Variation of a polychaete community in nearshore soft bottoms of Admiralty Bay, Antarctica, along austral winter (1999) and summer (2000–2001)

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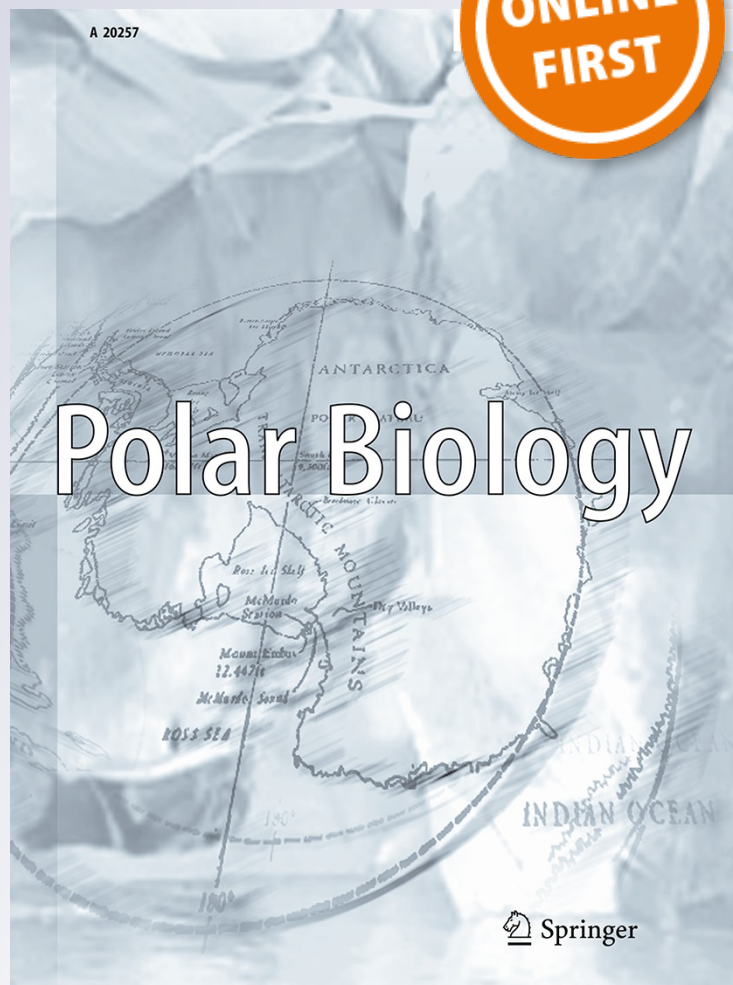
Paulo Cesar Paiva[1,2] · Victor Corrêa Seixas[1,2] · Carlos Alejandro Echeverría[3,4]

Abstract Studies on community structure of Antarctic benthos are mostly conducted on summer samplings, when ice-impacts and productivity blooms are intense. Few surveys performed during winter demonstrated that, despite temperatures and productivity stability, community structure is variable. In order to assess how polychaete community is influenced by seasonality and depth along a discontinuous year, six replicate samples were taken in nine surveys during winter and four in summer at two depths (12 and 25 m) in Admiralty Bay, King George Island. Spatial patchiness was more intense at 12 m presupposing ice-mediated and wave-induced disturbances, whereas 25-m patchiness among replicates was restricted to summer surveys. A pattern of temporal stability was partially confirmed in 12-m site. Deeper site was characterized by seasonality with dominant-species replacement reflecting shifts in organic matter availability. Diversity was higher in early and midwinter following both summer productivity blooms and macroalgal decomposition that extend the energy budget into the winter, analogous to microbial biomass supply of "food banks" that sustains the benthic ecosystem functions over winter in Antarctic Peninsula shelf deeper areas. Despite the opportunistic status of several nearshore polychaetes, it was possible to distinguish those that responded to organic enrichment (i.e., *Capitella perarmata* and *Ophryotrocha notialis*), from those associated with physical disturbances (i.e., *Aphelochaeta cincinnatus* and *Levinsenia gracilis*). Awareness of such patterns and their spatial and temporal variations will facilitate future studies on community assessment, especially those based on indicator species of benthic communities.

Keywords Depth partitioning · Seasonality · Benthic · Ice-impacts

We dedicate this paper to Edmundo Ferraz Nonato who passed away on April 14, 2014. He was a Brazilian expert in marine benthic studies, taxonomy and biology of polychaetes and a pioneer of Brazilian Antarctic research.

✉ Paulo Cesar Paiva
paulo.paiva@gmail.com

1 Laboratório de Polychaeta, Departamento de Zoologia, Instituto de Biologia, Universidade Federal do Rio de Janeiro, Av. Carlos Chagas Filho, 373, CCS, Ilha do Fundão, Rio de Janeiro, RJ CEP 21941-902, Brazil

2 Programa de Pós-graduação em Biodiversidade e Biologia Evolutiva, Instituto de Biologia, Universidade Federal do Rio de Janeiro, Av. Carlos Chagas Filho, 373, CCS, Ilha do Fundão, Rio de Janeiro, RJ CEP 21941-902, Brazil

3 Instituto Virtual Internacional de Mudanças Globais, COPPE, Universidade Federal do Rio de Janeiro, Anexo ao CT, Ilha do Fundão, Rio de Janeiro, RJ CEP 21945-970, Brazil

4 Laboratório de Pesquisas Costeiras e Estuarinas (LABCOEST), Núcleo Interdisciplinar UFRJ-Mar, Universidade Federal do Rio de Janeiro, Rua Octávio Cantanhede s/n, Ilha do Fundão, Rio de Janeiro, RJ CEP 21941-902, Brazil

Introduction

Studies on the structure of benthic communities in Antarctica are mostly based on summer samplings. During this season, environmental processes, such as ice-impact, bottom wave action, primary production and light availability, are more variable or intense (Arntz et al. 1994; Clarke and Johnson 2003; Gutt 2007). The few surveys conducted during austral winter have demonstrated that community structure is not so stable, despite the season-long constancy in temperatures and productivity

(Battershill 1990). This is more noticeable in some nearshore areas of the Antarctic peninsula, with yearly variation in both the intensity and level of ice-impacts, and surface water often unfrozen (Peck et al. 2006) or restricted to floating pack-ice, as usually occurs in Admiralty Bay (Jażdżewski et al. 2001; Echeverría and Paiva 2006).

Austral winters and summers differ regarding primary production and coastal organic matter input and through the amplitude of physical disturbances by wave or ice-impacts themselves as well as by their intensity and frequency (Brown et al. 2004; Barnes and Conlan 2007). Biophysical habitat heterogeneity exerts stronger influence on benthic community density and composition, affecting β-diversity patterns, at smaller spatial scales, while the effects of biological productivity are more significant in rather larger scales (Thursh et al. 2010).

On comparing austral winters and summers, analysis of benthic communities gives important information on main environmental and biological processes driving community and also on their timing. This is especially important when considering that nearshore Antarctic communities are among the most likely to be affected by ice-melting and global-warming-related impacts (Aronson et al. 2009).

Admiralty Bay (King George Island) is one of the most studied marine ecosystems of Antarctica, owing chiefly to the effort of Polish and Brazilian Antarctic Programs, which have run scientific stations in the area for ca. 40 years (Siciński et al. 2011). Mega- and macrobenthic communities have been investigated in a great range of depths in the bay (e.g., Arnaud et al. 1986; Jażdżewski et al. 1986, 1991; Pabis et al. 2011), while other studies were restricted to the more unstable intertidal or nearshore regions (Nonato et al. 2000; Jażdżewski et al. 2001; Echeverría et al. 2005; Echeverría and Paiva 2006; Bick and Arlt 2013). Polychaete taxocoenoses was the focus of investigation of several studies (Siciński 1986, 2000; Sicinski and Janowska 1993; Bromberg et al. 2000; Siciński 2004; Barbosa et al. 2010; Pabis and Siciński 2010).

Even though temporal and bathymetric variations in macrobenthic communities in the survey area at taxonomic group level have already been assessed (Jażdżewski et al. 2001; Echeverría and Paiva 2006), species variation is more likely to provide more realistic information as to responses to environmental and biological impacts. This is mainly true in taxonomic groups that involve a wide range of functional and ecological roles, as in polychaetes (Fauchald and Jumars 1979). In both number of species and biomass, polychaetes comprise one of the dominant groups in Antarctic benthic communities, in shallow/shelf and slope/deep-sea waters (Hilbig et al. 2006). As they are accountable for a large part of the benthic community structure, their responses to environmental factors are most likely to reflect conditions of the community as a whole (Bromberg et al. 2000).

The material analyzed here came from our previous study (Echeverría and Paiva 2006), for which two soft-bottom stations (at 12 and 25 m) were sampled in Admiralty Bay (King George Island, Antarctica) from March to September 1999 (winter) and from December 2000 to March 2001 (summer). Analyses involved data on polychaete species in order to evaluate (1) diversity patterns, (2) depth distribution, (3) within-site spatial variation and (4) temporal variation in community structure.

Materials and methods

Survey area and sampling

Surveys were undertaken in a nearshore area, east to the Brazilian Antarctic Station (052°23.2′W 062°5.1′S) in Admiralty Bay, King George Island, Antarctica (Fig. 1 and see Echeverría and Paiva 2006). 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 September 1999 (winter): W1 (16 Mar), W2 (2 Apr), W3 (22 Apr), W4 (10 May), W5 (31 May), W6 (7 Jul), W7 (4 Aug), W8 (25 Aug) and W9 (20 Sep). In December 2000 and March 2001(summer), four surveys were carried: S1 (29 Dec), S2 (12 Jan), S3 (7 Feb) and S4 (26 Feb).

Six replicate samples were collected from each of two stations (12 and 25 m) using a 0.056-square meter Van Veen grab. Samples were sieved with a 0.5-mm mesh. Environmental characteristics of the sampling area and abiotic patterns at both stations throughout all surveys are described in more detail in Echeverría et al. (2005) and Echeverría and Paiva (2006). Water temperature at 1 m depth ranged from 1 °C (March) to −1.9 °C (August) during winter. Sea surface froze from August 30 to September 15, 1999. Icebergs grounded in the studied area at 11 m depth (July 16, 1999) and at the 25-m site (February 22, 2011). Average sediment organic matter content was slightly different between depths (ca. 4 % in 12 m and 5 % in 25 m) with lowest values (3 %) in midwinter (June) at the 25-m site. Bottoms in both depths also differ in grain size; 12-m site is composed of very fine sands, with an average of 65 % of sand (>0.062 mm) and 33 % of mud (<0.062 mm), while the 25-m site is composed mainly of muddy bottoms, with an mean of 27 % of sand and 64 % of mud.

Data analysis

Diversity and richness

Diversity of each station and sampling periods were measured by using Renyi entropy (Tóthmérész 1995;
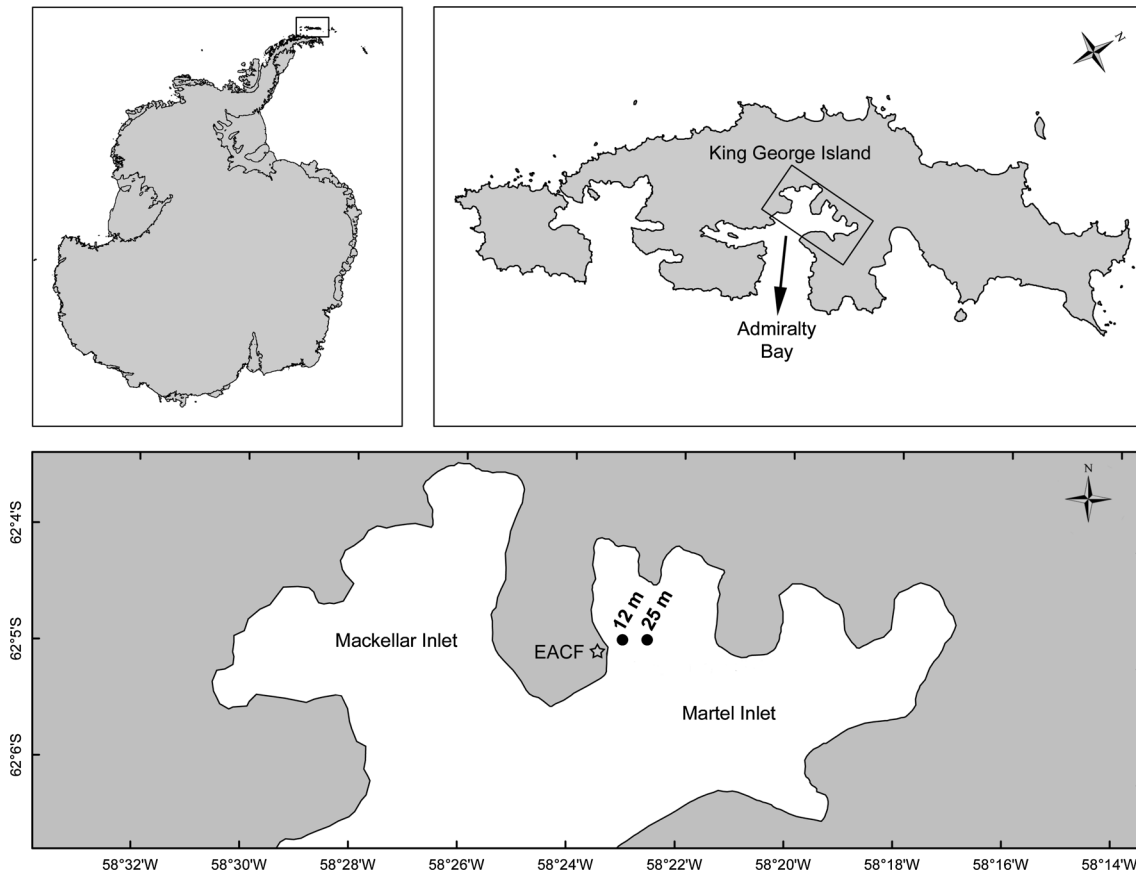
Fig. 1 Study area, showing the location of the 12 and 25 m depth sample sites, adjacent to the Brazilian Antarctic Station "Comandante Ferraz" (EACF)

Maurer and McGill 2011) for producing diversity profiles of Renyi values (R). These profiles, which are based on various levels of the alpha parameter ($\alpha = 0, 0.5, 1, 1.5, 2, 2.5, 3\ldots$), are functionally related to traditional diversity indices. They represent special cases of Renyi entropy (e.g., for $\alpha = 0$, R is equal to the logarithm of the number of species, for $\alpha = 1$, equal to the Shannon index, and for $\alpha = 2$, equal to the negative logarithm of the Simpson index). Diversity profiles show how diversity changes as the emphasis shifts from rare to common species (Leinster and Cobbold 2012).

Apart from the actual number of species collected, the asymptotic number of species was also estimated by using nonparametric abundance-based (ACE and Chao 1) and incidence-based (ICE, Chao 2, Jacknife 1, Jacknife 2) estimators (Colwell and Coddington 1994; Gotelli and Colwell 2010). These provide not only the total number of species, but also those expected to occur in the survey station, but which have not been sampled. EstimateS software (Colwell 2010) was used to calculate species richness estimators.

Community composition

Permutational multivariate analysis of variance (PERMANOVA Anderson 2001) was applied to a Bray–Curtis similarity matrix of log-transformed data, in order to assess significant differences in species densities and composition between depths and surveys. Patterns of temporal variation were further assessed through dimensions reductions, pooling replicates for each sampling and applying a nonmetric multidimensional scaling ordination (Meulman 1992) in a matrix of Bray–Curtis distance of log abundances ($\log x + 1$). Only species with a frequency of occurrence higher than 10 % (17 species) were included in the analysis, i.e., excluding species that occurred in only one or two surveys. Principal component analysis (PCA) was applied to assess temporal or successional patterns for each depth separately thereby reducing the 17 species to only two components (latent variables), which represented main temporal patterns of dominant polychaete species. PCA scores obtained for replicates were plotted to assess both common species patterns (Jassby and Powell 1990) and spatial variability among replicates.

A mixed ANOVA model, considering surveys (time) as the random variable and depth as the fixed (Quinn and Keough 2002), was applied to assess depth partitioning of species that frequently occurred at both depths. Thus, the main effect of depth in species density could be taken into consideration only when their patterns were significantly greater than the depth × survey interaction. Community composition analysis and diversity profiles were calculated using R environment (R Development Core Team 2011) and "vegan" package (Oksanen et al. 2011).

Results

Depth distribution

Among the 26 species sampled throughout all surveys, seven occurred only at 12-m site (Table 1). Of these, five were collected once and one twice throughout all the surveys, thus possibly reflecting under-sampling of this site. *Cirrophorus brevicirratus* was the only species restricted to 12-m site, which was relatively frequent, occurring in 5 out of 13 surveys. The 25-m site had no exclusive species.

Depth distribution over time was assessed for six dominant species that occurred at both depths (Table 2; Fig. 2). *Apistobranchus glacierae*, *Leitoscoloplos geminus*, *Leitoscoloplos kerguelensis* and *Ophelina syringopyge* dominated the shallower site (12 m). *Lenvinsenia gracilis* was more abundant in the deeper. *Aphelochaeta cincinnatus* presented no depth preference. Other frequent, although less abundant species, were also more recurrent in the shallower site than the deeper, viz., *Sphaerodoropsis arctowskyensis* (11 vs. 2 surveys), *Ophryotocha notialis* (10 vs. 2), *Scoloplos* (*Leodamas*) *marginatus* (8 vs. 2) and *Capitella perarmata* (7 vs. 2). Nevertheless, the inverse also occurred, as was the case with *Brada villosa* (4 vs. 12). Species more frequent in shallower stations than in deeper ones occurred mainly in summer surveys.

Except for *A. cincinnatus*, variations in species patterns differed between both sites (Table 2). The main temporal pattern, as also presented by NMDS analysis (see below), was the decrease in densities observed for *A. glacierae* and *O. syringopyge* in the late winter (W9) and the first summer survey (S1) at both depths, and *A. cincinnatus* shifting from the 12- to 25-m site over the same period (Table 2; Fig. 2). Another noticeable pattern was that certain dominant species at the 12-m site, i.e., *A. glacierae, L. geminus* and *L. kerguelensis*, were also common at the 25 m during the summer. However, during mid- and late winter, they maintained high densities at 12-m site and almost disappeared at 25 m.

Pooling sampling surveys, assessment of asymptotic species richness for both sites, indicated higher species richness for both incidence and abundance estimators in 12 m (Table 3). The difference between both sites ranging from 9 to 23 clearly indicated this higher richness, as well as under-sampling of the shallower site.

Diversity patterns

In order to better visualize diversity profiles, these were plotted separately (Fig. 3). The role of rare species was noticeable at the two sites, indicating the occurrence of more rare species during the summer (Fig. 3, curves S2, S3, S4). During the first winter survey (W1), the main difference noticed between depths was the very reduced diversity at 25-m site, owing to the dominance of very few species, whereas evenness, here represented by the right size of the profile ($\alpha = 5$), in the 12-m site was higher. Another different pattern was the lower diversity in the last winter survey (W9), mainly at 12 m, which presented less than half the number of species of the remainder. At the 25-m site, lower diversities also occurred in the late winter in W7 and W9. In both cases, but mainly in W7, the pattern was reflected by lower richness (lower α values) and evenness (higher α values). This pattern of lower-diversity profiles in W9 at 12 m and in W1, W7 and W9 at 25 m, also expressed by two traditional diversity indices, viz., Shannon ($\alpha = 1$) and Simpson = ($\alpha = 2$), reflects the dominance of only two species, *A. cincinnatus* and *L. gracilis.* It is also noteworthy that the diversity profile at 12 m indicates an increasing diversity over time, mainly owing to increased evenness. This diversity pattern starts with lower values in late winter (W9), followed by summer (S2 and S4) and reached higher values in early (W1) and mainly midwinter (W3–W6). Thus, early and midwinter seem to be characterized by more stable conditions at 12 m. In 25 m, conditions are slightly different, with higher diversities mainly associated with the summer and early winter.

Temporal variation in community composition

As assessed by PERMANOVA (depth: pseudo-$F = 46.53$; $p < 0.0001$, time pseudo-$F = 2.67$, $p < 0.0001$, and the interaction of both: pseudo-$F = 2.44$, $p < 0.0001$), community composition and relative species abundance differed substantially between depths and among periods. NMDS analysis (Fig. 4) (stress = 0.09) clearly distinguished both depths in the first axis, as it was expected when considering the difference in community composition between depths. Seasonal variation between summer (S) and winter (W) was slightly discriminated by the lower position in the second axis (NMDS2), with the noticeable exception of S1 (at 12 m). Temporal variation was more noticeable at the 25-m site with surveys more dispersed in

Table 1 Species abundance (with respective code for figures) for each depth site and survey

Species/Surveys/Sites	Code	W1		W2		W3		W4		W5		W6		W7		W8		W9		S1		S2		S3		S4		Total		Both
		12	25	12	25	12	25	12	25	12	25	12	25	12	25	12	25	12	25	12	25	12	25	12	25	12	25	12	25	
Apistobranchus glacierae	Ag	277	0	405	13	50	10	74	72	356	0	101	0	10	0	236	0	0	2	15	1	28	445	338	49	825	411	2715	1003	3718
Aphelochaeta cincinnatus	Ac	165	165	217	127	44	10	124	58	88	10	124	45	96	15	87	91	122	58	8	125	206	192	504	69	443	56	2228	1021	3249
Levinsenia gracilis	Lgr	0	43	14	50	0	37	2	6	0	10	4	42	26	32	1	21	4	117	0	185	6	115	6	151	14	190	77	999	1076
Leitoscoloplos geminus	Lg	138	0	83	6	12	10	44	6	77	1	90	2	18	0	34	5	11	0	52	2	91	22	133	1	109	80	892	135	1027
Ophelina syringopyge	Os	4	2	178	9	79	12	43	21	51	0	123	2	10	0	117	3	0	1	1	0	2	21	47	1	77	41	732	113	845
Leitoscoloplos kerguelensis	Lk	60	3	71	14	38	15	31	18	53	4	38	1	17	1	43	4	24	1	6	0	16	40	34	14	76	28	507	143	650
Rhodine antarctica	Ra	34	2	46	1	12	4	21	0	13	2	19	1	14	0	24	2	4	0	2	1	26	5	16	4	47	7	278	29	307
Capitella perarmata	Cp	12	0	0	0	1	0	5	0	0	0	9	0	0	0	0	0	0	0	22	1	0	5	1	0	72	0	122	6	128
Ophryotrocha notialis	Op	10	0	0	0	3	0	7	0	18	0	36	0	0	0	1	0	0	0	11	0	3	1	5	1	1	0	95	2	97
Sphaerodoropsis arctowskyensis	Sar	1	0	26	0	3	0	5	0	4	0	3	0	0	0	0	0	1	0	1	0	14	3	14	0	8	5	80	8	88
Brada villosa	Bv	2	3	2	17	0	4	0	7	0	2	0	4	1	1	0	19	0	2	0	0	0	2	0	6	2	1	7	68	75
Cirrophorus brevicirratus	Cb	0	0	40	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	5	0	2	0	4	0	52	0	52
Asychis amphiglypta	Aa	1	3	11	0	0	0	0	0	0	0	0	1	3	0	5	0	0	1	0	3	2	4	0	0	11	1	33	12	45
Petiboneia hartmanae	Ph	0	0	2	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	4	1	2	0	13	1	4	4	23	27
Barrukia cristata	Bc	0	0	1	1	1	0	2	2	3	1	1	0	3	0	1	0	0	0	1	1	0	0	0	0	3	0	16	6	22
Scoloplos (Leodamas) marginatus	Sm	0	0	2	0	0	0	2	0	3	0	4	1	0	0	0	0	1	0	0	0	1	0	2	0	2	1	17	2	19
Aglaophamus trissophyllus	At	1	0	0	0	0	0	3	1	2	0	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	9	1	10
Maldane sarsi antarctica		0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	6	0	0	0	0	1	6	7
Lumbrineris magalhaensis		0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2
Aricidea (Acmira) strelzovi		0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2
Fabriciinae gen. sp.		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	0	2
Lumbrineris sp.		0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Perinereis falklandica		0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Eteone sculpta		0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Pista cristata		1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Lysilla loveni macintoshi		1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Total number of individuals		706	221	1099	239	243	102	363	192	672	30	553	99	199	49	552	145	167	182	119	323	401	863	1102	309	1698	825	7874	3579	11,453
Number of species		13	7	15	10	10	8	13	10	15	7	13	9	11	4	12	7	7	7	10	9	13	14	12	10	18	12	26	19	26

Table 2 ANOVA table of species density by depth (fixed factor) and survey (random factor)

Factor	Depth		Survey		Depth × Survey	
Species	F^{a}	p	F	p	F	p
Apistobranchus glacirae	12.11	**0.0045**	3.91	**<0.0001**	3.29	**0.0004**
Aphelochaeta cincinnatus	0.09	0.7646	2.57	**0.0049**	1.69	0.0774
Levinsenia gracilis	38.98	**<0.0001**	3.32	**0.0003**	2.51	**0.0061**
Leitoscoloplos kerguelensis	17.54	**0.0012**	2.02	**0.0291**	1.22	0.2783
Ophelina syringopyge	15.65	**0.0019**	4.96	<0.0001	2.46	**0.0069**
Leitoscoloplos geminus	55.00	**<0.0001**	3.21	**0.0005**	1.99	**0.0309**

Significative reults in bold ($p < 0.005$)

[a] For F ratios used to test effects, see restricted version in Quinn and Keough (2002) p. 236
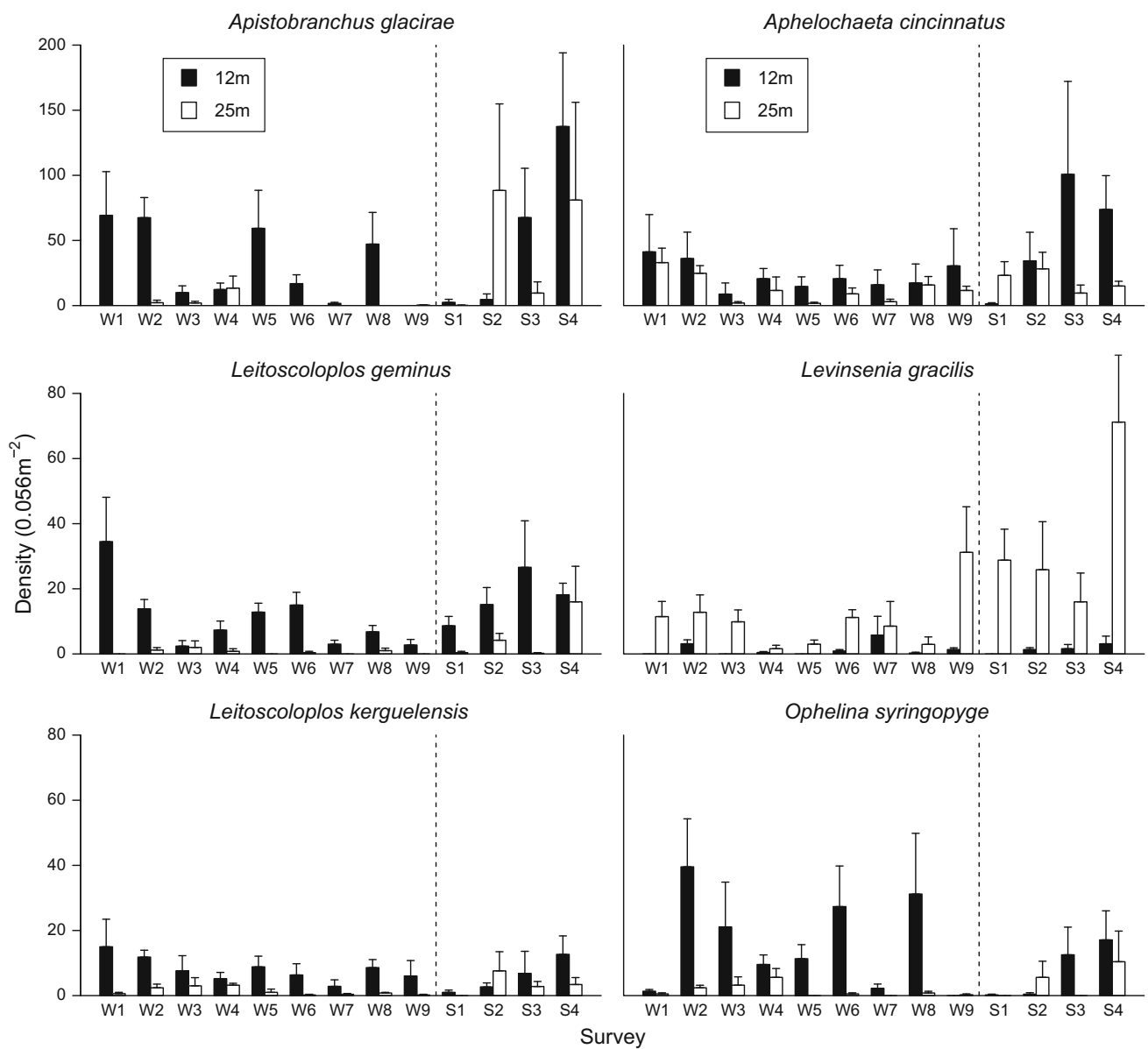
Fig. 2 Temporal variation by depth for dominant species with means and standard errors ($n = 5$)

Table 3 Asymptotic estimators of species richness for each depth

Estimator[a]	Number of species	
	12 m	25 m
ACE	45.31	27.90
ICE	40.87	32.06
Chao1	48.00	27.33
Chao2	50.77	27.23
Jack1	39.20	30.50
Jack2	46.92	32.51

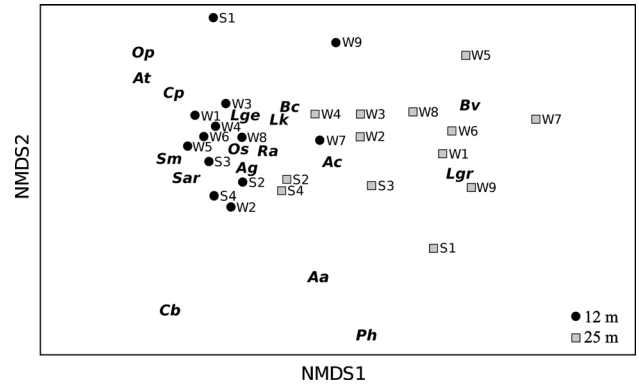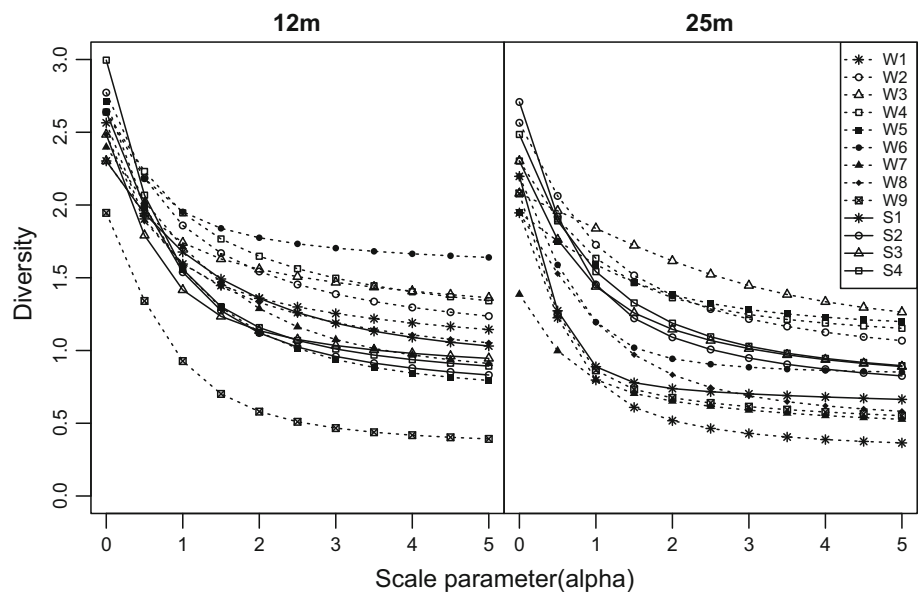[a] According to Gotelli and Colwell 2010

Fig. 4 Multi-dimensional scaling plot based on a Bray–Curtis distance matrix in log-transformed data. Stress value is 0.09 (code of species as in Table 1, W1, W2… = winter surveys, S1, S2,… = summer surveys)

the plot than at the shallower site. Concerning community composition, winter surveys were very similar at the 12-m site. While at 25 m, surveys are gathered in two main groups: early winter (W2–W4) in the center of the ordination diagram and midwinter to late winter (W5–W9) at the right side. Early winter surveys at 25 m were more associated with 12-m surveys and to the dominance of *A. cincinnatus*, *Barrukia cristata* and *L. kerguelensis,* while mid- and late-winter surveys (W5–W9) were more associated with *B. villosa* and *L. gracilis*.

Two late-winter surveys from the 12-m site (W7 and W9) were clearly different from all the other surveys at the same depth, being more associated with the 25-m site. Such pattern is due to an overall decrease in species densities (Fig. 2), with the exception of surface dwellers *A. cinncinatus* and *L. gracilis* that dominate (Figs. 2, 4). In both depths, summer was the most variable season, mainly due to the higher abundance of *C. perarmata* and *O. notialis*, in the first summer survey (S1), whereas the following summer surveys were characterized by an increase in abundance of *S. (Leodamas) marginatus*, *S. arctowskyensis* and *A. glacierae*.

Briefly, community analyses indicated sudden seasonal shifts in specific surveys at 12-m site (e.g., S1, W7 and W9 at 12 m), although temporal patterns were mainly due to continuous changes of species dominance. However, seasonality was stronger at 25-m site, clearly distinguishing summer and two winter groups.

Within-site spatial variability

Spatial variability among replicates (=patchiness) and temporal patterns were assessed by plotting scores derived from PCA, as applied to individual scores of each replicate producing a latent variable with the corresponding spatial variability (i.e., standard error). At the 25 m depth, PC1 indicated spatial variability (error bars) as being higher during summer (except for S1), intermediate in early winter and lower in mid- and late winter (Fig. 5). When
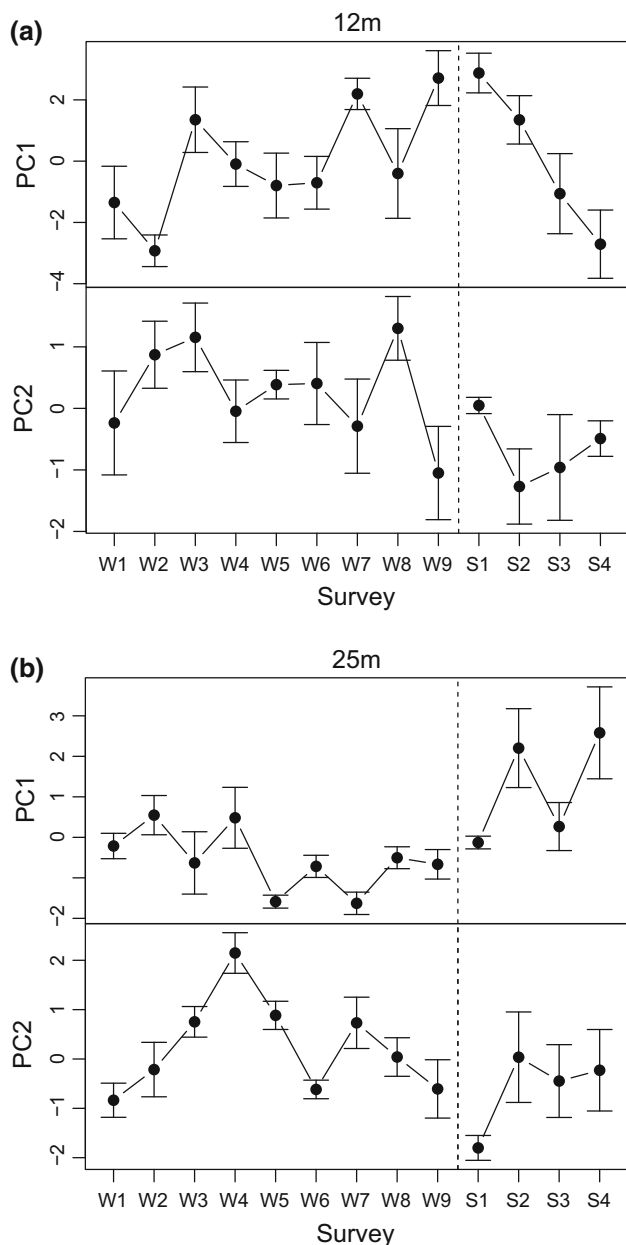
Fig. 3 Diversity profiles of Renyi numbers by scale parameter of both sampling sites. Only main patterns are presented

(a)

(b)

Fig. 5 Plot of sample scores of first (PC1) and second (PC2) principal components along surveys with mean and confidence intervals (*error bars*)

comparing variances from S2, S3, S4 with middle/late winter (W5–W9) and S1, this variability proved to be significantly different according to an *F* test ($F = 7.15$–37.19, $p = 0.025$–0.005). The general pattern of the first axis also demonstrated the similarity among mid- and late-winter surveys, when compared to summer. PC2, also associated with larger spatial variability during summer (Fig. 5), remained homogenous throughout winter. There was a more noticeable temporal pattern, with scores increasing from early to midwinter, with a peak in W4, followed by a decrease in late winter. The exception was

the lower score in W6, possibly related to the increase in dominance of *L. kerguelensis*, *O. syringopyge* and *B. villosa*.

Spatial variability at the 12-m station was higher than at the 25-m station in all the surveys (Fig. 5), thereby indicating that patchiness in this area was greater, with no difference over time. Owing to this spatial variation, temporal patterns were indistinct. The exception was the tendency for scores to increase in late winter, especially of W7 and W9. This was mainly due to the maintenance of *L. gracilis* and *A. cincinnatus* abundance levels. PC2 was also associated with even higher variability and reflected the dominance of those species that maintained higher densities during mid- and late winter, i.e., *B. cristata*, *L. geminus* and *A. cincinnatus*, as against the decrease in other species.

Discussion

Diversity patterns

The structure of nearshore Antarctic benthic communities is usually highly conditioned by abiotic factors, mainly by those associated with either ice-impacts from icebergs during summer (Peck et al. 1999), or ice-foot and anchor-ice during winter (Barnes and Conlan 2007). Wind generated waves are also likely to disturb benthic communities. This is mainly so in late winter and early summer, when surface waters are partially or completely ice-free, thereby conditioning accentuated spatial (mainly bathymetric) and temporal variation in benthic community structure (Echeverría and Paiva 2006). This variation is more intense in those macrobenthic groups inhabiting the upper layers of the sediment, such as polychaetes. Nevertheless, diversity patterns are also affected by several biotic factors, such as recruitment, food supply, predation and competition (Ricklefs and Schluter 1993).

Regarding diversity profiles, 12-m station, although presenting an increase in diversity from summer to mid-winter, was seasonally the most stable of the two sites, with only a pronounced reduction in winter survey 9 (W9), which followed a heavy storm that affected the entire benthic community (Echeverría and Paiva 2006). Physical disturbances cause local high dominance of few species, thereby contributing considerably to the high beta-diversity in shallow waters (Gutt 2007). The imperceptible effect along time on either local diversity or richness at the 12 m depth possibly indicated quick recovery of polychaete populations, due to the dominance of opportunistic species (Smale 2007). Beta-diversity had a noticeably different pattern in the deeper area (25 m), where W9 diversity profile was not very different from those of other winter surveys (W1 and W7). The lowest diversity observed at

25 m in the (W7) survey was probably due to a general decrease in diversity during winter followed by a recovery in summer and early winter, which was not related to physical impacts. At the 12-m site, winter survey 7 (W7) was also associated with physical disturbance, in this case by ice-impacts, since it took place 9 days after the grounding of an iceberg. However, this impact affected community structure only at the level of higher taxonomic groups (Echeverría and Paiva 2006).

Nonetheless, observed diversity patterns are more likely to result from the interaction of disturbances and certain local environmental conditions, such as productivity, organic matter content and oxygen supply (Levin and Gage 1998). This seems to be reflected by the rather different patterns between both depths with diversities reaching higher values at 12 m in early and midwinter following productivity blooms of shallow environments during the summer (Clarke 1996). Corbisier et al. (2004) found that both omnivorous and depositivorous polychaetes present an isotopic signature of macroalgal fragments, whose decomposition would extend the energy budget until midwinter, when the levels of local organic matter in the sediment start to decrease (Echeverría and Paiva 2006). These processes based on macroalgal debris being analogous to the benthic–pelagic coupling of deeper waters (500–600 m) on the west Antarctic Peninsula shelf, where the strong seasonality of phytoplankton summer blooms produce seafloor deposits of phytodetrital material that provides food for the benthic community (Smith et al. 2012). Thus, particulate organic matter and associated microbial biomass on the bottom accumulate as a "food bank" that sustains the benthic ecosystem functions over winter (Smith and DeMaster 2008). Such energy budget delay would thereby maintain early winter diversity levels and postpone the impact of winter resource limitation (sensu Nedwell et al. 1993; Peck et al. 2006) on polychaete community structure until late winter/summer, when diversity normally decreases.

Community composition and richness

The total number of species (26) was similar to the number of polychaete species recorded by other authors for near-shore sites (4–30 m) in Admiralty Bay (Sicinski and Janowska 1993; Bromberg et al. 2000). Richness pattern, with more species observed and estimated in the 12-m site than in the 25 m, contrasted from that observed previously in the same region, which found less species at 12 m (11–14, against 26 here; Sicinski and Janowska 1993; Bromberg et al. 2000). This different pattern can be the result of temporal integration, which led to the collection of more rare species not observed in the shallower site when sampling design was restricted temporally (Jażdżewski

et al. 1991; Echeverría and Paiva 2006). Thus, owing to this rare species, asymptotic estimators provide a quite different richness picture for the shallower site than previously observed, estimating almost twice as many species as the apparently more environmentally stable 25-m site (Nonato et al. 2000; Siciński et al. 2011).

Despite the high similarity in species composition with several other surveys in King George Island (Bromberg et al. 2000; Siciński 2000, 2004; Bick and Arlt 2013), relative dominance and distribution were a little different. Some species referred only to deeper areas of the nearshore region (>20 m), such as *O. syringopige*, *A. glacirae*, *L. kerguelensis* and *S. arctowskyensis* (e.g., Siciński 2000), were common in the shallower site (12 m) in this survey, and pattern also previously observed in the same locality (Bromberg et al. 2000). Densities were also similar to those observed by Bromberg et al. (2000) but quite different, threefold to sixfold higher (ca. 10,000 and 23,500 ind.m^{-2}, respectively, at 25 and 12 m) than observed for other nearshore sites in Admiralty Bay (Jażdżewski et al. 1986; Siciński 2000). These differences can be related both to particularities of sampled localities in the bay generally related to bottom slope, sediment composition and grain-size characteristics (Siciński 2004; Siciński et al. 2011).

Depth distribution and patchiness

Despite similarities of diversity profiles between both depths, the shallow area was considerable richer and denser. As regards species that occurred in both depths, the opportunist *A. cincinnatus* was the only species whose abundance did not differ between depths. All others species were more abundant at 12 m depth, except for *L. gracilis* which dominated at 25 m. Considering local bottom topography and grain size, apparently the 12-m site is a transitional community, with a mixture of species typical for more shallow sites, with those with a wider range and also shared with the deeper 25-m station (Nonato et al. 2000). Despite differences in sediment composition between depths, this probably has little effect on depth distribution, mainly when considering that most polychaetes from Antarctic environments present a wide range of depths distribution, sediment types and feeding strategies (Pabis and Siciński 2010) and thus do not present the traditional animal–sediment relationships common for temperate or tropical environments. This absence of correlation of fauna and substrate in the Antarctic benthos was defined by Gutt (2007) as the "opportunistic choice of the substrates," since other environmental characteristics are more relevant toward explaining community structure.

Even though patchiness was more intense in the shallow site, variation was constant over time, thereby presupposing that ice-mediated (Gutt 2001; Bowden 2005) and wave-

induced disturbances are constant and frequent, thus not allowing the establishment of more stable communities, leading to the year-long dominance by several opportunistic species, such as *L. kerguelensis*, *A. cincinnatus*, *L. gracilis* and *A. glacierae* (Bromberg et al. 2000; Conlan et al. 2004). According to Smale (2007), shallower areas can be subject to such extreme disturbance conditions that even pioneer species, abundant only under moderately disturbed conditions, as those observed in the 12-m area, become rare.

Conversely, the 25-m site presented a more pronounced seasonal pattern, with higher patchiness among replicates (metric scale) during the summer, most likely the result of physical disturbances by ice, which, owing to their patchy nature, can cause local high dominance by pioneer species, contributing considerably toward differences in the pattern of dominance and composition of macrobenthic assemblages within small scales (Gutt and Piepenburg 2003). As previously recorded in the studied area (Nonato et al. 2000), among ice effects, iceberg scouring is usually associated with patchiness (Hall 1994). Even though no iceberg was recorded in this site during the survey, depressions from old scours accumulate macroalgal debris during the summer. Such debris provides deposit feeders with organic matter (Corbisier et al. 2004) or, even, in some cases, make the scour anoxic and practically azoic during the summer season (Bromberg et al. 2000).

Temporal community patterns

Opportunistic species, common throughout all surveys in the 12-m site, are likely to dominate after the occurrence of physical or biological disturbance. In the early summer, *C. perarmata* and *O. notialis,* both belonging to genera comprising species known as enrichment opportunists in nearshore Antarctic waters, were predominant (Stark 2000; Conlan et al. 2010). Such enrichment could possibly arise from productivity blooming in shallow environments during this period (Clarke 1996). Other disturbances, such as the recorded grounding of an iceberg at 25 m just before W7, and the strong storms at W9, which affected both sites, apparently did not lead to colonization by pioneer species, but on the contrary, and with the exception of *A. cincinnatus* and *L. gracilis*, to an overall decrease in species abundance, as also observed by Echeverría and Paiva (2006) at the level of taxonomic groups. These two species also dominated during summer surveys, when wave-induced impacts are fairly frequent and intense, and surface waters do not freeze. Both species are normally considered as pioneers or opportunists in nearshore studies (Bromberg et al. 2000; Conlan et al. 2004, 2010). Thus, in spite of the opportunistic status of several polychaete species in nearshore Antarctic waters, it was possible to distinguish those

that are more prone to an increase in density through organic enrichment (i.e., *C. perarmata* and *O. notialis*) from those that remain unaffected when ice- and wave-generated physical disturbances disrupt nearshore benthic communities (i.e., *A. cincinnatus* and *L. gracilis*). Echeverría and Paiva (2006) did not observe any pattern for polychaetes as a group, while oligochaetes did present a common response of increased densities for both organic enrichment (summer) and physical disturbances (late winter). Thus, specific responses for polychaetes, masked at group level, are likely to give clues on suggested opportunistic behavior of some antarctic polychaete species since they are likely to discriminate the nature of the disturbance factor.

A pattern of year-long temporal stability in benthic community nearshore polychaete taxocoenosis in the 12-m area was partially confirmed. Although this pattern was interrupted by both storm- and ice-provoked physical disturbances, subsequent recovery was almost complete in the next sampling survey. As could be expected for a nearshore area, this pattern is associated with communities subject to highly seasonal production (Kim et al. 2010). On the other hand, the 25-m area presented a more seasonal pattern of year-long dominant-species replacement, a probable reflection of changes in the availability of organic matter. This could be indirectly assessed in the area by associating light intensity and sediment organic matter content (Echeverría and Paiva 2006). This content reflects the seasonal trend from high production in the summer (Arntz et al. 1994) to resource limitation in the mid- and late winter (Peck et al. 2006).

Nonetheless, the pattern of species common to both depths, but whose density is strongly reduced during mid- and late winter only in the deeper site, precluded a straightforward explanation. Two of these, *L. geminus* and *O. syringopyge*, are burrowers, and *A. glacierae*, a tubiculous surface dweller (Bromberg et al. 2000; Pabis and Siciński 2010). Their reduction in density at 25 m was not accompanied by other community descriptors, as richness and diversity, which differed only slightly between depths and thus could not be associated with the observed physical disturbances, since this reduction normally follows iceberg grounding and storms. Although disturbance by anchor-ice, which is more likely to occur in the austral winter (Dayton 1989; Barnes 1999), could also be involved in these processes, detection and assessment of its impacts is difficult (Gutt 2001). Even though the synergy of biotic and physical disturbances could be involved, evaluation would require both further field experiments and visual monitoring.

The assessment of temporal variation in diversity patterns and community structure not only allowed the assessment of environmental factors underlying community structure, but also provided some cues of possible

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human impacts and their effect on community composition (Aronson et al. 2011), and hence, resilience capacity in an area located only 200 m from a research station. Impacts from Antarctic research stations, although small and locally restricted, over time are likely to affect the adjacent marine environment (Stark et al. 2003). Awareness of such patterns and their spatial and temporal variations will facilitate community assessment, when endangered, besides indicating how and when action is required to avoid impacts that are likely to impinge irreversible damages to benthic communities.

References

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecol 26:32–46

Arnaud PM, Jażdżewski K, Presler P, Siciński J (1986) Preliminary survey of benthic invertebrates collected by Polish Antarctic expeditions in Admiralty Bay (King George Island, South Shetland Islands, Antarctica). Pol Polar Res 7:7–24

Arntz WE, Brey T, Gallardo VA (1994) Antarctic zoobenthos. Oceanogr Mar Biol Annu Rev 32:241–304

Aronson RB, Moody RM, Ivany LC, Blake DB, Werner JE, Glass A (2009) Climate change and trophic response of the Antarctic bottom fauna. PLoS One 4:e4385

Aronson RB, Thatje S, McClintock JB, Hughes KA (2011) Anthropogenic impacts on marine ecosystems in Antarctica. Ann N Y Acad Sci 1223:82–107

Barbosa LS, Soares-Gomes A, Paiva PC (2010) Distribution of polychaetes in the shallow, sublittoral zone of Admiralty Bay, King George Island, Antarctica in the early and late austral summer. Nat Sci 2:1155–1163

Barnes DKA (1999) The influence of ice on polar nearshore benthos. J Mar Biol Assoc UK 79:401–407

Barnes DKA, Conlan KE (2007) Disturbance, colonization and development of Antarctic benthic communities. Philos Trans R Soc B 362:11–38

Battershill CN (1990) Temporal changes in antarctic marine benthic community structure. NZ Antarct Rec 10:23–27

Bick A, Arlt G (2013) Description of intertidal macro- and meiobenthic assemblages in Maxwell Bay, King George Island, South Shetland Islands, Southern Ocean. Polar Biol 36:673–689

Bowden D (2005) Seasonality of recruitment in Antarctic sessile marine benthos. Mar Ecol Prog Ser 297:101–118

Bromberg S, Nonato EF, Corbisier TN, Petti MAV (2000) Polychaete distribution in the near shore zone of Martel Inlet, Admiralty Bay (King George Island, Antarctica). Bull Mar Sci 67:175–188

Brown KM, Fraser KPP, Barnes DKA, Peck LS (2004) Links between the structure of an Antarctic shallow-water community and ice-scour frequency. Oecologia 141:121–129

Clarke A (1996) Marine benthic populations in Antarctica: patterns and processes. In: Foundations for ecological research west of the Antarctic Peninsula. Antarct Res Ser 70:373–388

Clarke A, Johnson NM (2003) Antarctic marine benthic diversity. Oceanogr Mar Biol Annu Rev 41:47–114

Colwell RK (2010) EstimateS: statistical estimation of species richness and shared species from samples. Version 8.2. User's guide and application. http://purl.oclc.org/estimates. Accessed 29 Nov 2012

Colwell RK, Coddington JA (1994) Estimating terrestrial biodiversity through extrapolation. Philos Trans R Soc Lond B 345:101–111

Conlan KE, Kim SL, Leninhan HS, Oliver JS (2004) Benthic changes during 10 years of organic enrichment by McMurdo Station, Antarctica. Mar Poll Bull 49:43–60

Conlan KE, Kim SL, Thurber AR, Hendrycks E (2010) Benthic changes at McMurdo Station, Antarctica following local sewage treatment and regional iceberg-mediated productivity decline. Mar Poll Bull 60:419–432

Corbisier TN, Petti MVA, Skowronski RSP, Brito TAS (2004) Trophic relationships in the nearshore zone of Martel Inlet (King George Island, Antarctica): δ13 C stable-isotope analysis. Polar Biol 27:75–82

Dayton PK (1989) Interdecadal variation in an Antarctic sponge and its predators from oceanographic climate shifts. Science 245:1484–1486

Echeverría CA, Paiva PC (2006) Macrofaunal shallow benthic communities along a discontinuous annual cycle at Admiralty Bay, King George Island, Antarctica. Polar Biol 29:263–269

Echeverría CA, Paiva PC, Alves VC (2005) Composition and biomass of shallow benthic megafauna during an annual cycle in Admiralty Bay, King George Island, Antarctica. Antarct Sci 17:312–318

Fauchald K, Jumars PA (1979) The diet of worms: a study of polychaete feeding guilds. Oceanogr Mar Biol Annu Rev 17:193–284

Gotelli NJ, Colwell RK (2010) Estimating species richness. In: Magurran AE, McGill BJ (eds) Frontiers in measuring biodiversity. Oxford University Press, New York, pp 39–54

Gutt J (2001) On the direct impact of ice on marine benthic communities, a review. Polar Biol 24:553–564

Gutt J (2007) Antarctic macro-zoobenthic communities: a review and an ecological classification. Antarct Sci 19:165–182

Gutt J, Piepenburg D (2003) Scale-dependent impact on diversity of Antarctic benthos caused by grounding of icebergs. Mar Ecol Prog Ser 253:77–83

Hall SJ (1994) Physical disturbance and marine benthic communities: life in unconsolidated sediments. Oceanogr Mar Biol Annu Rev 32:179–239

Hilbig B, Gerdes D, Montiel A (2006) Distribution patterns and biodiversity in polychaete communities of the Weddell Sea and Antarctic Peninsula area (Southern Ocean). J Mar Biol Ass UK 86:711–725

Jassby AD, Powell TM (1990) Detecting changes in ecological time series. Ecology 71:2044–2052

Jażdżewski K, Jurasz W, Kittel W, Presler E, Presler P, Siciński J (1986) Abundance and biomass estimates of the benthic fauna in Admiralty Bay, King George Island, South Shetland Islands. Polar Biol 6:5–16

Jażdżewski K, Teodorczyk W, Sicinski J, Kontek B (1991) Amphipod crustaceans as an important component of zoobenthos of the shallow Antarctic sublittoral. Hydrobiologia 223:105–117

Jażdżewski K, DeBroyer C, Pudlarz M, Zielinski D (2001) Seasonal fluctuations of vagile benthos in the uppermost sublittoral of a maritime Antarctic fjord. Polar Biol 24:910–917

Kim S, Hammerstom KK, Conlan KE, Thurber AR (2010) Polar ecosystem dynamics: recovery of communities from organic

enrichment in McMurdo Sound, Antarctica. Integr Comp Biol 50:1031–1040

Leinster T, Cobbold CA (2012) Measuring diversity: the importance of species similarity. Ecology 93:477–489

Levin LA, Gage JD (1998) Relationships between oxygen, organic matter and the diversity of bathyal macrofauna. Deep-Sea Res Pt II 45:129–163

Maurer BA, McGill BJ (2011) Measurement of species diversity. In: Magurran A, McGill BJ (eds) Biological diversity—frontiers in measurement and assessment. Oxford University Press, Oxford, pp 55–65

Meulman JJ (1992) The integration of multidimensional scaling and multivariate analysis with optimal transformations. Psychometrika 57:539–565

Nedwell D, Walker T, Ellis-Evans J, Clarke A (1993) Measurements of seasonal rates and annual budgets of organic carbon fluxes in an Antarctic coastal environment at Signy Island, South Orkney Islands, suggest a broad balance between production and decomposition. Appl Environ Microbiol 59:3989–3995

Nonato EF, Brito TAS, Paiva PC, Petti MAV, Corbisier TN (2000) Benthic megafauna of the nearshore zone of Martel Inlet (King George Island, South Shetland Islands, Antarctica): depth zonation and underwater observations. Polar Biol 23:580–588

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H (2011) Vegan: community ecology package. R package version 2.0-1. http://cran.r-project.org

Pabis K, Siciński J (2010) Distribution and diversity of polychaetes collected by trawling in Admiralty Bay—an Antarctic glacial fiord. Polar Biol 33:141–151

Pabis K, Siciński J, Krymarys M (2011) Distribution patterns in the biomass of macrozoobenthic communities in Admiralty Bay (King George Island, South Shetlands, Antarctic). Polar Biol 34:489–500

Peck LS, Brockington S, Vanhove S, Beghyn M (1999) Community recovery following catastrophic iceberg impacts in a soft-sediment shallow-water site at Signy Island, Antarctica. Mar Ecol Prog Ser 186:1–8

Peck LS, Convey P, Barnes DKA (2006) Environmental constraints on life histories in Antarctic ecosystems: tempos, timings and predictability. Biol Rev 81:75–109

Quinn G, Keough M (2002) Experimental design and data analysis for biologists, 1st edn. Cambridge University, Cambridge

R Development Core Team (2011) R: A language and environment for statistical computing. R Foundation for statistical computing, Vienna. http://www.R-project.org/. Accessed 29 Nov 2012

Ricklefs RE, Schluter D (1993) Species diversity in ecological communities: historical and geographical perspectives. The University of Chicago Press, Chicago and London

Siciński J (1986) Benthic assemblages of polychaeta in chosen regions of the Admiralty Bay (King George Island, South Shetland Islands). Pol Polar Res 7:63–78

Siciński J (2000) Polychaeta (Annelida) of Admiralty Bay: species richness, diversity, and abundance. Pol Polar Res 21:153–169

Siciński J (2004) Polychaetes of Antarctic sublittoral in the proglacial zone (King George Island, South Shetland Islands. Pol Polar Res 25:67–96

Siciński J, Janowska E (1993) Polychaetes of the shallow sublittoral of Admiralty Bay, King George Island, South Shetland Islands. Antarct Sci 5:161–167

Siciński J, Jażdżewski K, De Broyer C, Presler P, Ligowski R, Nonato EF, Corbisier TN, Petti MAV, Brito TAS, Lavrado HP, Błażewicz-Paszkowycz M, Pabis K, Jażdżewska J, Campos LS (2011) Admiralty Bay Benthos diversity—A census of a complex polar ecosystem. Deep Sea Res II 58:30–48

Smale DA (2007) Ice disturbance intensity structures benthic communities in nearshore Antarctic waters. Mar Ecol Prog Ser 349:89–102

Smith CR, DeMaster DJ (2008) Preface and brief synthesis for the FOODBANCS volume. Deep Sea Res II 55:2399–2403

Smith CR, DeMaster DJ, Thomas C, Sršen P, Grange L, Evrard V, DeLeo F (2012) Pelagic-benthic coupling, food banks, and climate change on the West Antarctic Peninsula Shelf. Oceanography 25:188–201

Stark JS (2000) The distribution and abundance of soft sediment macrobenthos around Casey Station, East Antarctica. Polar Biol 23:840–850

Stark JS, Riddle MJ, Simpson RD (2003) Human impacts in soft-sediment assemblages at Casey Station, East Antarctica: spatial variation, taxonomic resolution and data transformation. Austral Ecol 28:287–304

Thursh SF, Hewitt JE, Cummings VJ, Norkko A, Chiantore M (2010) β-Diversity and species accumulation in Antarctic coastal benthos: influence of habitat, distance and productivity on ecological connectivity. PLoS One 5:e11899

Tóthmérész B (1995) Comparison of different methods for diversity ordering. J Veg Sci 6:283–290