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Ectosymbiosis associated with cidaroids (Echinodermata: Echinoidea) promotes benthic colonization of the seafloor in the Larsen Embayments, Western Antarctica

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ABSTRACT

Ice-shelf collapses in the Larsen A and B embayments along the Weddell side of the Antarctic Peninsula resulted in new open-water areas that are likely reorganizing benthic communities. It is a natural laboratory to assess colonization of the sea bottom under new conditions. We tested the hypothesis that the epibionts associated to cidaroid echinoids could promote or enhance the colonization of hard surfaces. In fact, being vagile, cidaroids might improve dispersal capabilities of the sessile animals that are attached to their spines, e.g., promoting the colonization of areas where the fauna has been eradicated by iceberg scouring. If this hypothesis is correct, pioneer sessile species present locally on stones might have affinities with ectosymbionts on cidaroids, and the sessile fauna present both on cidaroids and stones should be more similar in the Larsen embayments than in undisturbed areas. We therefore compared sessile species living on cidaroids with those living on stones in three areas: Larsen A and B embayments and two undisturbed and geographically different areas, Atka Bay and Elephant Island. Overall, richness, evaluated as 'morphotypes' richness, was lower in the Larsen area than in other areas, but levels of species diversity were similar among the three zones. The estimate of similarity between assemblages (using the C_{22} index of Chao et al., 2008) also suggests that cidaroid epibionts are either species-specific or specific to cidaroids, while the composition of sessile fauna on stones is more variable and probably dependent on local factors. In the two undisturbed areas, sessile fauna are highly different between stones and cidaroids. This contrasts with the Larsen embayments where cidaroids share more than 80% of epibionts with the surrounding stones. These results suggest that ectosymbioses linked to cidaroids strongly contribute to benthic colonization of the seafloor in the Larsen embayments. With time, secondary successions are expected to occur, increasing the difference between epibiotic communities on cidaroids and those on stones, and lead to the situations observed in unperturbed sites.

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1. Introduction

Biodiversity has a paramount role in the ecosystems functioning (Duffy et al., 2007), and the dynamics of colonization of new habitats is of particular interest in assessing processes of recovery. However, the onset of ecosystem settlement in newly free areas is often difficult to assess. Well-studied cases concern large-scale catastrophic events (such as volcanic eruptions, forest fires, hurricanes, meteorite impacts) that caused the complete destruction of life and former habitats (Brown and Lomolino, 1998; Thornton et al., 2001; Rampino and Koeber, 2006). Small-scale disturbances can be equally important by removing, for instance,

dominant plants or animals and modifying inter-specific competition inside a community. Such disturbances occur in terrestrial (e.g., falling trees in tropical forests) and in aquatic ecosystems (e.g., predatory sea-stars removing dominant mussels on intertidal rocky shores) (Brown and Lomolino, 1998). Few studies have been carried out in the marine realm (Tomascik et al., 1996; Lock et al., 2009). For instance, benthos recovery after human-induced disturbances has been investigated (including in the deep sea). In addition to small-scale recolonization studies of artificial trays devoid of fauna (e.g., Kline and Stekoll, 2001), a broad-scale attempt was made in the Peru trench at 4150 m depth (Thiel et al., 2001). This disturbance covered an area of 10 km² in which 2 km² sections were intensively disrupted to 10–15 cm depth. Seven years later, the macrofaunal taxa had largely recovered (Borowski, 2001), with an enhanced heterogeneity and, for some taxa, even greater abundances than before (Bluhm, 2001).

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Recolonization takes time. Early stages correspond to the settlement of pioneers in discrete patches that then expand and coalesce. Later stages involve species replacements. For plants on lava, the pioneer colonization stage lasts more than 20 years (Abe, 2006; Cutler et al., 2008). For corals it takes fewer than five years for diversification to begin (Tomascik et al., 1996). For a complex ecosystem, complete recolonization might take centuries (Rampino and Koeber, 2006; Cutler et al., 2008). In contrast, deep-sea benthos may show a rapid colonization of physically disturbed seafloor presumably because the sediment disruption enhances food accessibility, at least for deposit feeders (Ingole et al., 2005).

The recent changes in the Larsen ice shelves along the Weddell side of the Antarctic Peninsula provide an opportunity to observe the effects of large-scale disturbances due to ice melting. After a period of steady retreat, concomitant with ice thinning up started in the late 1980s, the ice shelves of Larsen A (to the north) and Larsen B (central embayment) collapsed in 1995 and 2002, respectively. This last event corresponds to the largest surface of ice shelf ever disintegrated, equalling a surface of more than 3000 km² which rapidly collapsed over a few weeks (Shepherd et al., 2003; Rack and Rott, 2004). Each collapse event released a huge amount of thick ice that scoured the seafloor down to several hundred meters depth. In the two years after the collapse and disappearance of the buttressing ice shelf, ice discharge from ice streams has increased 3–8 fold, producing many large icebergs (Rignot et al., 2004; Scambos et al., 2004). Discharge of these icebergs has slowed to a new equilibrium (Rott et al., 2007). The impact of iceberg scouring on the benthos has been well characterized in Antarctica (Gutt et al., 1996; Smale et al., 2008), and it is known that in the Weddell Sea, even in 'standard' conditions, ice scouring prevented the Antarctic benthos from reaching maturity and can affect up to the 20% of the seafloor (Gutt and Starman, 2001). Therefore, the catastrophic events recorded in Larsen A and B can be expected to have dramatically impacted the benthos and, especially, the sessile organisms formerly present under the ice shelves.

Studies of recovery after intense ice disturbances showed that a variety of factors may affect the successive stages of settlement of Antarctic benthic communities. These include dispersal capabilities and growth rates of colonizing species, as well as competition between species (Teixido et al., 2004, 2007). Teixido et al. (2007) also suggested ectosymbiosis might contribute to benthic colonization.

The general role of symbiotic relationships in early stages of the process of species colonisation is still unclear. In plants, mutualist relationships may be either an advantage for early colonization (e.g., mycorrhization facilitates resources acquisition in pioneers, Cuenca and Lovera, 1992), or a limiting factor (e.g., plants and pollinators need synchronicity, Shanahan et al., 2001). Ectosymbiosis, the inter-specific relationship in which a species (the symbiont) lives on another species (the basibiont), whatever the nature of the relationship, is suspected to facilitate colonization (Hétérier et al., 2008). Ectosymbiosis has been identified as a key factor that structures benthic communities in the Antarctic as it decreases the level of competition between benthic species for hard substrates which are often scarce (Gutt and Schick, 1998). The most studied Antarctic basibionts are bivalves (Cerrano et al., 2009) and cidaroid echinoids (Hétérier et al., 2008; Linse et al., 2008; Cerrano et al., 2009). Primary spines of cidaroids lack an epithelium, thereby providing an accessible hard substrate for numerous sessile species (David et al., 2009). As they harbour sessile species distinct from those attached to the surrounding stones, cidaroids are expected to play a key role in maintaining and possibly enhance biodiversity in deep environments of Weddell Sea (Hétérier et al., 2004, 2008). A similar role is suggested to occur in shallow waters as well (Linse et al., 2008).

Ectosymbionts are thought to promote the colonization of disturbed marine areas because dispersion is improved through the mobility of their basibionts (Cerrano et al., 2006). The collapse of Larsen A and B offered the opportunity to study the early stages of colonization of newly vacated large areas of the seafloor. In this regard, two different dynamics may occur, allowing to test two alternative hypotheses. According to the first one, if sessile species attached to cidaroids are species-specific (this is the case in deep waters, see Hétérier et al., 2008), they must be the primary-colonizers. When these primary-colonizers subsequently colonize the surrounding area, the community settled on stones should reflect the ectosymbiotic community living on cidaroids. This pattern should depart from unperturbed situations, where sessile communities of stones and cidaroids usually differ (Hétérier et al., 2008). An alternative hypothesis is that sessile species colonizing the newly vacated area of Larsen firstly settle on stones and, only secondarily, on the spines of cidaroids. In this latter case, primary-colonizers should be composed by generalist sessile species, and the sessile fauna settled on cidaroids in new colonized areas should differ from that of undisturbed areas. These two alternative hypotheses are here tested through a comparative study of the sessile organisms fixed on rocks versus those fixed on cidaroids, in three contrasting areas: the impacted Larsen embayments and two relatively undisturbed control sites located on each side of the Weddell Sea.

2. Material and methods

Sampling was done during the expedition *ANTARKTIS-XXIII/8* of the RV *'Polarstern'* in the Weddell Sea and South Shetlands from November 2006 to January 2007 (Gutt, 2008). Cidaroids and stones were collected, during the same trawl, on the continental shelf, using either a Bottom or an Agassiz trawl. On the whole, a total of 15 stations, distributed in the three contrasting areas between 146 and 391 m deep: one station at the entrance of Atka Bay in the East Weddell Sea, five stations in Larsen A and B embayments (where ice shelves recently collapsed) and nine stations off Elephant Island (Fig. 1, Table 1). In each station, both substrates (stones and cidaroids) were collected during the same trawl.

All collected cidaroids were studied. Spine length, test diameter, and height were measured with digital vernier calliper to the precision of a tenth of a millimeter. Cidaroid size was estimated using a size index determined as the sum of the test height and lengths of the longest aboral spine and the longest adoral spine. Many parameters may affect the quality and integrity of samples. For example, the bottom type, the trawl size and the trawling time may lead to the damage of the collected cidaroids in different ways and, above all, by breaking their spines. Therefore, a Kruskal–Wallis test was performed to test whether the number of spines found on collected cidaroids was the same in all three areas. Moreover, a Wilcoxon Signed Ranks Test was used to assess the evenness of the number of specimens sampled by the two types of trawl.

To obtain 'biotic' (cidaroids) and 'abiotic' (stones) substrates of comparable size, only stones with a size within the size range of cidaroids (i.e. between 10 and 100 mm) were taken into account. Because trawls sometimes collect stones in large numbers, a random sub-sample of about a hundred stones was considered for the analyses. All studied stones were measured, considering the largest measure as stone length, and its perpendicular measure as stone width. A size index was calculated by multiplying length by width. Finally, each encrusted stones and cidaroid specimens were fixed (separately) in 95% ethanol for further analysis and subsequent identification of their sessile organisms.

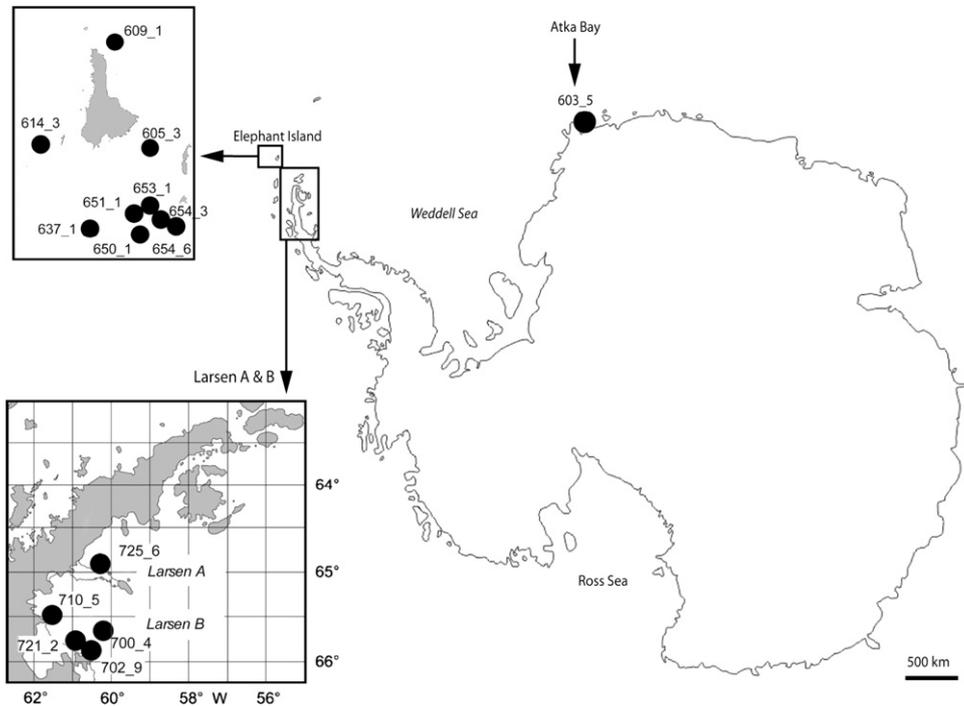


Fig. 1. Map of Antarctica with location of sampling stations (black dots) in Atka Bay, Larsen A and B and Elephant Island (black circles show precise station locations). Modified after Gutt (2008).

Table 1
Sampling station position, average depth, used trawl and number of stones and cidaroids sampled in each with the proportion of individuals colonized by at least one sessile species.

Station	Position	Average depth (m)	Trawl	Area	Number of individuals					Proportion of colonized individuals			
					S	C				S	C	P	
						Am	Cp	Cg	Nm				Rt
PS69/603_5	70°30.99'S 08°48.08'W	285.5	AGT	AB	49	0	15	1	1	3	0.67	1.00	0.0003
PS69/605_3	61°20.33'S 55°31.53'W	145.8	ACT										
PS69/609_1	61°12.04'S 54°37.10'W	317.4	BT										
PS69/614_3	60°52.37'S 55°29.80'W	253.3	AGT	EI	96	15	0	0	3	26	0.24	1.00	<0.0001
PS69/637_1	61°05.31'S 56°14.65'W	391.3	BT										
PS69/650_1	61°17.41'S 56°12.28'W	322.3	BT										
PS69/651_1	61°17.42'S 55°58.46'W	305.7	BT										
PS69/653_1	61°18.54'S 55°57.92'W	359.1	BT										
PS69/654_3	61°21.52'S 56°02.28'W	353.6	ACT										
PS69/654_6	61°22.80'S 56°03.84'W	342.5	ACT										
PS69/700_4	65°55.40'S 60°19.95'W	438.6	AGT										
PS69/702_9	65°57.85'S 60°28.42'W	218.2	AGT										
PS69/710_5	65°32.86'S 61°38.33'W	240.6	AGT										
PS69/721_2	65°55.41'S 60°34.01'W	296.6	AGT										
PS69/725_6	64°54.80'S 60°37.46'W	180.6	ACT										

AB: Atka Bay, EI: Elephant Island, L: Larsen. AGT: Agassiz trawl, BT: Bottom trawl. S: stones, C: cidaroids, Am: *Aporocidaris milleri*, Cg: *Ctenocidaris gigantea*, Cp: *Ctenocidaris perrieri*, Nm: *Notocidaris mortenseni*, Rt: *Rhynchocidaris triplora*. P: Likelihood ratio χ^2 testing for the difference in the proportion of colonized individuals between stones and cidaroids in each area. The number of individuals pertains for each area. For EI and L areas, they are cumulated numbers of several stations.

Identification and counting of sessile organisms present both on cidaroid spines and stone surfaces was made in the laboratory with the aid of a stereomicroscope. Most epibionts were determined at least to the class level, and at a lower taxonomic level when possible. Because of the diversity of the sessile organisms present, very few could be determined to the species level. The solution adopted was to determine 'morphotypes' and consider them as species proxies for further analyses. The prevalence of sessile organisms on cidaroids or stones was

calculated as the ratio of the number of colonized individuals to the total number of individuals (Table 1). Abundance data were obtained by counting the number of individuals attached to each colonized substrate (cidaroid or stone). For colonial species (e.g., sponges, bryozoans, hydrozoans), for which the notion of 'individual' is ambiguous, it is conservative to consider that a single colony was founded by only one propagule and that each spatially discrete colony represents one single event of colonization (Hétérier et al., 2008). Species abundance distribution (SAD)

of sessile assemblages was analysed according to the methods reviewed by McGill et al. (2007). Such methods are independent of taxon identity and result more robust for comparison of communities that do or do not share species (or morphotypes). By using these methods, it is possible to capture most of the information in rank-abundance plots (McGill et al., 2007). Abundance data on a \log_{10} scale were plotted against the rank for each morphotype, from the most abundant (Rank 1) to the least abundant, and the distributions were inspected visually to look for differences between communities (Whittaker, 1965; Krebs, 1989; Magurran, 2004).

Data were analysed using indices for richness (\hat{S}_{ACE}), diversity (\hat{H}) and similarity (C_{22}) as suggested by Chao and Lee (1992), Lee and Chao (1994), Chao and Shen (2003), and Chao et al. (2008). These indices, calculated using the software SPADE (Chao and Shen, 2009), are an extension of classical indices used in community ecology (Krebs, 1989). They take into account 'unseen' species, as estimated by the probability of missing rare species and computed from abundance-based data. These indices use replicates to compute confidence intervals which make possible comparisons of heterogeneous data. To obtain these indices for a given sampling station, we used individual cidaroids or stones as replicates for describing the cidaroid or stone assemblages respectively (as suggested by Shaw and Dobson (1995) for host-parasite relationships). Therefore, the width of the confidence intervals computed will depend on the number of cidaroids and stones collected at a given station. When the number of replicates (cidaroids and stones) collected at a station was too low, one single index was computed for all stations in a zone (Table 1). Finally, a 95% confidence interval (CI) based on 200 bootstrap iterations was obtained for each index. The estimate of S , the richness index of a given assemblage, was obtained using the abundance-based coverage estimator \hat{S}_{ACE} (Chao and Lee, 1992). The estimate of H , the alpha diversity index of a given assemblage, was obtained using the extended Shannon index \hat{H} of Chao and Shen (2003) based on the frequency and abundance of species. Finally, the estimate of similarity between assemblages used the non-parametric index C_{22} of Chao et al. (2008) that is derived from a Morisita index. Comparisons of average C_{22} values between cidaroids and stones for all the sampling stations were tested using a Wilcoxon test, and not just estimated according to 95% CI of C_{22} values. Statistical analyses were made using the softwares SPADE (Chao and Shen, 2009) and JMP (SAS Institute).

3. Results

On the whole, 70 cidaroid specimens were collected: 20 in Atka Bay, 44 off Elephant Island and six in Larsen areas. Cidaroids belonged to five species with different spine morphologies: *Ctenocidaris gigantea* (H.L. Clark, 1925), *Ctenocidaris perrieri* Koehler, 1912, *Notocidaris mortenseni* (Koehler, 1900), *Rhynchocidaris triploporea* Mortensen, 1909 and *Aporocidaris milleri* (A. Agassiz, 1898). *R. triploporea* and *N. mortenseni* are widely distributed all around Antarctica (David et al., 2005). We only found one species in Larsen, *N. mortenseni* (Table 1). Comparison among cidaroids showed that the number of spines found on collected cidaroids was the same in all three areas (for *N. mortenseni* and *R. triploporea*; Kruskal–Wallis $Z=1.63$, $p=0.44$). Moreover there was no significant difference in the number of cidaroids sampled by the two types of trawl in Elephant Island area (Wilcoxon Signed Ranks Test, $W=14.5$, $p=0.32$). We therefore considered our samples similar in quality among the different areas.

In the three geographic zones, stones were always more abundant than cidaroids. However, while all cidaroid spines had ectosymbionts, only a small fraction of stones had sessile animals (Table 1). It is likely that some bare stones were partially buried into the mud as they were collected, the sediment cover preventing them from being colonized by epizoa. However, there was no evidence to generalize this fact to the majority of them. One hundred and seventeen morphotypes (hereafter called 'species') belonging to 10 taxa were counted in the three geographic areas. Bryozoans were the dominant group in terms of number of species (Fig. 2). Protozoans were numerically dominant in number of individuals, but showed a lower diversity (Fig. 2). Plots of the species abundance distribution (SAD) showed no major difference between the different geographic zones (Fig. 3). There were always numerical dominant species (500–1000 individuals) and a slight excess of rare species. Nevertheless, there were more rare species in the Atka Bay station than in others and the Larsen zone had slightly fewer species than the other two (Fig. 3).

Sessile species richness is higher on cidaroids (all species grouped) than on stones in Atka Bay and Elephant Island zones, while no significant differences were found in Larsen (Fig. 4A). The estimated total richness is also lower in Larsen than in the two other zones. Diversity shows contrasting patterns among the

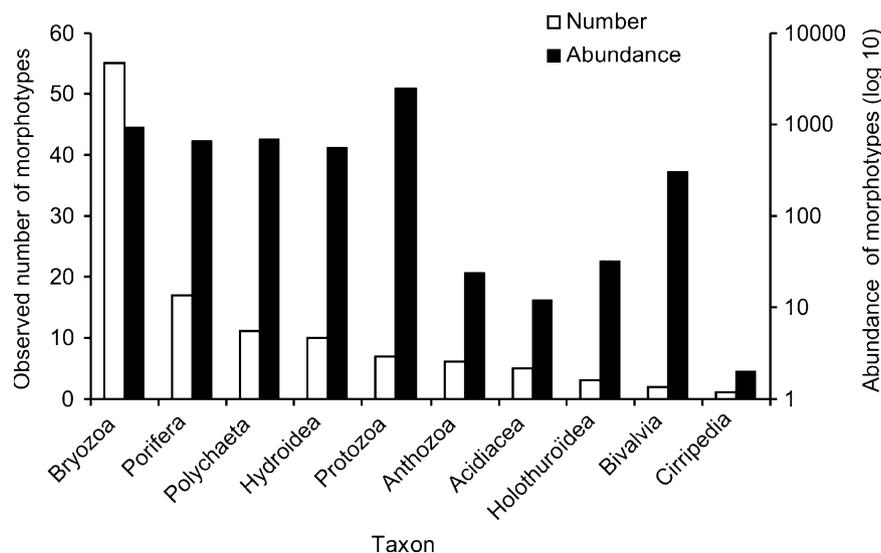


Fig. 2. Total number (white bars) and abundance (black bars) of morphotypes found in the 10 sessile taxa, in all sites and all substrate types.

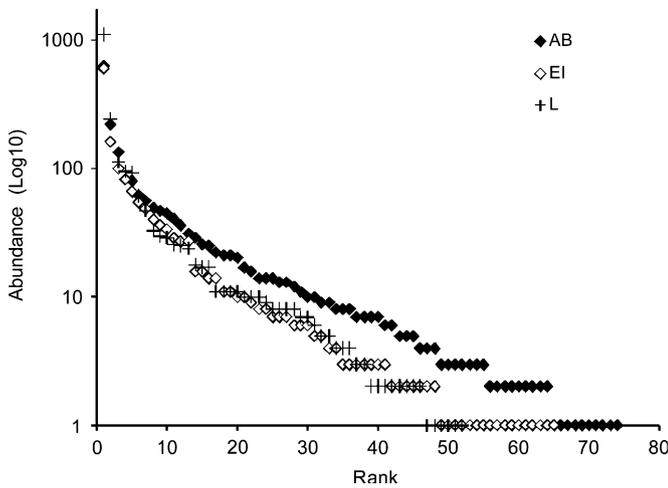


Fig. 3. Species abundance distribution (rank-abundance plot) of total sessile fauna for the three zones (fauna found on both stones and cidaroids). AB: Atka Bay, EI: Elephant Island, L: Larsen.

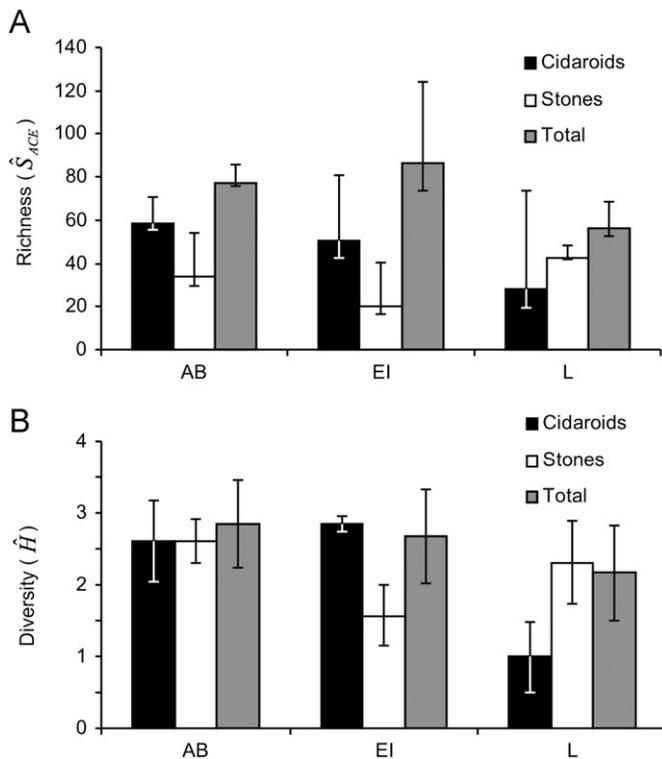


Fig. 4. Characteristics of sessile fauna within each geographic zone: (A) estimate of species richness (\hat{S}_{ACE}) according to the type of substrate and (B) estimate of specific diversity (\hat{H}) according to the type of substrate. For each zone, the total of all cidaroid species is considered. AB: Atka Bay, EI: Elephant Island, L: Larsen. Error bars are 95% confidence intervals based on 200 bootstrap iterations.

three zones (Fig. 4B). While no pattern was found between stones and cidaroids in Atka Bay, diversity was lower on stones than on cidaroids at Elephant Island. The reverse pattern was found in Larsen. Global diversities are not significantly different between the three zones but ectosymbiont diversity found on cidaroids in Larsen is lower than in the two other stations (Fig. 4B). Since the different zones harboured different cidaroid species, this difference might be due to differences in the qualities of substrate provided by these different species. We therefore compared Richness and Diversity for the only cidaroid species

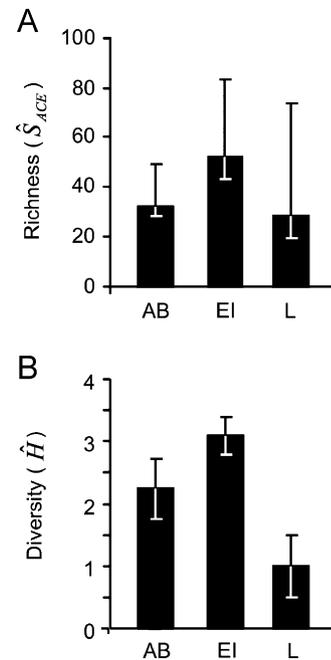


Fig. 5. Characteristics of sessile fauna fixed on *Notocidaridus mortensenii* within each geographic zone: (A) estimate of species richness (\hat{S}_{ACE}) and (B) estimate of specific diversity (\hat{H}). AB: Atka Bay, EI: Elephant Island, L: Larsen. Error bars are 95% confidence intervals based on 200 bootstrap iterations.

present in all three zones. The ectosymbiont richness on *N. mortensenii* is not significantly different between stations, while overall diversity is much lower in Larsen than in other zones (Fig. 5).

The similarity between sessile communities was compared at three different levels. We first compared, within each zone, the similarities of fauna between the different types of substrates (e.g., between stones and a given species of cidaroid, or between two cidaroid species). In Atka Bay and Elephant Island, similarities are much higher between the different cidaroid species than between stones and cidaroids (Fig. 6), with the exception of the low similarity between *R. triplopora* and *C. perrieri* in Atka Bay. In Larsen, the level of similarity between stones and cidaroids is significantly higher than in the two other zones and is at the same level (around 80%) as similarities between cidaroid species at the two other zones (Fig. 6). We then compared the similarities in sessile fauna between the different geographic zones. This was done for the substrates common to the three zones, i.e. the cidaroid *N. mortensenii* and stones. Sessile fauna living on *N. mortensenii* is highly similar between zones, while similarities of the fauna fixed on stones are very low and always significantly lower than those between cidaroids (Fig. 7). The similarity of the fauna fixed on stones between Larsen and Elephant Island is nevertheless higher than for the other comparisons (Fig. 7).

4. Discussion

We only found one cidaroid species in Larsen, *Notocidaridus mortensenii*. Its epibiotic fauna is less diverse but as rich as the one found on stones. In addition, the two faunas are very similar since approximately 80% of species are common to the two substrates. This last result contrasts sharply with what is found in the two other zones, where similarities between the epibiotic fauna present on cidaroids and the one present on stones are very low. Hétériér et al. (2008) found a similar pattern in the Weddell Sea at deeper stations (depth > 1000 m), where general

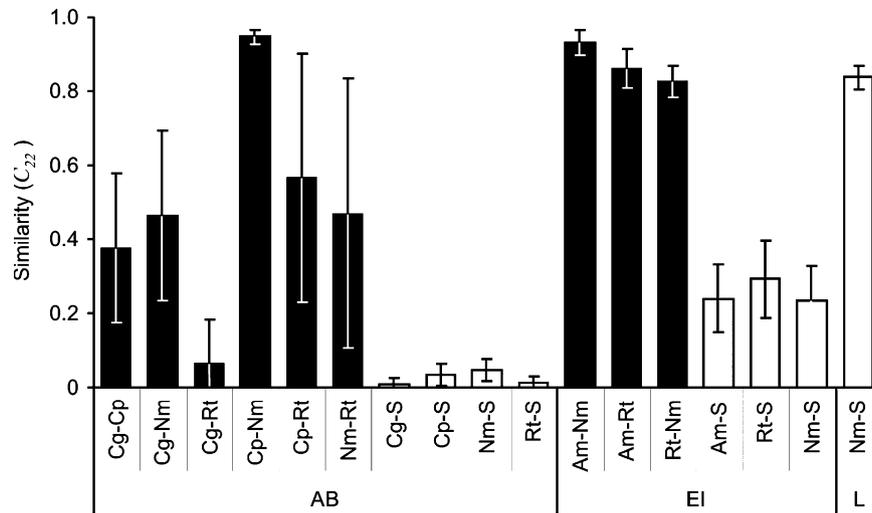


Fig. 6. Inter-substrate pairwise similarities (C_{22}) of sessile fauna at each geographic zone. AB: Atka Bay, EI: Elephant Island, L: Larsen. Am: *Aporocidaris milleri*, Cg: *Ctenocidaris gigantea*, Cp: *Ctenocidaris perrieri*, Nm: *Notocidaris mortenseni*, Rt: *Rhynchocidaris triplopora*, S: stones. Black bars stand for similarities between cidaroids, white bars for similarities between cidaroid and stone. Error bars are 95% confidence intervals based on 200 bootstrap iterations.

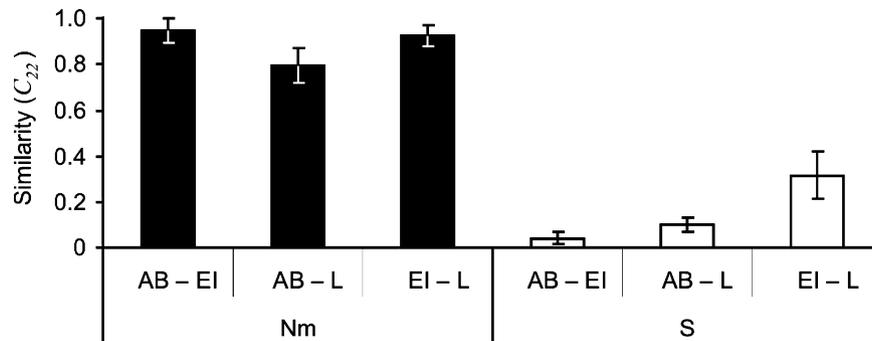


Fig. 7. Similarities (C_{22}) of sessile fauna between the different geographic zones, according to the substrate types. AB: Atka Bay, EI: Elephant Island, L: Larsen. Only substrates common to the 3 zones were considered. Nm: *Notocidaris mortenseni*, S: stones. Error bars are 95% confidence intervals based on 200 bootstrap iterations.

biodiversity is low (Clarke and Johnston, 2003). The present study extends the conclusions of H  tierier et al. (2008) to shallower environments, showing that sessile species harboured by cidaroids are complementary with those living on stones and that ectosymbiosis makes an important contribution to biodiversity in the Antarctic.

A striking result in the present study is that the epibiotic communities on *N. mortenseni* are very similar among the three distantly related geographic zones while the epibiotic communities on stones are very different. This means that the structure of the stone-borne epibiotic communities relies upon local environmental factors while cidaroid epibiosis is highly species-specific.

Overall, sessile communities are poorer in terms of number of species in the Larsen areas freed after the ice shelves collapse, while community diversities (\hat{H}) are very similar in all three zones. This means that colonization is not just the action of a few dominant pioneer species, but that numerically various species contribute to increasing local diversity (otherwise a much lower diversity would have been found in Larsen). Cerrano et al. (2006) proposed that ectosymbiosis might facilitate the colonization of an ecosystem by sessile organisms after a perturbation, because living substrates (basibionts) are actively motile while mineral substrates are not.

Two observations suggest that colonizing processes of Larsen bottoms are helped by the presence of *N. mortenseni*: (1) in Larsen the epibionts found on *N. mortenseni* are similar to those found in

the other studied sites, and (2) these Larsen cidaroids share more than 80% of their epibionts with the surrounding stones. This means that cidaroids might have colonized Larsen bottoms as adults and that cidaroid epibionts have settled in the surroundings via their propagules, producing a local sessile community (i.e. on stones and other hard substrates). This would support the hypothesis of Cerrano et al. (2006) that ectosymbiosis might facilitate the colonization of an ecosystem by sessile organisms. Appearance of *N. mortenseni* in the Larsen area may also have resulted from larval dispersal without direct involvement in the settlement of ectosymbionts. Indeed, planktonic larvae of cidaroids are not colonized by epibionts, nor are juveniles because their spines are still protected by an epithelium. Therefore, adult *N. mortenseni* are likely the main agents in the dispersion of epibiotic species. Our results also suggest that the 20% of the species specificity to stones might be due to local recruitment. Similarities of the sessile faunas fixed on stones in Larsen and Elephant Island, which are in relative proximity, are very high. This contrasts with the situation between Larsen and Atka Bay that are more distant. These two simultaneous sources of recruitment could explain the high diversity of epibionts in this recently perturbed ecosystem. With time, secondary successions with new colonization and species replacement will most probably occur on stones (and other abiotic hard substrate in the area) rather than on cidaroids (their epibiotic communities being rather specific and constant). This could thus increase the difference between cidaroid and stone epibiotic communities and

lead to the usual situation observed in unperturbed sites (see Hétériér et al., 2008) where epibiotic communities differ for stones and cidaroids.

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