylum) on each ascidian species was estimated by their contribution to the total percent cover of sessile macro-epibionts on each basibiont.

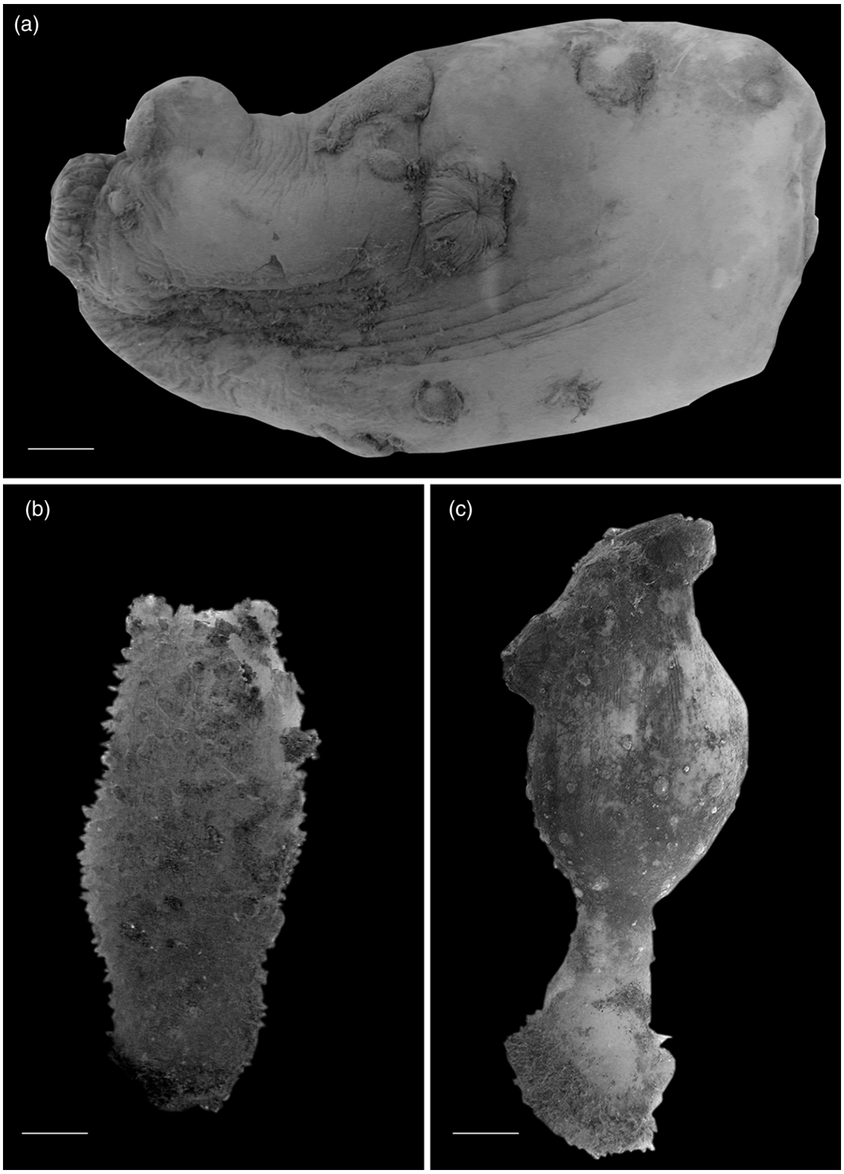

Fig. 1 Studied basibiont ascidian species: (a) *Corella antarctica*, dorsal view; (b) *Cnemidocarpa verrucosa*, lateral view; (c) *Molgula pedunculata*, lateral view. Scale bars: 1 cm.

The diversity of sessile macro-epibionts was estimated by means of Shannon-Wiener (H′) and Evenness (J′) indices. The Jackknife procedure was performed to compare diversity and evenness among the three ascidian species by ANOVA. When significant ($p < 0.05$), a post-hoc Bonferroni test was applied to determine differences between basibiont species.

Estimation of the area available for colonization

Colonization by benthic organisms varies according to the degree of exposure of the available substrate to colonize (Bowden 2005). The body surfaces of the erect species, *M. pedunculata* and *C. verrucosa*, are equally exposed. *Corella antarctica* has a depressed shape (dorso–ventral axis), and therefore there is an evident difference in the exposure of its dorsal and ventral surface (the latter being the area of attachment).

To avoid bias in comparisons, only the exposed (dorsal) surface of *C. antarctica* and one of the two surfaces (randomly selected) of the other two species were considered. The available area for colonization by sessile macro-epibionts was estimated using the software Image J (freely available from the National Institute of Health, USA, at http://rsbweb.nih.gov/ij/). The relationship between the area available for colonization and the percent cover of sessile epibionts in the three ascidian species was tested by linear regression analysis.

pH measurements on ascidian tunics

The pH on the outer tunic surface was determined using analytical pH strips (range 1–14; resolution 1 pH unit). All pH measurements were made by removing the ascidians from seawater and then placing the pH strip against the "dry" outer tunic for a period of 10 min (according to Koplovitz et al. 2009). These measurements were performed on specimens of *C. antarctica* ($n = 4$), *C. verrucosa* ($n = 10$) and *M. pedunculata* ($n = 5$).

Results

A total of 21 sessile macro-epibiotic taxa were found on 28 individuals (basibionts) of the three ascidian species. Macro-epibionts belonged to six different animal phyla and one macroalgal species. With seven species, Bryozoa was the most diverse phylum, followed by Chordata, with five different ascidian species belonging to Styelidae and Molgulidae (Table 1).

The richness of sessile macro-epibionts varied significantly in the three ascidian species ($p = 0.042$), with the highest richness observed in *Corella antarctica*. Significant differences between the three ascidians were also found in the diversity of sessile macro-epibionts, Shannon-Wiener (H′) ($p < 0.01$) and Evenness (J′) ($p < 0.01$). *Corella antarctica* revealed the highest H′ and J′, while these indices were lowest in *Cnemidocarpa verrucosa*. The total percent cover varied significantly in the three ascidian species ($p < 0.01$), reaching the highest percent cover in *C. verrucosa*. Considering the relative abundance of the different higher sessile macro-epibiotic taxa, it is notable that Porifera reached over 95% of the total percent cover in *C. verrucosa* and 61% in *Molgula pedunculata*. *C. antarctica* showed the highest density of Bryozoa, with almost 45% of the total percent cover (Fig. 2, Table 2).

The highest area available for colonization of sessile macro-epibionts was estimated in *C. antarctica* (23–78 cm^2), with lower areas in *C. verrucosa* (10–36 cm^2) and *M. pedunculata* (12–40 cm^2). There was a clear trend between the percent cover of epibionts and the area

Table 1 List of epibiotic taxa found on the three ascidian species. Asterisks indicate presence of a given taxa.

					Basibiont ascidian species		
Phylum/division	Class	Order	Suborder	Family/genus/species	*Corella antarctica*	*Cnemidocarpa verrucosa*	*Molgula pedunculata*
Porifera	Demospongiae			Species P1	*	*	*
				Species P2		*	
				Species P3		*	*
Cnidaria	Anthozoa	Actiniaria		Species C1	*		
	Hydrozoa			Species C2		*	
				Species C3	*		
Bryozoa	Gymnolaemata	Cheilostomata	Anasca	Species B1	*		
				Species B2	*		
				Species B3	*	*	*
				Species B4			*
				Species B5	*		*
			Ascophora	Species B6		*	
				Species B7	*	*	*
Annelida	Polychaeta			Species A1	*		
Mollusca	Gastropoda	Sorbeoconcha	Hypsogastropoda	Buccinidae/*Neobuccinum eatoni*	*		*
Chordata	Ascidiacea	Stolidobranchia		Styelidae/*Cnemidocarpa verrucosa*	*	*	
				Styelidae sp.			*
				Molgulidae/*Molgula enodis*	*		
				M. pedunculata	*		
				Molgula sp.		*	
Heterokontophyta	Phaeophyceae	Desmarestiales		Desmarestiaceae/*Desmarestia* spp.	*		*

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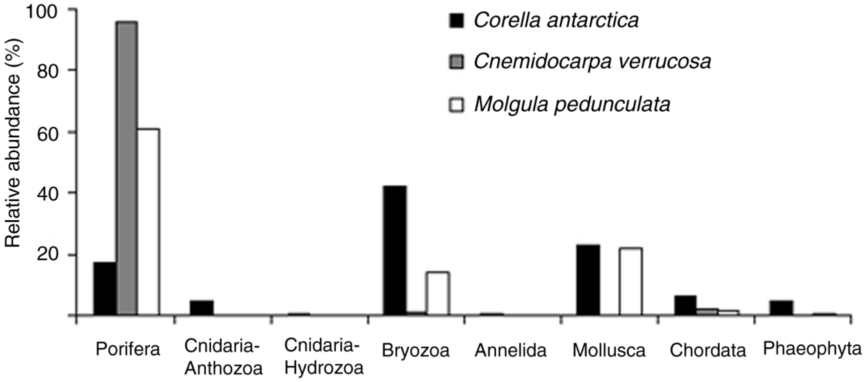

Fig. 2 Relative abundance (%) of higher epibiotic taxa (phylum/division) on the three basibiont ascidian species.

available for colonization in each of the three ascidian species. Nevertheless, this relationship was statistically significant only in the case of *C. antarctica* (linear regression analysis: $R^2 = 74.88$, $n = 10$, $p < 0.01$) (Fig. 3).

The pH values measured on the tunic of the different ascidian individuals were: *C. antarctica* 1–2 ($n = 4$); *C. verrucosa* 7–8 ($n = 10$); *M. pedunculata*: 7–8 ($n = 5$).

Discussion

At Potter Cove, a diverse macrobenthic community has been described, set on primary substrates, particularly soft bottoms. This community is dominated by sessile suspension feeders, such as ascidians, sponges, clams (*Laternula elliptica*) and pennatulids, as well as by motile species such as asteroids, ophiuroids and gastropods (Sahade et al. 1998; Sahade et al. 2008). Previous studies, performed with phototransects, did not reflect the totality of the macrobenthic organisms, since they did not consider the macro-epibionts settled on secondary substrates, like the ascidian tunics. Besides, these organisms were underestimated in cases where they were visually hidden in three-dimensional microhabitats. The present results report for the first time the sessile macro-epibiotic communities developed on three solitary ascidian species that are important members of that rich macrobenthic community.

The rapid warming experienced by the Antarctic Peninsula in recent decades is said to be responsible for profound environmental and biological changes (Cook et al. 2005; Ducklow et al. 2007; McClintock et al. 2008; Smale 2008; Montes- Hugo et al. 2009; Rückamp et al. 2011; Schloss et al. 2012). It may also be related to shifts detected in the structure of the benthic community at Potter Cove, particularly the abundance and distribution of ascidians. The latter was the dominant taxon found in 1994, but has almost disappeared at 20 m depth, and showed a great decline from 1998 to 2010 at 30 m (Sahade et al. 1998; Sahade et al. 2008; Sahade et al. unpubl. ms.). The ascidian species most affected is *Molgula pedunculata*, which was dominant in terms of density. The ascidians *Corella antarctica* and *Ascidia challengeri* also showed some reduction in density. The importance of changes that affect ascidian density seems to be higher than that estimated so far, considering the role of these animals as live substrate for the macrobenthic community of this area. On the

Table 2 Comparative parameters of basibiont ascidian species and their epibiotic community: basibiont body size (range), species richness (S′) (number of epibiotic taxa), percent cover (%), Shannon-Wiener (H′) and Evenness (J′) indices (expressed as mean ± standard error). Values of *F* and *P* corresponding to ANOVA analyses between basibiont species are also indicated. Letters in parentheses indicate significant differences between species (Bonferroni post-hoc test, $p < 0.05$).

Basibiont ascidian species	Range size in cm^2 (mean ± SD)	S′ (number of macro-epibiotic taxa)	% cover	H′	J′
Corella antarctica ($n = 10$)	23–76 (45 ± 19)	14(A)	10.63 ± 3.38(A)	2.23 ± 0.03(A)	0.85 ± 0.01(A)
Cnemidocarpa verrucosa ($n = 9$)	23–36 (19 ± 9)	9(B)	31.25 ± 3.57(B)	0.27 ± 0.03(B)	0.13 ± 0.01(B)
Molgula pedunculata ($n = 9$)	16–40 (25 ± 11)^a	9(A, B)	11.79 ± 3.57(A)	1.53 ± 0.03(C)	0.66 ± 0.01(C)
$F_{(2,\ 25)}$		3.61	10.73	1176.24	2338.21
p		0.042	< 0.01	< 0.01	< 0.01

[a] The area in *Molgula pedunculata* does not include the stalk.

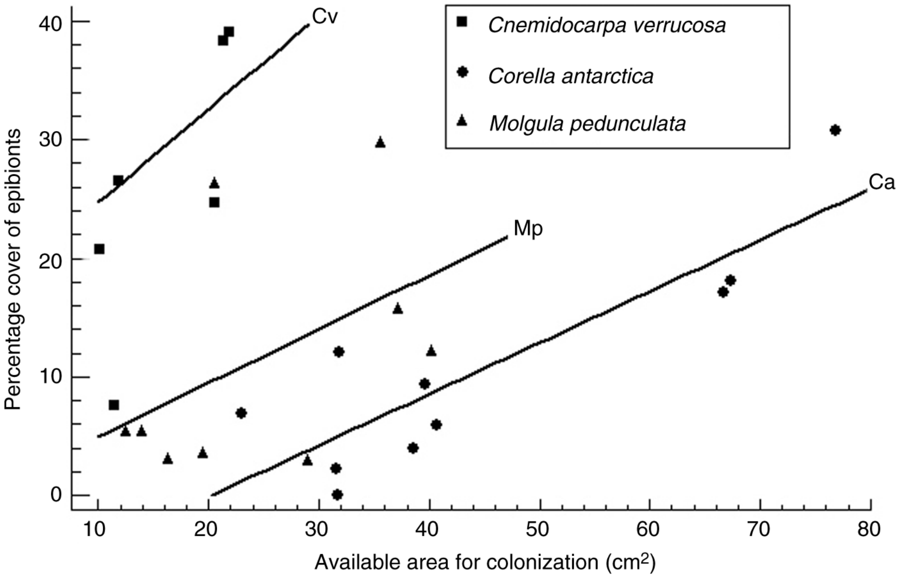

Fig. 3 Linear regression analyses between percent cover of epibionts and available area for colonization on the basibiont ascidian individuals of *Corella antarctica* (Ca), *Cnemidocarpa verrucosa* (Cv) and *Molgula pedunculata* (Mp).

high Antarctic shelf, Gutt & Schickan (1998) reported 374 different epibiotic relationships, comprising 47 different epibionts and 96 substratum taxa, only one of which was an ascidian, *Synoicum* sp. In these assemblages, this ascidian was colonized by a large number of epibiotic taxa (13), slightly less than bryozoan (16) and hexactinellid sponges (23).

On soft bottoms, ascidian tunics form a particularly suitable substrate for bryozoans. The latter have been described as common and often the most abundant epibionts on a wide range of abiotic and biotic substrata (Stebbing 1972; Jackson 1979; Witman & Suchanek 1984; Rubin 1985; Landman et al. 1987; Frazier et al. 1992; Barnes 1999). The fine (muddy) sediment prevailing in the inner Potter Cove is not suitable substrate for bryozoans, and they were practically absent in previous studies (Sahade et al. 1998; Sahade et al. 2008). The presence of ascidians is essential for their establishment in that area.

There were significant differences between the three ascidian species in terms of richness, percent cover and diversity of sessile macro-epibiotic taxa. A high degree of specialization has been previously found in epibiotic communities, depending on the morphological features of the basibiont, that is, shape, texture, surface area (Sebens 1991). Since the selected ascidian species show marked differences in their tunic structure, the percent cover and diversity of sessile macro-epibionts also vary. While the tunic surface of *C. antarctica* and *M. pedunculata* is smooth, the tunic of *C. verrucosa* is contractile, rough, with conical papillae arranged transversely and bearing thorns. The latter species supported the highest percent cover of sessile epibionts, probably favoured by the variability in its tunic morphology.

Area and time are difficult to separate when interpreting the diversity and intensity of epibiosis (Huston 1994). The size of basibionts, constituting the area available for colonization by epibionts, seems to be directly related to their age (Kowalke et al. 2001). Since both factors promote diversity, a higher diversity of epibionts is to be expected on larger individuals. The upper size reported for *C. antarctica, C. verrucosa* and *M. pedunculata* is higher than any individuals measured in the study reported here. Haphazardly collected by divers who were not particularly seeking large specimens, the individuals examined in this study were probably not old specimens. The individuals of *C. antarctica* were larger and with greater diversity of sessile macro-epibionts than those of the other two species. *Molgula pedunculata* showed larger sizes and higher diversity than *C. verrucosa*. However, *C. antarctica* and *M. pedunculata* supported a lower cover of macro-epibionts compared with *C. verrucosa*. A single species (Porifera) was predominant on *C. verrucosa*, with 90% of the total relative abundance.

It has been previously reported that the larvae of some Porifera prefer shaded microhabitats such as ruts and cracks (Voultsiadou et al. 2010), like the tunic surface of *C. verrucosa*. Larval recruitment to the tunic surface could be facilitated by a chemical cue from the tunic that triggers settlement (Hadfield & Paul 2001). Given its smaller size, along with the short period of development of the sessile epibiotic community on this ascidian, this phenomenon could be probably explained by a recruitment event of the epibiotic sponge.

Considerable progress has been made in understanding chemical ecological interactions among marine organisms. Some Antarctic Porifera produces sea star feeding deterrents and inhibitors of fouling organisms (Amsler et al. 2001). According to Koplovitz et al. (2009) the acidity of the tunic of five species of Antarctic ascidians: *Corella eumyota* (probably *Corella antarctica* Alurralde et al. 2013), *Distaplia cylindrica*, *D. colligans*, *Sycozoa gaimardi* and *Trididemnum* sp. may prevent their predation by starfishes; for these authors, colonial forms may be under greater selective pressure to employ chemical defences, since solitary ascidians have tougher, more protective outer tunics than colonial forms, a characteristic that seems to be useful to prevent predation. According to Stoecker (1978, 1980), acidic pH surface in ascidians may prevent epibiosis. In contrast, Davis & Wright (1989) have suggested that secondary metabolites rather than acidic pH are responsible for antifouling defences. The measured pH values ranged from very acidic to moderately alkaline. These values matched those in previous studies: Koplovitz et al. (2009) reported pH 2 in *C. eumyota* (=*C. antarctica*); pH values of 6.9–8.6 and 8 were measured in *C. verrucosa* (McClintock et al. 1991; Koplovitz & McClintock 2011), while other molgulids (*Molgula occidentalis*) reached a slightly alkaline pH value of 8 (Koplovitz & McClintock 2011). The pH variations may also be related to epibiosis cover: *C. antarctica* showed the most acidic tunic and a lower percent cover than expected, considering the size of specimens, which are far larger than those of the other two species. McClintock et al. (2004) measured acidic outer colony surfaces (pH 1.5) in the colonial ascidian *Distaplia cylindrica,* a species that also possesses potent antifouling secondary metabolites. According to Pisut & Pawlik (2002), there is no clear trade-off between the presence of secondary metabolites and inorganic acid defences in ascidians, suggesting that these defences are redundant or that alternative chemical defences may have evolved for different predators or for different stages in the life history of the ascidians producing them. Chemical defences against sea stars and fish that are attributable to secondary metabolites are not as prevalent in Antarctic ascidians as they are in tropical or temperate ascidians or in other Antarctic organisms such as macroalgae and sponges (Koplovitz et al. 2009). Nonetheless, inorganic chemical defences (acids) are not uncommon in Antarctic ascidians and may deter sea star predation or, as in the present study, may produce a reduction in epibiosis.

The marked differences observed in sessile epibiotic communities and their patterns suggest that, at intraspecific level, the diversity and percent cover of epifaunal communities are related to the size (age) of the basibiont individuals. At interspecific level, the diversity of sessile macro-epibiotic communities seems to be also related to the size (age) of the basibionts, while structural features of the ascidian tunics and pH value may determine epibiosis.

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References

Alurralde G., Torre L., Schwindt E., Castilla J.C. & Tatián M. 2013. A re-evaluation of morphological characters of the invasive ascidian *Corella eumyota* reveals two different species at the tip of South America and in the South Shetland Islands, Antarctica. *Polar Biology 36*, 957–968.

Amsler C.D., McClintock J.B. & Baker B.J. 2001. Secondary metabolites as mediators of trophic interactions among Antarctic marine organisms. *American Zoologist 41*, 17–26.

Barnes D.K.A. 1994. Communities of epibiota on two erect species of Antarctic Bryozoa. *Journal of the Marine Biological Association of the United Kingdom 74*, 863–872.

Barnes D.K.A. 1999. Do life patterns differ between two Scotia Arc localities? A preliminary investigation of three erect Antarctic bryozoan species. *Antarctic Science 11*, 275–282.

Barnes D.K.A. 2001. The contribution of secondary space to benthic richness of a coral reef: colonization of *Dendrostrea frons* (Mollusca). *Marine Ecology 22*, 189–200.

Bowden D.A. 2005. Seasonality of recruitment in Antarctic sessile marine benthos. *Marine Ecology Progress Series 297*, 101–118.

Castilla J.C., Lagos N.A. & Cerda M. 2004. Marine ecosystem engineering by the alien ascidian *Pyura praeputialis* on a mid-intertidal rocky shore. *Marine Ecology Progress Series 268*, 119–130.

Connell J.H. & Keough M.J. 1985. Disturbance and patch dynamics of subtidal marine animals on hard substrata. In S.T.A. Pickett & P.S. White (eds.): *The ecology of natural disturbance and patch dynamics*. Pp. 125–151. New York: Academic Press.

Cook A.J., Fox A.J., Vaughan D.G. & Ferrigno J.G. 2005. Retreating glacier fronts on the Antarctic Peninsula over the past half-century. *Science 308*, 541–544.

Davis A.R. & Wright A.E. 1989. Interspecific differences in fouling of two congeneric ascidians (*Eudistoma olivaceum* and *E. capsulatum*): is surface acidity an effective defense? *Marine Biology 102*, 491–497.

Ducklow H.W., Baker K., Martinson D.G., Quetin L.B., Ross R.M., Smith R.C., Stammerjohn S.E., Vernet M. & Fraser W. 2007. Marine pelagic ecosystems: the West Antarctic Peninsula. *Philosophical Transactions of the Royal Society B 362*, 67–94.

Frazier J.G., Winston J.E. & Ruckdeschel C.A. 1992. Epizoan communities on marine turtles. III. Bryozoa. *Bulletin of Marine Science 51*, 1–8.

Gutt J. & Schickan T. 1998. Epibiotic relationship in the Antarctic benthos. *Antarctic Science 10*, 398–405.

Hadfield M.G. & Paul V. J. 2001. Natural chemical cues for settlement and metamorphosis of marine invertebrate larvae. In J. McClintock & B. Baker (eds.): *Marine chemical ecology*. Pp. 431–462. Boca Raton: CRC Press.

Harder T. 2008. Marine epibiosis: concepts, ecological consequences and host defence. In H.C. Flemming et al. (eds.): *Marine and industrial biofouling*. Pp. 219–232. New York: Springer.

Häussermann V. & Försterra G. (eds.) 2009. *Marine benthic fauna of Chilean Patagonia*. Santiago: Nature in Focus.

Herdman W.A. 1882. Preliminary report on the Tunicata of the Challenger Expedition, IV. Molgulidae. *Proceedings of the Royal Society Edinburgh 11*, 233–240.

Huston M.A. 1994. *Biological diversity: the coexistence of species on changing landscapes*. Cambridge: Cambridge University Press.

Jackson J.B.C. 1979. Overgrowth competition between encrusting cheilostome ectoprocts in a Jamaican cryptic reef environment. *Journal Animal Ecology 48*, 805–823.

Jones C.G., Lawton J.H. & Shachak M. 1994. Organisms as ecosystem engineers. *Oikos 69*, 373–386.

Koplovitz G. & McClintock J.B. 2011. An evaluation of chemical and physical defenses against fish predation in a suite of seagrass-associated ascidians. *Journal of Experimental Marine Biology and Ecology 407*, 48–53.

Koplovitz G., McClintock J.B., Amsler C.D. & Baker B.J. 2009. Palatability and chemical anti-predatory defenses in common ascidians from the Antarctic Peninsula. *Aquatic Biology 7*, 81–92.

Kott P. 1969. *Antarctic Ascidiacea*. Washington, DC: American Geophysical Union.

Kowalke J., Tatián M., Sahade R. & Arntz W. 2001. Production and respiration of Antarctic ascidians. *Polar Biology 24*, 663–669.

Landman N.H., Saunders W.B., Winston J.E. & Harries P.J. 1987. Incidence and kinds of epizoans on the shells of live nautilus. In W.B. Saunders & N.H. Landman (eds.): *Nautilus*. Pp. 163–177. New York: Plenum Press.

McClintock J., Ducklow H. & Fraser W. 2008. Ecological responses to climate change on the Antarctic Peninsula. *American Scientist 96*, 302–310.

McClintock J.B., Amsler M.O., Amsler C.D., Southworth K.J., Petrie C. & Baker B.J. 2004. Biochemical composition, energy content and chemical antifeedant and antifoulant defenses of the colonial Antarctic ascidian *Distaplia cylindrica*. *Marine Biology 145*, 885–894.

McClintock J.B., Heine J., Slattery M. & Weston J. 1991. Biochemical and energetic composition, population biology, and chemical defense of the Antarctic ascidian *Cnemidocarpa verrucosa* Lesson. *Journal of Experimental Marine Biology and Ecology 147*, 163–175.

Monteiro S.M., Chapman M.G. & Underwood A.J. 2002. Patches of the ascidian *Pyura stolonifera* (Heller, 1878): structure of habitat and associated intertidal assemblages. *Journal of Experimental Marine Biology and Ecology 270*, 171–189.

Montes-Hugo M., Doney S.C., Ducklow H.W., Fraser W., Martinson D., Stammerjohn S.E. & Schofield O. 2009. Recent changes in phytoplankton communities associated with rapid regional climate change along the western Antarctic Peninsula. *Science 323*, 1470–1473.

Nylund G.M. & Pavia H. 2005. Chemical versus mechanical inhibition of fouling in the red alga *Dilsea carnosa*. *Marine Ecology Progress Series 299*, 111–121.

Odate S. & Pawlik J.R. 2007. The role of vanadium in the chemical defense of the solitary tunicate, *Phallusia nigra*. *Journal of Chemical Ecology 33*, 643–654.

Pisut D.P. & Pawlik J.R. 2002. Anti-predatory chemical defenses of ascidians: secondary metabolites or inorganic acids? *Journal of Experimental Marine Biology and Ecology 270*, 203–214.

Rubin J.A. 1985. Mortality and avoidance of competitive overgrowth in encrusting Bryozoa. *Marine Ecology Progress Series 23*, 291–299.

Rückamp M., Braun M., Suckro S. & Blindow N. 2011. Observed glacial changes on the King George Island ice cap, Antarctica, in the last decade. *Global Planet Change 79*, 99–109.

Sahade R., Tarantelli S., Tatián M. & Mercuri G. 2008. Benthic community shifts: a possible linkage to climate change? *Reports on Polar Research 571*, 331–337.

Sahade R., Tatián M., Kowalke J., Kühne S. & Esnal G.B. 1998. Benthic faunal associations on soft substrates at Potter Cove, King George Island, Antartica. *Polar Biology 19*, 85–91.

Schloss I.R., Abele D., Ferreyra G.A., González O., Moreau S., Bers V. & Demers S. 2012. Response of Potter Cove phytoplankton dynamics to long term climate trends. *Journal of Marine Systems 92*, 53–66.

Sebens K.P. 1991. Habitat structure and community dynamics in marine benthic systems. In S.S. Bell et al. (eds.): *Habitat structure. The physical arrangement of objects in space*. Pp. 211–234. London: Chapman & Hall.

Smale D.A. 2008. Continuous benthic community change along a depth gradient in Antarctic shallows: evidence of patchiness but not zonation. *Polar Biology 31*, 189–198.

Stebbing A.R.D. 1972. Preferential settlement of a bryozoan and serpulid larvae on the younger parts of *Laminaria* fronds. *Journal of the Marine Biological Association of the United Kingdom 52*, 765–772.

Stoecker D. 1978. Resistance of a tunicate to fouling. *The Biological Bulletin 155*, 615–626.

Stoecker D. 1980. Relationships between chemical defense and ecology in benthic ascidians. *Marine Ecology Progress Series 3*, 257–265.

Tatián M., Sahade R., Doucet M. & Esnal G. 1998. Ascidians (Tunicata, Ascidiacea) of Potter Cove, South Shetland Islands, Antartica. *Antarctic Science 2*, 147–152.

Torre L., Servetto N., Eöry M.L., Momo F., Tatián M., Abele D. & Sahade R. 2012. Respiratory responses of three Antarctic ascidians and a sea pen to increased sediment concentrations. *Polar Biology 35*, 1743–1748.

Vasconcelos P., Curdia J., Castro M. & Gaspa M.G. 2007. The shell of *Hexaplex* (*Truncalariopsis*) *trunculus* (Gastropoda: Muricidae) as a mobile hard substratum for epibiotic polychaetes (Annelida: Polychaeta) in the Ria Formosa (Algarve coast—southern Portugal). *Hydrobiology 575*, 161–172.

Voultsiadou E., Kyrodimou M., Antoniadou C. & Vafidis D. 2010. Sponge epibionts on ecosystem-engineering ascidians: the case of *Microcosmus sabatieri*. *Estuarine, Coastal and Shelf Science 86*, 598–606.

Voultsiadou E., Pyrounaki M.M. & Chintiroglou C. 2007. The habitat engineering tunicate *Microcosmus sabatieri* Roule, 1885 and its associate peracarid epifauna. *Estuarine Coastal and Shelf Science 74*, 197–204.

Wahl M. 1989. Marine epibiosis. I. Fouling and antifouling: some basic aspects. *Marine Ecology Progress Series 58*, 175–189.

Wahl M. 2009. Epibiosis: ecology, effects and defences. In M. Wahl (ed.): *Marine hard bottom communities*. Pp. 61–72. Berlin: Springer.

Ward M.A. & Thorpe J.P. 1991. Distribution of encrusting bryozoans and other epifauna on the subtidal bivalve *Chlamys opercularis*. *Marine Biology 110*, 253–259.

Witman J.D. & Suchanek T.H. 1984. Mussels in flow: drag and dislodgement by epizoans. *Marine Ecology Progress Series 16*, 259–268.

Wright P.J. & Jones C.G. 2006. The concept of organisms as ecosystem engineers ten years on: progress, limitations and challenges. *BioScience 56*, 203–209.