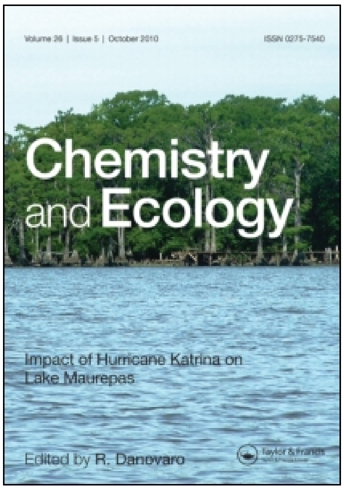

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C. Cerrano[a]; B. Calcinai[b]; M. Bertolino[a]; L. Valisano[a]; G. Bavestrello[b]
[a] Dipartimento per lo Studio del Territorio e delle sue Risorse, Università di Genova, Genoa, Italy [b] Dipartimento di Scienze del Mare, Università Politecnica delle Marche, Ancona, Italy

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Epibionts of the scallop *Adamussium colbecki* (Smith, 1902) in the Ross Sea, Antarctica

C. CERRANO*†, B. CALCINAI‡, M. BERTOLINO†, L. VALISANO†
and G. BAVESTRELLO‡

†Dipartimento per lo Studio del Territorio e delle sue Risorse, Università di Genova, C.so Europa 26,
I-16132, Genoa, Italy
‡Dipartimento di Scienze del Mare, Università Politecnica delle Marche, Via Brecce Bianche,
60131 Ancona, Italy

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Although it is characterized by a patchy distribution, *Adamussium colbecki* is considered the most important bivalve of Antarctica, mainly in relation to its functional role in the transfer of energy from the water column to the benthos. Here, we compare the epibionts of *A. colbecki* from three different areas, highlighting the importance of their shells as a natural secondary hard bottom for many taxa. In this way, we show that due to its ability to swim, the scallop may contribute to the dispersion of epibiotic species, and this probably increases their survival. These data amplify the ecological roles of *A. colbecki*, which, along with its shells, can be considered an important ecosystem engineer in Antarctic communities.

Keywords: Epibiosis; Ecosystem engineer; Phoresy; Substratum; Marine molluscs

1. Introduction

The spatial distribution and structure of marine benthic communities are due to numerous abiotic and biotic factors, which are in turn influenced by the presence of organisms, in a mutual exchange of inputs. Among the biotic factors, an important role is traditionally assigned to food availability and competition [1, 2], although particularly in highly diversified habitats, co-evolutive interactions also have a role in the structuring of communities [3]. Epibiosis is considered to be particularly important in the highly diversified Antarctic communities. Indeed, in the Lazarev and Weddel Seas, 347 different epibiotic relationships of the megafauna have been described [4], highlighting that the Antarctic benthic communities are predominantly biologically accommodated rather than physically controlled.

Several groups of Antarctic benthos, such as sponges, hydroids, gorgonians, and bryozoans, are mainly limited to hard substrata, although they can easily colonize soft bottoms using several kinds of secondary hard substrata [5]. In this way, the particular role of mollusc shells

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*Corresponding author. Email: cerrano@dipteris.unige.it

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in providing a secondary hard substratum has been highlighted recently using an ecosystem engineering perspective [6], a useful approach when an organism creates, modifies, and maintains habitats [7].

In the Antarctic waters, the endemic scallop *Adamussium colbecki* (Smith, 1902) represents the most abundant bivalve [8], and it is considered as an important step in the transfer of energy from the water column to the benthos [9]. In Terra Nova Bay, the scallop shells host a rich epibiotic community which consists of diatoms, forams, sponges, hydroids, gorgonians, ascidians and polychaets [10, 11]. Another common epibiont is the spat of the scallop itself, which generally lives for about 3–5 yr attached to the adult shell by means of its byssus [12, 13].

To highlight the importance of *A. colbecki* shells as a natural substratum for many epibiotic groups, differences in the total coverage and in the coverage of the different taxa between the right and left valves are presented here, comparing data from three different populations sampled along the Victoria Land. Moreover, the role of epibiosis on *Adamussium* population dynamics and the possible role of the bivalve in epibiont dispersion in the areas damaged by ice-scouring and in the survival of epibiotic organisms are also discussed.

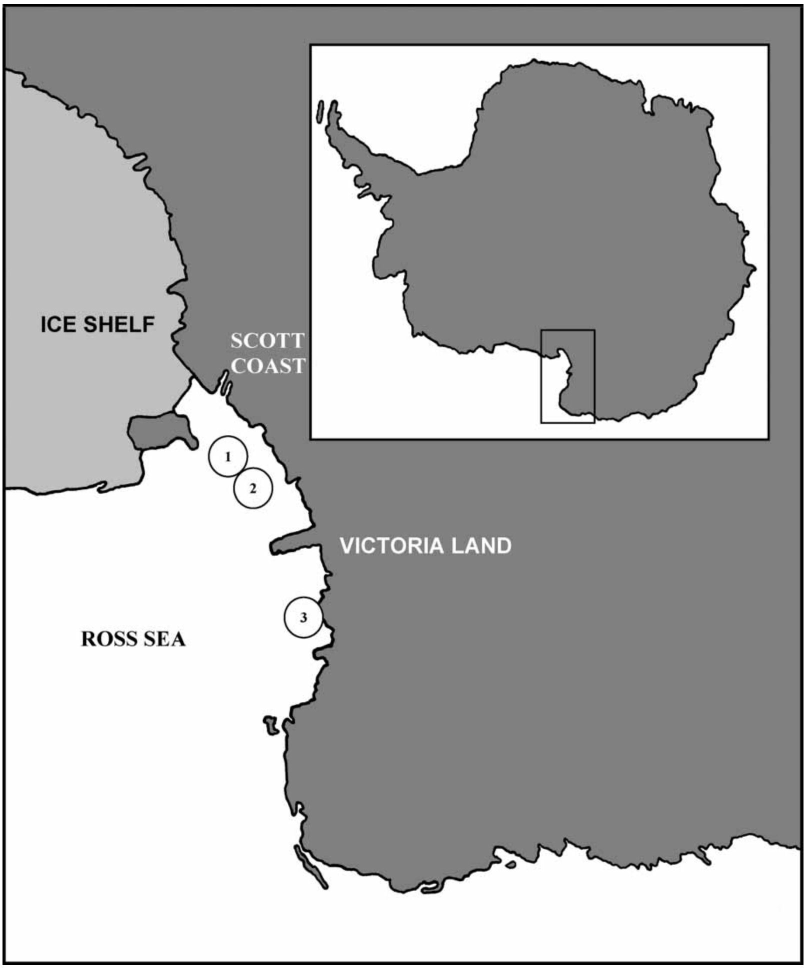

Figure 1. Map of study site. 1: New Harbor; 2: Dunlop Island; 3: Terra Nova Bay.

2. Materials and methods

The samples were collected from Terra Nova Bay during the XIVth (1998/99) and the XVth (1999/2000) Italian Expeditions, and from Dunlop Island and New Harbor during the Scott Base–Cape Roberts traverse that was performed in collaboration with the New Zealand Expedition (Event K081, 2002/03) (figure 1).

Terra Nova Bay extends from Cape Washington to the Drygalsky glacier. The sea bed consists of pebbles of various sizes in the shallow zone, changing to fine-grained, muddy sediments below 40–50 m in depth. The heterogeneity of this area contributes to the creation of a mosaic structure of the communities and explains the high richness of species diversity and biomass [5].

Dunlop Island and New Harbor lie in the zone of the McMurdo Sound, on the north side of the Scott Coast. In the area of McMurdo Sound, the variations in the surface of the frozen sea and the nearness of the Ross Ice Shelf mean that this zone is characterized by a constant water temperature of around $-1.9\,^{\circ}\mathrm{C}$ and oligotrophic conditions that result from the very low primary productivity [14]. At Dunlop Island, the sea bottom is made of a coarse sediment, with

Table 1. Comparisons among the coverage of valves in the three stations.

New Harbor	Valves	ANOVA $p < 0.001$	
Terra Nova Bay	Valves	ANOVA $p < 0.001$	
Dunlop Island	Valves	ANOVA $p < 0.001$	
Macrobenthos			
Demosponges	Stations	Two-way ANOVA $p < 0.01$	
		Tukey Test	New Harbor vs. Dunlop Island $p < 0.05$ New Harbor vs. Terra Nova Bay $p < 0.05$
Hydrozoa	Stations	Two-way ANOVA $p < 0.01$	
		Tukey Test	New Harbor vs. Terra Nova Bay $p < 0.05$ Dunlop Island vs. Terra Nova Bay $p < 0.05$
Bryozoans	Stations	Two-way ANOVA $p < 0.01$	
		Tukey Test	Terra Nova Bay vs. New Harbor $p < 0.05$
Tubes of tanaidaceans	Valves × stations	Two-way ANOVA $p < 0.01$	
		Tukey Test	New Harbor vs. Terra Nova Bay $p < 0.05$ New Harbor vs. Dunlop Island $p < 0.05$ Dunlop Island vs. Terra Nova Bay $p < 0.05$
Microbenthos			
Spirorbids	Valves × stations	Two-way ANOVA $p < 0.01$	
		Tukey Test valves $p < 0.05$	
		Tukey Test	New Harbor vs. Terra Nova Bay $p < 0.05$ Dunlop Island vs. Terra Nova Bay $p < 0.05$
Diatoms	Valves × stations	Two-way ANOVA $p < 0.01$	
		Tukey Test	New Harbor vs. Dunlop Island $p < 0.05$ New Harbor vs. Terra Nova Bay $p < 0.05$ Dunlop Island vs. Terra Nova Bay $p < 0.05$
Foraminifera	Valves	Two-way ANOVA $p < 0.001$	
		Tukey Test $p < 0.05$	
	Stations	Two-way ANOVA $p < 0.01$	
		Tukey Test	New Harbor vs. Dunlop Island $p < 0.05$ New Harbor vs. Terra Nova Bay $p < 0.05$

few and scattered specimens of *A. colbecki*, *Sterechinus neumayeri*, and *Odontaster validus*, while at New Harbor, the sea bed consists of a fine-grained, muddy sediment [10]. In this area, the *A. colbecki* population can reach several hundreds of specimens per 10 m^2, although this density decreases with depth [12]; there are also numerous sponge species and ophiuroids (mainly *Ophionotus victoriae*).

For the present study, we considered specimens with a diameter of between 6 and 7 cm. From Terra Nova Bay, 36 specimens of *A. colbecki* were collected in January at depths between 20 and 35 m; from the other two stations, Dunlop Island and New Harbor, 45 specimens were collected in October at depths between 15 and 25 m. All of the scallops were collected by scuba divers by visually selecting the specimens with the highest amounts of epibionts.

The samples were fixed in 4% formaldehyde, rinsed with water, and stored in 70% alcohol. Some samples were stored dried. The valve surface of *A. colbecki*, which can be considered as being roughly flattened [10], was analysed at the stereomicroscope, to identify the epibionts and to determine the percentage coverage of the valves (table 1). The epibionts were divided in two groups on a dimensional basis: macrobenthic (sponges, cnidarians, bryozoans, and tanaidaceans) and microbenthic (diatoms, foraminifera, and spirorbids).

The abundance on the valves was expressed as a percentage of the coverage and is given as mean ± standard errors. The data were analysed with ANOVA and multicomparison tests, after Freeman and Tukey transformations of frequency percentage data and $\log(x + 1)$ transformations of density data, performed to make the assumptions of variance.

3. Results

In every station, the epibionts on the valves analysed showed different coverage rates depending on the valve considered (ANOVA: New Harbor, $p < 0.001$; Dunlop Island, $p < 0.001$; Terra Nova Bay, $p < 0.001$), with the left valve being generally more colonized.

Among macrobenthic organisms, the most common were the sponge *Homaxinella balfourensis* (figure 2A–C), gorgonians belonging to the genus *Thouarella* (figure 2D and E), and the hydrozoan *Hydractinia angusta*; among microbenthic organisms, diatoms, spirorbids, and phorams were the most represented groups.

3.1 *Macrobenthos*

Regarding the macrobenthic community in its complexity, no differences were detectable between the two valves of the scallop (figure 3). A more detailed analysis conducted on the different groups highlighted qualitative and quantitative differences among the three sites (figure 4).

Demosponges appeared to be more abundant on the right valve than on the left. Significant differences arose between the stations (two-way ANOVA, $p < 0.01$), with New Harbor showing a higher coverage rate than that for Dunlop Island and Terra Nova Bay (Tukey test, New Harbor vs. Dunlop Island, $p < 0.05$; New Harbor vs. Terra Nova Bay, $p < 0.05$).

For the cnidaria, hydrozoa colonized the right and the left valves with similar values, but showed differences between the stations (two-way ANOVA, $p < 0.01$); for New Harbor and Dunlop Island, they covered a higher percentage frequency than for Terra Nova Bay (Tukey test, New Harbor vs. Terra Nova Bay, $p < 0.05$; Dunlop Island vs. Terra Nova Bay, $p < 0.05$). Gorgonians were present only in Terra Nova Bay and Dunlop Island, at very low levels (1–2%), and they uniquely colonized the right valves.

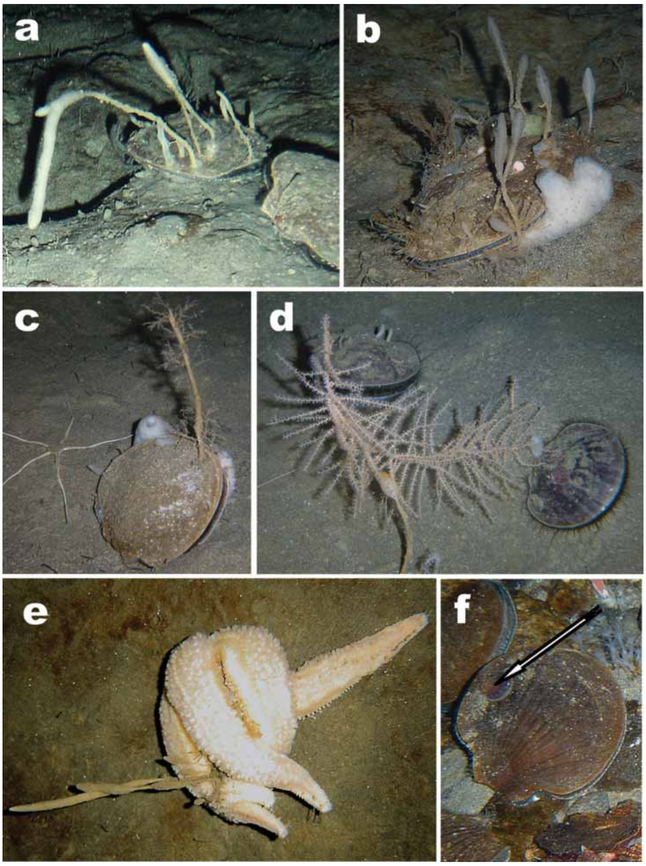

Figure 2. *Adamussium colbecki* specimens with some of the most common epibionts. (a) *Homaxinella balfourensis* is among the commonest epibionts species; (b) sponges can also easily colonize the lower valve; (c) when preyed on by starfishes, *H. balfourensis* leaves its axial skeleton, which represents a good substratum for other organisms such as hydrozoans; (d) the octocoral *Thouarella* sp.; (e) *Notasterias armata* preying on an *A. colbecki*: sponges do not protect the bivalve from this kind of predators; (f) spat (arrow) of *A.colbecki* settled on an adult shell.

Bryozoans, which, at Terra Nova Bay and New Harbor, colonized the right and left valves equally, showed differences between the stations (two-way ANOVA, $p < 0.01$), with a higher presence at Terra Nova Bay than at New Harbor (Tukey test, $p < 0.05$). Their coverage rates were always about 10% across the three stations studied.

The tubes of tanaidaceans, which were absent from Terra Nova Bay, covered the valve surfaces differently in the other stations (two-way ANOVA, $p < 0.01$), with New Harbor showing frequency percentages higher than those at Dunlop Island (Tukey test, New Harbor vs. Terra Nova Bay, $p < 0.05$; New Harbor vs. Dunlop Island, $p < 0.05$; Dunlop Island vs. Terra Nova Bay, $p < 0.05$).

The byssus of *A. colbecki*, the finding of which suggests the presence of young specimens and a recruitment of the species, was only found at Dunlop Island, with values of 1%, on the left valves.

3.2 *Microbenthos*

The microbenthic assemblages showed significant differences between the valves, being more represented on the left (upper valve) than on the right (figure 3). Spirorbids covered different

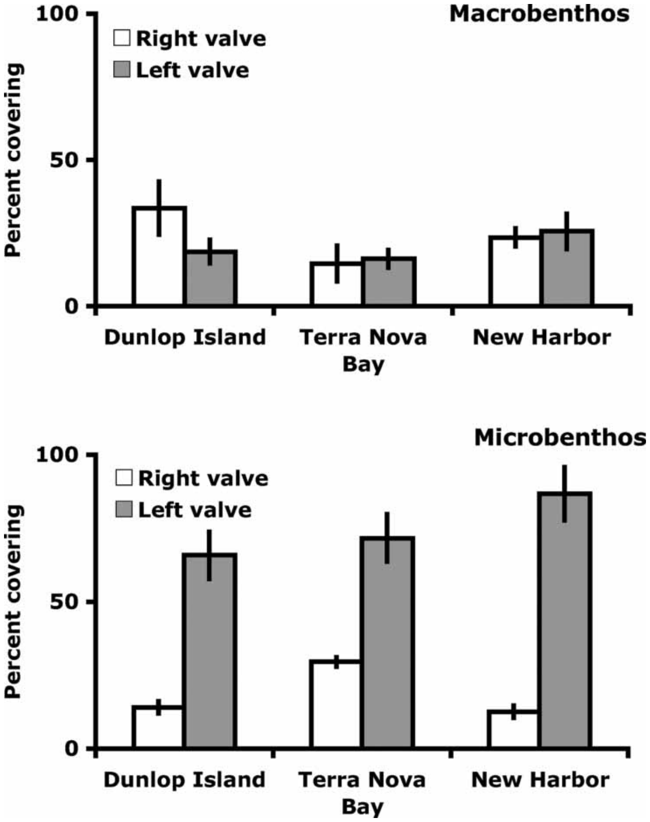

Figure 3. Percentage coverage of macrobenthos and microbenthos on the two valves at the three stations of Terra Nova Bay, Dunlop Island, and New Harbor.

percentages of the surfaces of the valves in all three stations (two-way ANOVA, $p < 0.01$), colonizing mainly the right valves of *A. colbecki* at Terranova Bay (Tukey test, $p < 0.05$), and with a coverage of mainly the left valves at New Harbor (Tukey test, New Harbor vs. Terra Nova Bay, $p < 0.05$; Dunlop Island vs. Terra Nova Bay, $p < 0.05$).

The coverage of diatoms was different across the different stations and between the two valves (two-way ANOVA $p < 0.01$), with a 60% cover at Dunlop Island, and 35% of the surface of the left valves at Terra Nova Bay and New Harbor, while the coverage of the right valves was negligible (Tukey test, New Harbor vs. Dunlop Island, $p < 0.05$; New Harbor vs. Terra Nova Bay, $p < 0.05$; Dunlop Island vs. Terra Nova Bay, $p < 0.05$).

Foraminifera covered the left valve significantly more than the right (two-way ANOVA, $p < 0.001$; Tukey test, $p < 0.05$), and at Dunlop Island they were less prevalent than at the other two sites (two-way ANOVA, $p < 0.01$; Tukey test, New Harbor vs. Dunlop Island, $p < 0.05$; New Harbor vs. Terra Nova Bay, $p < 0.05$), where they covered about 35% of the valves.

In summary, at Dunlop Island, the coverage of the left valve (about 80% complete) was mainly due to diatom mats and partially to foraminifera. On the right valve, the more abundant taxa, with a coverage rate lower than 10%, were diatoms, hydrozoa, bryozoans, and sponges. At Terra Nova Bay, the left valve was always covered by foraminifera, with a 30% coverage, followed by bryozoans, demosponges, and spirorbids, with coverage rates of between 5% and

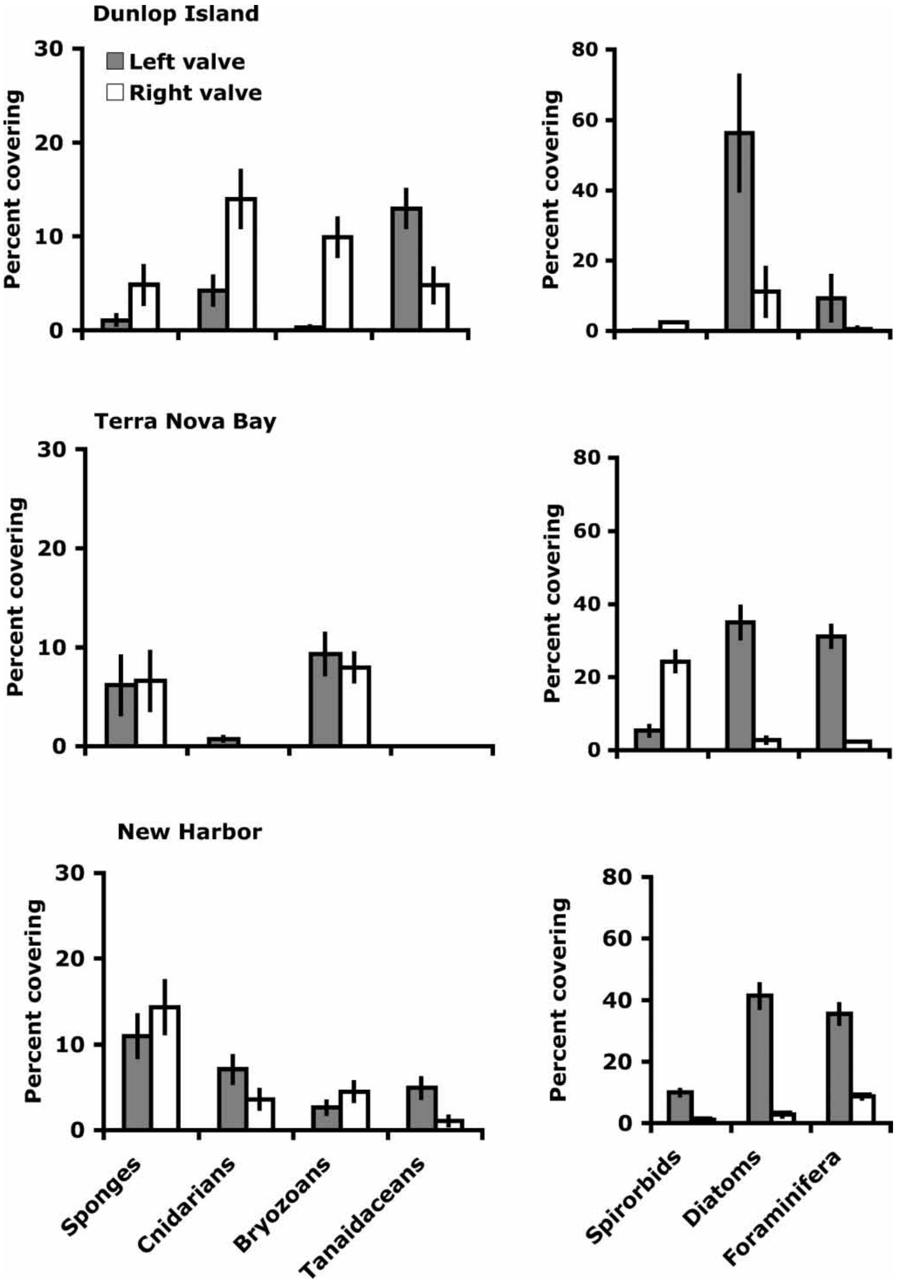

Figure 4. Coverage of the different taxa of epibionts on the two valves of *Adamussium colbecki* at the three considered stations.

10%. The left valve was covered by spirorbids and diatoms, to about 30%, and with coverage rates lower than 5% for bryozoans, demosponges, and foraminifera. At New Harbor, the left valve was covered by diatoms and foraminifera to 80% coverage, and sponges, hydrozoa, and the tubes of polychaetes completed the coverage of the surface; only in this station were coverage values of 100% reached.

4. Discussion

These results provide evidence that there are different groups of sessile organisms (at least diatoms, foraminifera, porifera, cnidaria, bryozoa, mollusca, anellida, and crustacea) that can utilize the shells of *A. colbecki* as a substratum.

The distribution of the different taxa is related both to the valve of the shell and to the characteristics of the different habitats. The site characterized by muddy bottoms (New Harbor) differs from the other two both for the greater coverage of the left valve and for the lesser coverage of the right, particularly due to the microbenthic organisms, which are more common on the left valve.

For the macrobenthic organisms, *e.g.* the sponges, these are present indifferently on the two valves, and this is due to the body plasticity of this group, which allows them to settle on the lower valve and to grow upwards (figure 2B). Hydrozoa occur more irregularly in the three stations, and they did not show any differences between the valves. This is probably due to the wide range of trophic resources that hydroids are able to exploit, from diatoms to pedicels of echinoderms [15].

For the epibionts, the scallop shells represent a particularly suitable substratum not just for the obvious reason that they allow the colonization of soft bottom habitats to organisms generally adapted to a life on hard substrata. As with other Pectinidae [16], *Adamussium* is a living and moving substratum. The clapping limits the activity of the grazers on the shells of *Adamussium*, and particularly the activity of the widely diffused *Sterechinus neumayeri*, which represents a continuous danger for the microbenthic community and for the larvae/juveniles of the macrobenthic species. Moreover, it has been demonstrated that the clapping of the scallops suspends organic matter that has settled to the bottom [17], so that it could be used by the epibionts [13]. Some species of Antarctic hydroids, and particularly *Hydractinia angusta* living on the scallops, use diatoms as trophic resources [15].

The moving ability of *Adamussium* could also be important for the re-colonization of areas damaged by ice scouring. In these situations, due to their vagility, the scallops are among the first colonizers, and in zones where the benthic community is completely erased, they may spread over their epibionts, working as phoretic organisms. However, with the scallop acting as a transport vehicle, this contributes in this way to a general dispersion of these pioneer species not just under iceberg-scouring conditions.

The known relationships between molluscs and their epibionts are generally considered to be positive. The most common epibionts on bivalve shells are generally sponges [1], and their presence usually increases the survival of the molluscs [17–22], limiting predation through the production of secondary metabolites. In Antarctica, the toxicity of sponges is not enough to protect them from predators, considering that sponges represent one of the most exploited food sources of starfishes (figure 2G) [23, 24].

Macrobenthic epibionts can reach high values of biomass, and this increased weight of the shells limits the escape strategy of the mollusc. Moreover, among the epibionts of the scallops there are young specimens of *A. colbecki*, which live byssally attached to the adult shells. The larvae of the scallops settle on any available hard substrata that they can find, but the grazers generally feed on them. In this way, the spats only survive on the adult shells due to the clapping activity, which prevents the grazing. As shown by the presence of *Hydractinia angusta* on shells of *Adamussium*, not only grazers but also epibionts can negatively affect recruitment [15], physically limiting the settlement of spats. Thus, an increase in colonization by macrobenthos produces a decrease in recruitment. This can result in partial genetic isolation of the *Adamussium* populations, as shown by recent genetic studies [25].

With all these considerations in mind, we can summarize with the following points: (1) *A. colbecki* can move from one area to another only when its shells are largely free from colonization by large epizoans; (2) this movement from one area to another with their newly settled epibionts can accelerate the colonization processes in disturbed areas (*e.g.* in ice-scoured areas); (3) this can increase the dispersal of epibiontic species, working as a phoretic organism; (4) vagility of *A. colbecki* provides an escape from predators for the epibionts as well, thus probably increasing the survival rate of the epibionts when newly settled; and (5) the epibionts can physically limit the settlement of spats of *Adamussium*, thereby limiting the renewal of the older populations.

In conclusion, shell production by *A. colbecki* creates and maintains a particular habitat allowing this species to be considered as an example of autogenic engineering [6]. The habitat modifications due to the occurrence of *A. colbecki* support an increase in species richness, which can involve species that are not specialized in this kind of association but that can widen their pattern of distribution through the use of the shells of the scallop.

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