Antarctic shallow subtidal echinoderms: is the ecological success of broadcasters related to ice disturbance?

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Abstract One characteristic pattern found in the marine Antarctic shallow environments is the unusually high proportion of species with protected and pelagic lecitotrophic development modes. However, species with planktotrophic development generally appear as the most conspicuous types of organisms in these environments. The Antarctic shallow benthos is considered as one of the most disturbed in the world, mainly due to the action of ice, thus one could hypothesize that such an environment should favor organisms with high dispersal capability. In order to test this general hypothesis, for two consecutive summers (2004–2005) and at two locations, we quantified the abundance and size distribution of most echinoderms present along bathymetric transects. Our results show the predominance of broadcasters (i.e., *Sterechinus neumayeri* and *Odontaster validus*) at a location where disturbances are common, while brooders (e.g., *Abatus*

agassizii) only occurred at shallower depths of the least disturbed location. These results not only corroborate the hypothesis that local disturbance is an important factor generating these ecological patterns, but also suggest how ice-related disturbances could represent a major selecting agent behind the patterns of species diversity at an evolutionary scale in Antarctica.

Introduction

Despite the high number of species with nonfeeding developmental modes (mainly brooding and pelagic lecithotrophy) among the Antarctic benthic marine invertebrates, it is currently recognized that few (Antarctic and sub-Antarctic) species with planktotrophic development (echinoderms in particular) correspond to the dominant macroinvertebrates in the shallow Antarctic subtidal environments (Pearse et al. 1991; Clarke 1992; Pearse 1994). More recently, a novel interpretation of this pattern has been proposed by Poulin et al. (2002), which considers separately the success of brooders and pelagic lecithotrophs at an evolutionary time scale and the present ecological success of pelagic planktotrophs. This perspective invokes the occurrence of differential rates of extinction among taxa with these contrasting developmental modes in the austral region since the Miocene. It was, however, during the Pleistocene that the alternation of glacial and interglacial episodes was more frequent (Imbrie et al. 1993) and the conditions were such that species with planktotrophic larvae were more prone to extinction through sorting at the species level (Jackson and Cheetham 1999). This interpretation, however, has been challenged lately by arguing that the current rarity of broadcasters among

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Antarctic marine benthic invertebrate species may be a consequence of evolutionary temperature adaptation (Thatje et al. 2005). Such explanation, however, assumes that the Antarctic community survival was only possible in the deep sea or in discrete shelters on the continental shelf. However, as argued by Pearse and Lockhart (2004), the more serious challenge concerns the hypothesis addressing the contrasting success between lecithotrophic development (whether pelagic or brooded) and planktotrophic development.

At an ecological time scale the occurrence of contrasting developmental modes (pelagic vs. benthic) should be reflected in the ecology of species by affecting fundamental demographic processes such as dispersion, recruitment and habitat selection. In particular, it is expected that the mode of development will have an important effect on the spatial distribution and the demography of these species (Poulin and Féral 1995). For brooding species, the release of juveniles in the close proximity of adults would allow the occurrence of discrete patterns of population distribution, with intraspecific competition acting as a key structuring process (e.g., *Abatus cordatus*: Poulin and Féral 1994, 1995). In the cases of species with pelagic development, where larval dispersal allows the colonization of new environments (microhabitats), processes that operate during or soon after settlement (e.g., competition, predation) are most likely responsible for the observed patterns. In either case, the occurrence of physical disturbance is also known to affect ecological patterns (e.g., Dayton 1971). Hence, the linkage between developmental modes and spatial distribution can be better understood if organisms with contrasting developmental modes can be found in a setting where strong disturbances show important local variability (Pearse et al. 1991; Poulin and Féral 1995). Shallow Antarctic benthic habitats have traditionally been considered among the most disturbed types of marine environments, even compared with highly disturbed terrestrial systems (Dayton et al. 1970; Raguá-Gil et al. 2004). Such disturbances are mainly exerted by the physical action of ice that assumes different forms and are believed to be responsible for the bathymetric zonation of Antarctic zoobenthos due to a gradient of decreasing frequency of disturbance by ice with depth (Dayton 1990). Freezing of the whole water column down to 10 m is referred as to icefoot, which prevents the development of stable shallow subtidal communities (Dayton et al. 1974). Additionally, the formation of anchor ice on the sea floor down to a depth of 100 m can entrap and kill benthic organisms (Dayton et al. 1970). Finally, floating ice of different sizes is more likely to exert an important effect on shallow benthic communities (Nonato et al. 2000; Gutt 2001).

Many examples exist that describe the patterns of bathymetric zonation of benthic organisms in the Antarctic shallow environments (Pugh and Davenport 1997; Sahade 1998; Nonato et al. 2000). In most cases, the shallower subtidal is almost depleted of conspicuous benthic invertebrates; however, species like the gastropod *Nacella concinna* and diverse amphipods are common (Nonato et al. 2000; Gutt 2001). Deeper portions of the shallow coastal Antarctic subtidal, however, are characterized by the presence of several invertebrates such as molluscs (e.g., *Neobuccinum eatoni*, *Laternula elliptica, Yoldia eightsi*) and echinoderms (e.g., *Sterichinus neumayeri, Odontaster validus*). Notwithstanding, echinoderms are particularly conspicuous and represented by echinoids, ophiuroids, asteroids and holothuroids (Pearse 1994; Sahade et al. 1998; Barnes and Brockington 2003; Manjón-Cabeza and Ramos 2001, 2003).

It is argued that the existence of a pelagic larval phase in some of the most abundant Antarctic echinoderms (i.e., *Sterechinus neumayeri* and *O. validus*) would allow a broader utilization (colonization) of different environments, particularly of those recently disturbed (Barnes and Brockington 2003; Raguá-Gil et al. 2004; Bowden 2005). Thus, our general working hypothesis states that highly mobile invertebrates, predominantly those with pelagic development, are more frequent in shallow, and highly disturbed settings, while less mobile, including brooding species, becomes more common along deeper, less disturbed, portions of the shallow Antarctic subtidal. The main objective of this study is to test, through in situ field observations, if the distribution of echinoderms with contrasting developmental strategies fits our predictions. Based on published information, as well as personal observations, echinoderms are common and conspicuous invertebrates in the Antarctic shallow subtidal, thus we chose to quantify the distribution and abundance of this group. We selected two locations along the Antarctic Peninsula representing scenarios subject to contrasting ice-related disturbance. At each location, equivalent surveys of echinoderms with known contrasting developmental strategies were performed along a bathymetric gradient.

Materials and methods

Study area and field surveys

Two locations along the Antarctic Peninsula were chosen for this study: a sheltered shore within Fildes Bay (62° 12′ S 58° 58' W) located in the south-east part of King George Island (South Shetlands), and the coastal

area next to the Chilean station Bernardo O'Higgins (63° 19' S 57° 54' W) 140 km to the south across the Bransfield Strait, on the west shore of to the tip of the Antarctic Peninsula (Fig. 1). Fildes Bay corresponds to a semienclosed system with its opening facing to the south, whereas O'Higgins is located on a more exposed shore. At each location, and in order to select appropriate study sites, we conducted preliminary surveys by SCUBA diving at different points in order to get a quick estimation of the type of bathymetry, bottom composition and the presence of echinoderms. The criteria for site selection considered the presence of different bottom types (i.e., sediment, rocky bottom, the presence of algae) and a slope that would include a depth gradient along a transect of manageable dimensions. After such rapid assessments, we selected one suitable site at each location where we placed the transect and conducted detailed surveys in order to obtain information on abundance of echinoderms at different depths. The transect at Fildes Bay (Fig. 1a) extended for 180 m and ranged between 3 and 33 m depth, while at O'Higgins, where the subtidal has a steeper slope, it was only 65 m long and ranged between 3 and 35 m (Fig. 1b). The maximum depth reached was mainly determined by the safety involving SCUBA diving. Each location was visited once during the austral summers of 2004 and 2005, Fieldes and O'Higgins, respectively.

The surveying methodology was similar at each site and consisted of a detailed quantification of the most common echinoderms present along the depth gradient. For conspicuous species occurring above the bottom, simple visual surveys were utilized by haphazardly tossing 1 m^2 frames at specific depths along the transect. At the same depth two divers surveyed several such frames

(at least four), where the number of samples was determined by the time it took to quantify all echinoderms present and the depth at which this happened. All individuals within each frame were identified and measured in situ and then released. Every time divers encountered sedimentary bottoms within the frame they carefully sieved through with their hands in search for hidden species (i.e., those buried in the sediment), if present, the whole frame area was surveyed using an air-lift suction device (Whale and Steneck 1991). Samples were collected inside a 1-mm mesh-size catch bag and transported alive for sorting in the laboratory.

We performed ANOVAs to compare differences in the number of individuals for each species along the bathymetric range surveyed at each site. Given the nature of these data (i.e., the occurrence of samples with zero values for some species) they were (log [$x + 1$]) transformed. A two-sample permutation test (Jadwiszczack 2003) was performed in order to test for differences in the average size between *Sterechinus* sampled at Fieldes and those collected at O'Higgins. Throughout the study the assumptions of normality, homogeneity of variance and independence of observations were tested and the appropriate transformations were performed when necessary (Sokal and Rohlf 1995).

Results

Distribution and abundance pattern of echinoderms

The overall echinoderm species composition at each site was similar, although conspicuous differences were

Fig. 1 Map of the study locations of **a** Fildes and **b** O'Higgins. ⊗ indicates position of transects and ★ indicates location of the Chilean bases
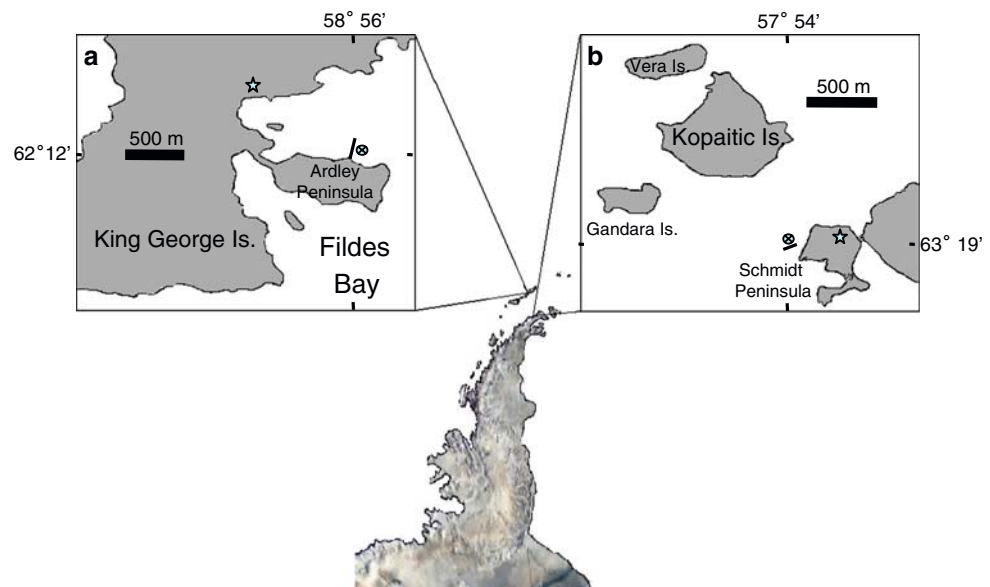
also evident such as the absence of *Abatus agassizii* and *Ophionotus victoriae* from the surveys at O'Higgins (Fig. 2). Besides the former differences, the bathymetric distribution of the most common species found at either site exhibited a greater abundance at shallower depths in Fildes compared to a clearly extended and even deeper distribution range in O'Higgins (Fig. 2a, b). The two most abundant species in Fildes were *A. agassizii* and *S. neumayeri* and they occurred primarily at shallow depths. *A. agassizii* was significantly more abundant between 3 and 5 m and no individuals were found below 12 m. Similarly, although with a slightly deeper distribution, *S. neumayeri* showed a significant peak of abundance around 8 m with a decreasing tendency towards deeper and shallower depths and it was also not found below 12 m. A similar distribution range, although less numerous, exhibited the asteroid *O. validus*. On the other hand, and although not so abundant, *Diplasterias brucei* was the species with the broadest bathymetric distribution (between 3 and 30 m) of all echinoderms considered here. Two other asteroids, *Neosmilaster* sp and *Lysasterias* sp. were
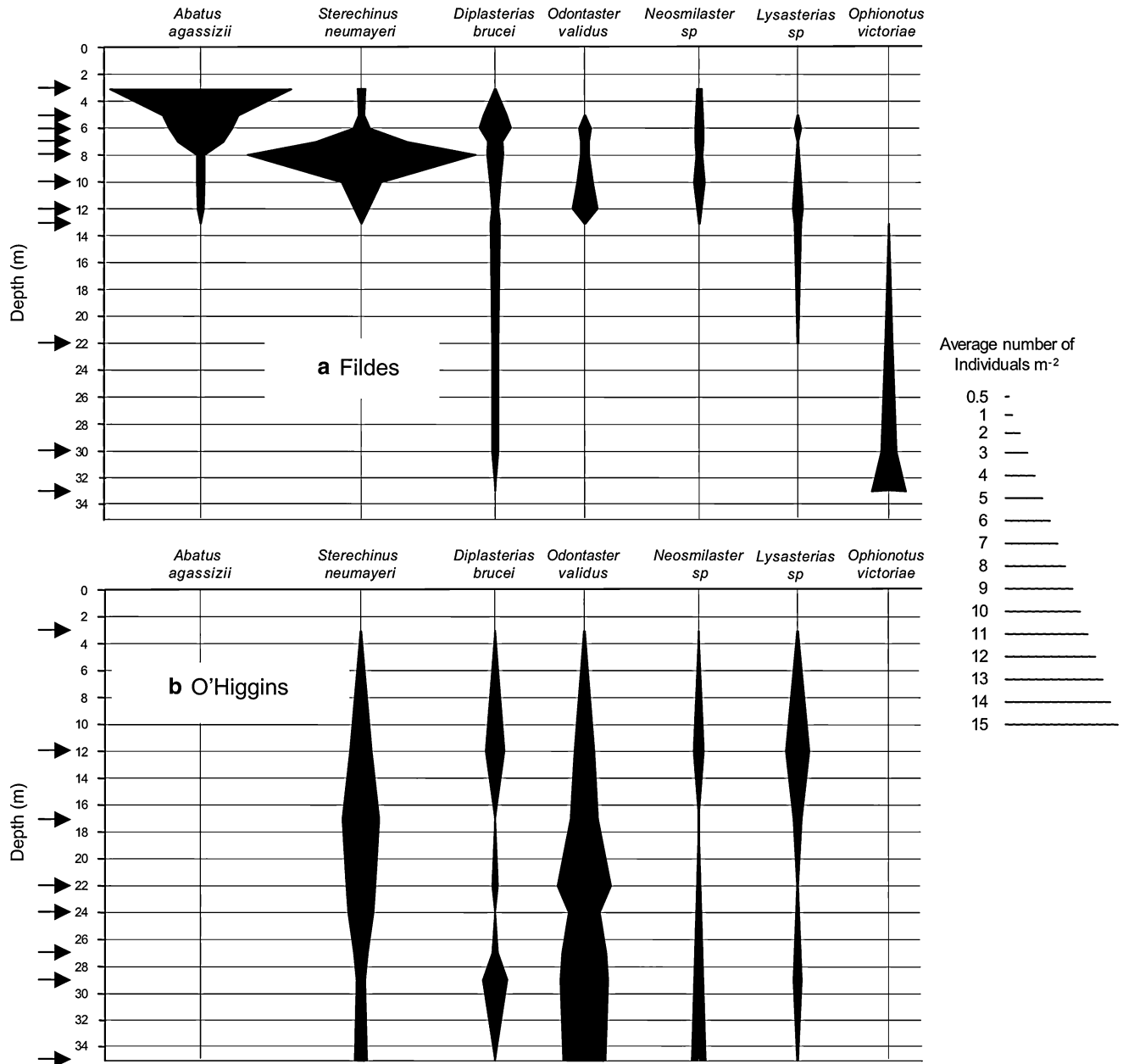

Fig 2 Spindle diagrams showing the bathymetric distribution of echinoderms present at the **a** Fildes and **b** O'Higgins locations. The *width* of spindles represents the average number of individuals per square meter. *Arrows* correspond to the depths where quadrants were surveyed

encountered, although comparatively less abundant and restricted to the shallow portion of the subtidal in Fildes. The ophiuroid, *O. victoriae*, had the deepest distribution range, only starting to appear in the samples collected at 22 m (Fig. 2a). In summary, most species at Fildes, with the exception of *Neosmilaster* sp. and *Lysasterias* sp., exhibited significant differences in their abundance along the bathymetric range considered. Noticeably was the fairly shallow distribution and greater abundance of at least 4 of the 7 species (Table 1).

A contrasting pattern of distribution and abundance of echinoderms was evident at O'Higgins (Fig. 2b). The most notorious pattern here compared with that at Fildes was the lack of either *A. agassizii* or *O. victoriae*. Furthermore, the distribution of all species at this location spanned more evenly throughout the depth gradient, without exhibiting significant differences in their abundance, except for *Lysasterias* sp. that was slightly more abundant at 12 m (Table 1).

Size frequency distribution of the two most important echinoids

The size distribution of *A. agassizii*, only present in Fildes, comprised individuals ranging from 4 to 45 mm in diameter, exhibiting an overall normal distribution with intermediate size-individuals being more abundant (Fig. 3a). However, on a closer look it is possible to distinguish several smaller modes, likely to represent different age classes (Mespoulhé and David 1992). On the other hand, *S. neumayeri* exhibited a very contrasting pattern of size distribution between locations; whereas individuals collected at Fildes were signifi-

cantly smaller than those found at O'Higgins ($P < 0.0001$) (Fig. 3b).

Discussion

Our field surveys at two locations within the Antarctic Peninsula revealed contrasting patterns of abundance and distribution of common benthic echinoderms within and between locations. These locations were originally chosen because they represent scenarios likely to experience differential ice-related disturbances. The northernmost location of Fildes, with a study site well within the bay, was considered a place
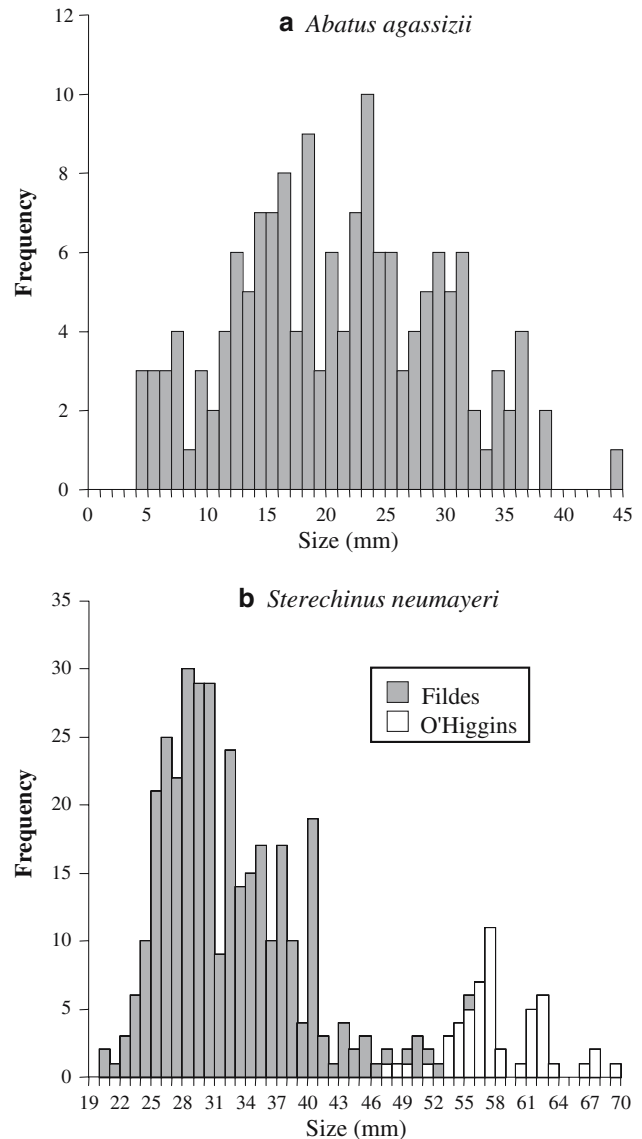

Fig. 3 Size frequency distribution of *Abatus agassizii* and *Sterechinus neumayeri*, the two echinoid species present at **a** Fildes and **b** Fildes and O'Higgins locations

Table 1 ANOVAs for differences in mean abundance of the main echinoderms present along each bathymetric transect within each location

Species	SS	df	MS	F	P
Fildes 2004					
Abatus agassizii	12.829	10	1.283	13.892	<0.0001
Sterechinus neumayeri	13.282	10	1.328	13.308	<0.0001
Diplasterias brucei	2.289	10	0.229	3.049	0.00036
Odontaster validus	1.545	10	0.154	2.872	0.0056
Neosmilaster sp.	0.233	10	0.023	0.936	0.5074
Lysasterias sp.	2.017	10	0.202	1.658	0.1132
Ophiunotus victoriae	78.638	10	7.864	32.578	<0.0001
O'Higgins 2005					
Sterechinus neumayeri	0.349	6	0.058	0.583	0.7399
Diplasterias brucei	22.881	6	3.813	2.367	0.0664
Odontaster validus	71.0678	6	11.946	0.615	0.7157
Neosmilaster sp.	0.607	6	0.101	1.700	0.1704
Lysasterias sp.	16.357	6	2.726	4.580	0.0040

SS Sum squares, *df* degrees of freedom, *MS* mean square

likely to receive little such disturbance, whereas O'Higgins further to the south, was a priori considered more exposed to the effects of ice due to the presence of extensive glaciers surrounding the area (Fig. 4).

As expected from the extensive literature available, *S. neumayeri* and *O. validus* were the most abundant and conspicuous species inhabiting the shallow benthic ecosystem surveyed. This pattern has been commonly reported not only for the Antarctic Peninsula but also for several locations around the continent (Arnaud 1974; McClintock et al. 1988; Brey and Gutt 1991; Arntz 1994; Brey et al. 1995). However, the most notorious, and somehow surprising pattern emerging from our surveys, was the presence, only at Fildes, of large aggregations of the irregular echinoid *A. agassizii* at the shallower depths. Although several recent studies describe the shallow benthic fauna of the Antarctic

Fig. 4 Pictures of each study location. **a** View from the north of Ardley Peninsula at Fildes and **b** view from the north-west of the Schmidt Peninsula at O'Higgins with base buildings in orange. Although the photos were taken during the austral summers of 2004 and 2005, respectively, these are fairly representative of the predominant conditions at each location. Notice the lack of ice cover at Fildes compared with O'Higgins

Peninsula (Sahade et al. 1998; Nonato et al. 2000; Barnes and Brockington 2003; Raguá-Gil et al. 2004; Barnes et al. 2006; Echeverría et al. 2005), none reports the presence of this Schizasterid urchin. In spite of the lack of ecological information on this species, but considering its brooding developmental mode, its distribution pattern was originally expected to be deeper under the notion that deeper habitats, therefore less disturbed, would be more suitable for brooding species (Poulin et al. 2002; but see Pearse and McClintock 1990). However, the apparently mildly disturbed conditions present in Fildes could represent suitable conditions for this species, even in the very shallow subtidal. Furthermore, the markedly different size classes found (from 4 to 45 mm) suggest that several cohorts coexist within a very narrow spatial domain (Poulin et al. 1994). Based on the growth curve estimated for *A. cordatus* in Kerguelen Islands (Mespoulhé and David 1992), the larger individuals in our surveys could be up to 4–5 years old. Since *A. agassizii* is likely to have very restricted mobility, like several other burrowing schizasterids (e.g., Thompson and Riddle 2005), coexisting cohorts suppose a fairly undisturbed type of environment, at least for the span of several years. The observed pattern resembles also the very shallow distribution (few meters in depth) of the sub-Antarctic congeneric species (Kerguelen Is.) *A. cordatus* (Poulin and Feral 1995) and *A. cavernosus* in the Atlantic Patagonian shore (Héctor Zaixso, personal communication), both living in ice-free environments. Furthermore, this distributional pattern is very similar to those seen between Cape Evans and Hut Point on Ross Island, McMurdo Sound. These sites are about 20 km apart, and anchor ice is more abundant off Hut Point. *Abatus shackeltoni* is very abundant at Cape Evans (Pearse and McClintock 1990) and rare or absent at Hut Point.

The distribution and abundance pattern of the remaining echinoderms present in our surveys, however, corresponds well with other descriptions for this system, in particular referring to their bathymetric distribution. The predominance of *S. neumayeri*, mainly at intermediate depths along our transects, both in Fildes and O'Higgins, was expected (Sahade et al. 1998; Nonato et al. 2000; Barnes and Brockington 2003) as well as the comparatively deeper occurrence of *O. victoriae* in one of the sites (Nonato et al. 2000; Echeverría et al. 2005). In Fildes the comparatively shallower distribution of most echinoderms contrasted with the reduced abundance and broader bathymetric range in O'Higgins of the same species.

Although no direct measurements were made to evaluate differences in ice-related disturbance between
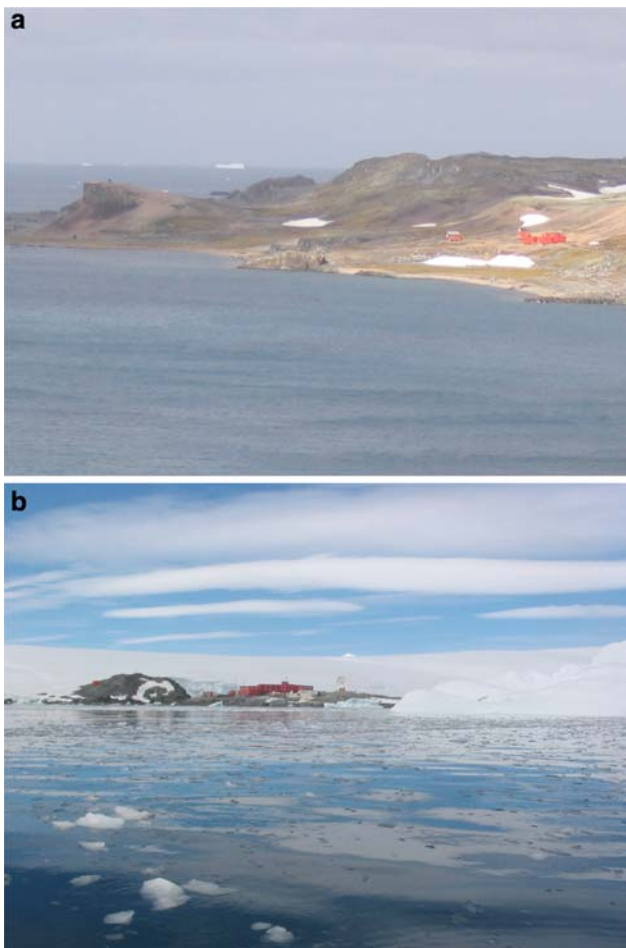
the two locations, evidence such as the notorious shift in the average size of *S. neumayeri* between locations indirectly indicates that O'Higgins might be more affected by ice. Such equivalent results were observed in other studies on *S. neumayeri* and *O. validus* (Brown et al. 2004; McClintock et al. 1988), where the average size distribution of these species was greater at a site more frequently scoured by ice compared to a nearby less disturbed site.

The explanation for such pattern is not clear; however, it might have to do with the greater recolonization capability of recently disturbed habitats by larger individuals (Brown et al. 2004).

For the most part our results conform with the general prediction, hence more mobile echinoderms with dispersive larvae appeared comparatively more abundant in the shallow subtidal. However, the shallow distribution of *A. agassizii*, a species with restricted mobility and direct development, was not expected. In general, the current pattern of species with either reproductive strategy (brooding vs. broadcasting) appears to be the result of factors operating at different temporal scales (Poulin et al. 2002). It is, however, likely that a gradient of harshness would exist along the latitudinal gradients within Antarctica, resembling those found along bathymetric ones. Thus, latitudes further away from the pole would exhibit milder (less disturbed by ice) conditions compared with higher latitudes. Thus, future research should consider quantifying the local (bathymetric) distribution and abundance of related species with contrasting developmental modes, as well as along latitudinal ranges within Antarctica and sub-Antarctic areas. It is even reasonable to hypothesize the occurrence of measurable changes in the patterns of Antarctic benthic assemblages at an ecological time scale if climatic (global) changes have an effect on environmental conditions (i.e., increase in the amount of ice as a disturbing agent).

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