Composition and biomass of shallow benthic megafauna during an annual cycle in Admiralty Bay, King George Island, Antarctica

CARLOS ALEJANDRO ECHEVERRÍA^{1,*}, PAULO CESAR PAIVA¹ and VINÍCIUS COUTO ALVES¹

¹Depto de Zoologia, Instituto de Biologia, Universidade Federal do Rio de Janeiro, CCS, Bloco A-Ilha do Fundão, 21940-590, Rio de Janeiro, RJ, Brazil * carlos, alciandroach everyig@betmail.com

 $* carlos_alejandroecheverria@hotmail.com$

Abstract: Composition and biomass of an Antarctic megafauna community were studied during a discontinuous 12 months cycle (March–December 1999 and December 2000–March 2001) at two stations (12 and 25 m depth) in Admiralty Bay, King George Island, Antarctica. During this period iceberg impacts were monitored in order to analyse their role in structuring the community. Organic matter content of the sediment showed a seasonal cycle for both depths, with lower values during winter and higher in summer. Composition and biomass of the megafauna were comparable to those described in previous surveys for the maritime Antarctica. Interannual or summer/winter changes in the density or biomass of the megafauna community were not significant, although significant differences between depths occurred during the whole survey. The observed community composition can be the considered result of a continuous invasion from a deeper fauna, constrained at shallower waters by the effects of ice and storms.

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Introduction

Antarctic benthic communities have been described as one of the most stable marine communities in the world (Cattaneo-Vietti et al. 2000). The marked seasonality that occurs at higher latitudes, on the other hand, affects primary production at sea (Fogg 1977), and it is expected to influence directly the benthic shallow maritime ecosystem, mainly due to winter resource limitation (Grebmeier & Barry 1991, Nedwell et al. 1993, Arntz et al. 1994, Clarke 1996). Summer increase in intensity and period of solar irradiance, together with the input of coastal runoff by the melt of coastal ice and snow (carrying organic phosphates and other nutrients in areas close to penguin and seal colonies), causes an increase in both planktonic and benthic algae growth. This production increase seems to be distributed by downhill bottom currents which may play an important role in carbon transportation to filter organisms that dominate deeper communities (Arnaud 1977, Arntz et al. 1994) by resuspension and lateral advection. Shallow soft-bottom communities, on the other hand, are influenced by this summer bloom (as a food/nutrient input), through primary production of:

- 1) benthic microalgae (Gilbert 1991),
- macroalgae with the input of its debris, fragmented by storms and icebergs, to the sediment (Zielinski 1981, Rakusa-Suszczewski & Zielinski 1993), and
- phytoplankton (Fogg 1977, Lipski & Rakusa-Suszczewski 1993), available to benthic community by direct sinking and through consumer's activity, in the

form of faecal pellets or falling dead bodies (Wägele & Schminke 1986, Clarke 1996).

During the winter primary production is restricted but secondary production is maintained at levels similar to summer, through bacterial decomposition (Rivkin & DeLaca 1990, Rivkin 1991, Nedwell *et al.* 1993). Some Antarctic algae can photosynthesize under very limited light conditions (Brouwer 1996, Rivkin & Putt 1987). Freezing ashore ends the input of meltwater and runoff, and solar irradiance becomes much less intense in the water column, due to the lower angle of incidence on the surface and to the shorter light period. The scarcity of plankton and the absence of terrestrial runoff makes the seawater very clear (Arntz *et al.* 1994), and may allow some productivity near the surface. However, many species seems to cease growth during winter (Clarke 1996 and references within).

Winter benthic studies in Antarctica are relatively scarce, owing mainly to difficulties in collecting during this period (Clarke 1996). Some seasonal studies were carried out on board polar vessels at more than 35 m depth (Gallardo & Castillo 1969, Mühlenhardt-Siegel 1989, Sáiz-Salinas *et al.* 1997). Studies in shallower water have been carried out at Signy Island (Hardy 1972, Brower *et al.* 1995), McMurdo Sound (Smith *et al.* 1986) and King George Island (Jazdzewski *et al.* 1986, 1995, Sahade *et al.* 1998). Yearround or comparative summer–winter studies are few. They have generally reported a high standing crop with small temporal differences in community density and composition (Lowry 1975, Kauffmann 1977, Tucker 1988, Mühlenhardt-Siegel 1989, Battershill 1990). Nevertheless, Zhang *et al.* (1986, p. 141), working in King George Island, found that "population density showed obvious seasonal variations". Clarke (1996, p. 385) considered that "winter is an important time in the ecology of many species and further year-round studies are badly needed".

Among the environmental factors that influence shallow benthic communities, ice is recognized as one of the most important (Kauffman 1977, Gutt et al. 1996, Peck et al. 1999). Sahade et al. (1998, p. 85), for example, working at depths down to 30 m in Potter Cove (King George Island), concluded that "ice impact (icebergs and anchor ice) seems to be the major regulating factor of benthic assemblages in shallow waters". These benthic communities seem to be composed of very long lived individuals (Arntz et al. 1994, Clarke 1996) and recovery from ice impacts could take years (Arntz et al. 1994). In contrast, after one iceberg impact, Peck et al. (1999) found that species return time, via locomotion from adjacent areas, is about 10 days. These authors also mention that strong storms with winds around 100 km h⁻¹ can cause water movement intense enough to advect meiofauna down to a depth of 9 m. Hydrodynamism caused by storms may therefore be considered one possible factor controlling shallow water community structure of the Antarctic benthos.

The megabenthic (*sensu* Gage & Tyler 1996) community structure in two shallow water sites in Admiralty Bay, King George Island, was studied from March–December 1999 (winter) and from December 2000–March 2001. The aim of this paper is to assess seasonal differences in composition and density of the shallow megafaunal community and relate them to environmental physical factors.

Material and methods

Study area

Admiralty Bay (King George Island, Antarctica) is a T-shaped bay with an area of 122 km^2 and a maximum depth of *c*. 535 m. Martel Inlet, where the Brazilian Antarctic station Comandante Ferraz is located, has a maximum depth of *c*. 250 m. The area adjacent to the Brazilian station slopes to a depth of 25 m at 100 m from the coast (Nonato *et al.* 1992, 2000, Bromberg *et al.* 2000). Sediment in this area becomes finer from shallow to deeper bottoms (Nonato *et al.* 1992), consisting mainly of very fine sand at 11 m and medium silt at 25 m (Bromberg *et al.* 2000), although it can change slightly from year to year (see Nonato *et al.* 2000, p. 582).

Inside this area, we selected two sites (12 m and 25 m depth) for a 12 month study. Depths were selected based on previous summer studies in the same area (Nonato *et al.* 2000, Bromberg *et al.* 2000) or in other shallow areas of Admiralty Bay (Sahade *et al.* 1998), that reported highest densities at 12–15 m and highest diversity at 25–30 m.

Stations were located respectively about 100 and 200 m east of the Brazilian station shore (052°23.2'W 062°5.1'S). At each site, six replicates were collected randomly using a 0.056 m² van Veen Grab. Samplings were carried out every 15-30 days (mean 22 days), when the weather conditions and equipment availability allowed. Nine surveys were carried out between March and December 1999 (winter), and four between December 2000 and March 2001 (summer). Winter surveys were carried out using a rubber boat with outboard engine; position was assessed through triangulation, and depth through a weighted rope. For summer surveys the research boat *Skua*, positioned by GPS, was used. Depth was assessed using a Magellan Fish Finder. Light incidence in the study area during winter was measured at 25 m depth, using a StowAway® Light Intensity Logger. Light intensity was expressed as percentage of surface light reaching 25 m, in order to avoid sensor deviations due to low temperatures. Continuous surface irradiance and other meteorological data were measured with a Campbell Scientific 21X data logger. During winter, sediment organic matter content was determined by ignition, using one sediment sample per replicate, except for the first survey, were only one sample was collected for each depth, resulting in 98 sediment samples. Iceberg scouring at the sites was monitored by assessing iceberg position by triangulation from shore for those grounded between 30 m and 10 m depth during the study period.

Megafauna was identified using a stereoscopic microscope and fixed in 4% formaldehyde. For each survey, six random replicates were pooled together, resulting in a sampling area of 0.336 m². Specimens were weighed using a 0.1 g balance. Rare species (less than four specimens in total) were not included in any statistical analysis. Megafauna density and biomass data were transformed using $x = \log_2 (x + 1)$, allowing the normalization of data for quantitative analysis. An unweighted cluster analysis was carried out for biomass data using Ward's method and Manhattan distances, in order to minimize the influence of double zeros. For density data, a Principal Components Analysis was carried out, and the resulting scores of the first two components were submitted to an ANOVA (Jassby & Powell 1990) in order to test the influences of depth, time, organic matter content and interactions of these factors on species distribution. A two-way ANOVA, using time and depth as factors, was also calculated comparing samples gathered in four temporal periods (see Stewart-Oaten et al. 1986); three along the Antarctic winter, with three temporal samples each, in early autumn (16/03, 02/04 and 22/04/1999), late autumn (10/05, 31/05 and 01/07/1999), and winter (04/08, 25/08 and 20/09/1999); plus one throughout summer, with four temporal samples (29/12/2000, 12/01, 07/02 and 26/02 2001).

Organic matter on sediment (Winter)





Results

Meteorology

During winter (1999) average wind speed was 76 km h⁻¹, with no preferential direction. Minimum air temperature was -16.3°C. Shallow water temperature ranged from 1°C to -2°C, with only one record of -2.5°C (2 September 1999). Sea surface froze from 30 August–15 September 1999, when the maximum wind speed of the studied period (159 km h⁻¹ direction south, on 15/09/1999) contributed to breaking the ice cover. During summer (2000/01) predominant winds were east (31% of the time) and northeast (20% of time). Minimum air temperature was -6.5°C.

Ice impact

During winter (1999), only one iceberg scoured at 11 m depth on the studied area (16 July 1999) and remained grounded for the next 12 days. In summer another iceberg grounded at the 25 m station (22 February 2001) and remained there until the end of the study.

Organic matter

Average sediment organic matter content was significantly different (P < 0.0001) between 12 (4.02%) and 25 m (4.88%). These values also showed a seasonal variation (Fig. 1), with significant differences between depths in mid winter (July, P < 0.01). By late summer (March/April) and at the winter's end (31 August) sediment organic matter contents were significantly higher (P < 0.001) than mid winter contents, at both depths.

Megafauna

A total of 2892 specimens were collected, distributed



Fig. 2. Cluster diagram of stations using species density (ind m⁻²).

among 26 taxa. The bivalve Lanternula elliptica (King & Broderip, 1831), although common in our samples, was discarded from the analysis due to its destruction in the remote sampling process. Mean biomass values (weightalcohol preserved) were 165 g m⁻² (S = 81, n = 13) at 12 m and 205 g m⁻² (S = 102, n = 13) at 25 m. Cluster analysis using either species density or biomass grouped stations mainly by depth (Fig. 2 for species density). In the plot of Principal Components Analysis (Fig. 3), samples were distributed along factor 1 (27.6% of the variance) axis which was explained mainly by depth. No clear pattern could be detected for the second axis, which explained 16.7% of the variance. The ANOVA analysis found no significant (P < 0.05) variation in community composition, density or biomass during winter 1999 or summer 2000/2001 period, or between years. Significant variations in specimens wet weight within each taxon through time were also not detected. In none of the analysed parameters could we detect any significant (P < 0.005) effects of season, only of depth. Interactions between community composition, depth and time were also non-significant. Distribution patterns of the six most abundant species along year and among depths is shown in Fig. 5. The observed pattern also indicated no strong temporal variation, except for the errantiate polychaetes Aglaophamus ornatus Hartman, 1967 and Barrukia cristata (Willey, 1902), not found in summer. All other species showed a depth differentiation with Serolis pollita Pfeffer, 1897 and Thracia meridionalis Smith, 1885 in 12 m and Ophionotus victoriae (Bell, 1902) at 25 m. Yoldia eightsii (Couthouy & Jay, 1839) was the only dominant species to show variation in depth preference along time, decreasing in density at 25 m in later winter periods.



Fig. 3. Plot of first (PC1) and second (PC2) principal components. Sampling stations are assigned to groups of season (w = winter, s = summer) and depth (12 and 25 m).

Discussion

Sampling

Although the sampled area (0.336 m^2) might be considered rather too small given the motility and size of the megafauna, the fact that it is constituted by six random 0.056 m² replicates increased the sample representativeness and minimized the effect of aggregation. Furthermore, species/area curves for both depths showed that 75% of the species could be collected with six samples, resulting in c. 2 m^2 as a good sample area. Even though some highly motile species (Serolis polita, Glyptonotus antarcticus Eights, 1853) can actively avoid the van Veen Grab, this gear allowed us to sample other invertebrates, e.g. Yoldia eightsii, Barrukia cristata and Brada villosa (Rathke, 1843), which are either not conspicuous enough for a visual method or too large to be sampled by a diver with a manual corer (area 0.008 m²; see Bromberg et al. 2000). A combination of visual methods (quadrats, transects) and van Veen sampling seems to be a better way for compensating for the drawbacks of both methods. A comparison between remote sampling (this work) and direct visual observations using 1 m² quadrats at exactly the same area (Nonato *et al.* 2000) indicated that remote sampling by grab was more effective in recovering megafauna density (226 ind m⁻² at 12 m and 420 ind m⁻² at 25 m against 121.7 ind m⁻² for 11 m and 21.7 ind m⁻² for 25 m) despite the nine year gap between both surveys.

Community patterns

Total biomass results are within the range of values described by Zamorano (1983), Mühlenhardt-Siegel (1988, 1989) and Jazdzewski et al. (1986) for Admiralty Bay. We found an average biomass of 165.4 g m⁻² (S = 81.3, n = 13) at 12 m compared to 79-1127.3 g m⁻² at 15 m found by Jazdzewski *et al.* (1986), and an average of 205.1 g m⁻² (S = 102.4, n = 13) at 25 m, compared to 139–2126 g m⁻² at 30 m found by these authors. Contrary to the observations of Bromberg et al. (2000) for polychaetes and Nonato et al. (2000) for the megafauna, in the same area, we found that diversity values were smaller at the deeper sites (sample area corrected). Megafaunal community variations between sampled years were not significant, and seems to be very small. Nonato et al. (2000) also found little variation in community composition between three non-consecutive sampled years, in the same area, although only in summer surveys.

The lack of temporally significant variation along 12 months suggests that megafauna is not strongly affected by the winter decrease in primary production. In Admiralty Bay such fauna is rather similar as regards specific composition in depths up to 500 m, but with shifts in the species' relative abundances (Jazdzewski & Sicinski 1993). Since metabolic adaptations to winter scarcity of food were not detected in Antarctic invertebrates (Arnaud 1977, Clarke 1980), mechanisms to overcome this processes seems to be related to the evolutionary spread of typical K-strategies (Clarke 1980) which can be characteristic of a

Table I. Survey date, name of site, depth, number of individuals, number of taxa, biomass (wet weight), and diversity.

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Date	Sample	Ind m ⁻²		No. taxa		Biomass g.m ⁻²		Diversity (H')	
		12 m	25 m	12 m	25 m	12 m	25 m	12 m	25 m
16.03.99	W1	27	87	7	10	125.3	223.1	1.72	1.80
02.04.99	W2	63	145	8	5	222.6	306.2	1.79	0.80
22.04.99	W3	32	80	11	7	91	151.2	2.53	1.29
10.05.99	W4	114	103	8	9	229.2	162.8	1.96	1.57
31.05.99	W5	111	178	6	10	228	190.5	1.28	1.08
01.07.99	W6	21	79	7	4	30.1	71.4	2.49	0.44
04.08.99	W7	88	27	5	5	206.6	51.8	1.86	0.68
25.08.99	W8	59	396	7	5	228	285.4	1.60	0.30
20.09.99	W9	31	217	4	5	79.2	102.1	1.22	1.00
29.12.01	S1	114	105	8	3	93.5	220.5	1.90	0.56
12.01.01	S2	90	251	6	6	217	215.5	1.08	0.89
07.02.01	S3	193	170	8	8	102	260.7	1.31	0.94
26.02.01	S4	81	160	9	8	298.2	425.6	2.14	1.38





deeper shelf fauna independent of light availablity. This pattern can be recurrent also in shallow water during winter, because light penetration in Antarctic waters is relatively shallow, owing to a low angle of sunlight incidence and a windy environment that provides rough sea surfaces. During this study, wind was below 20 knots (37 km h⁻¹) only 16% of time in summer, and only 7% in winter. This reduction in light penetration is also suggested by the fact that for several macroalgae species in Potter Cover (King George Island), maximum depth occurrence was around 40 m, which corresponds to 0.2% of surface light irradiation (Klöser et al. 1993 in Brouwer et al. 1995). Brouwer et al. (1995) mentions an even shallower limit for sheltered waters. Reduced light penetration, allied with a reduced suitable area due to the steepness of the shore, allows the shallow environment to be continuously invaded by a deeper fauna, and hence no seasonal variation would be detected, as expected in a typical light dependent shallow community. Hence, physical impacts (e.g. icebergs, storms) on shallow waters would be not as destructive for these communities as where their organisms were those restricted to the shallow waters only.

Several authors have pointed out the anchor ice and iceberg impact as the main causes of the differences on density and composition between communities around 12 and 25 m zones (Sahade *et al.* 1998, Bromberg *et al.* 2000, Nonato *et al.* 2000). However, these studies were carried

out in summer, and their authors did not observe the effects of ice directly. Anchor ice, being less frequent and restricted to shallower waters (up to 30 m) in the maritime Antarctica than at higher latitudes (Clarke 1996), seems to alter only a small fraction of the bottom, that can rapidly be colonized from adjacent areas (see Peck et al. 1999). More extensive impact by iceberg is less frequent. At Signy Island, for example, Barnes (1999) considers that iceberg impacts occur approximately biannually at 6 m, and every 25 years at 40 m. During winter, freezing of the sea surface also tends to immobilize icebergs, reducing their impact on shallow communities. We observed only two icebergs grounding in our study area over the 12 month period, and we found no alteration of mean density or diversity on the area after the impacts, nor for anchor ice during winter. Zamorano (1983) found a diminished total biomass at depths frequently disturbed by icebergs (15-20 m), compared with immediate shallower and deeper areas, and not a straight vertical increase in biomass, as it would be expected if vertical zonation were the result from continuous iceberg scouring. In areas were iceberg scouring is frequent, biomass and species richness are low. Frequent ice impact also reduces the availability of settling areas for benthic invertebrates. Since a very marked vertical zonation is characteristic of almost all marine ecosystems in the world, probably the ice is not the only cause for such zonation in Antarctic waters. Clarke (1996, p. 129), for example, mentions that "much of the continental shelf is too deep for direct impact by all but the largest icebergs". Antarctic shallow water soft bottom fauna seems to be the upper "boundary" of a deeper (shelf) fauna (White 1984, Clarke 1996), impoverished, at the upper levels, by physical constraints (ice and storms). This seems to explain the observed independence of seasonality and the temporal resilience (as Antarctica is one of the most physically constant ecosystems in the world). The fact that slopes are often steep in Antarctic coastal shelves may contribute to maintaining the constancy of communities' composition and diversity. Many species occurring at shallow depths are considered euribathic, as Ophionotus victoriae (Bell, 1902), Maldane sarsi Malmgren, 1865 and Sterechinus neumayeri (Meissner, 1900), although their relative densities seem to change at a 100 m depth boundary (Gallardo et al. 1977, Jazdzewski et al. 1986, Arntz et al. 1994).

Shallow benthic megafauna communities seem not to be directly affected by the organic input from primary production and, unlike shallow benthic macrofauna, are temporarily more stable and less affected by the physical constraints normally associated with ice effects such as anchor ice and ice scours. Nevertheless, the main causes for the noticeable vertical zonation of shallow megafauna are not clear and should be addressed in further investigations.

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