

# Normalized biomass size spectra in high Antarctic macrobenthic communities: linking trophic position and body size

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**ABSTRACT:** Normalized biomass size spectra (NBSS) and the stable nitrogen isotopic composition of food webs were analyzed to determine the inter-specific relationships between trophic level (measured as  $\delta^{15}\text{N}$ ) and body size in macrobenthic communities living on the continental shelf of the southeastern Weddell Sea (SEWS). We found that the relationship between trophic level and body size for the whole macrobenthic community was not significant ( $r^2 = 0.08$ ,  $p > 0.05$ ), probably associated with biomass accumulated in the larger body size fractions, which are represented particularly by suspension feeders such as sponges and tunicates. We used an alternative method of studying trophic structure of the aquatic communities based on the distribution of residuals of the NBSS. Here we demonstrate how residual distribution exhibited dome-like patterns, which may offer an additional quantitative tool for studying the relationship between trophic level and body size. These domes of biomass represent trophic positions derived from relationships between the body size distribution of the predators in one trophic position and their prey in another. We found 4 well defined domes of biomass, which appear when large benthic species are abundant, especially favored in an environment with high organic matter flux. A significant positive relationship ( $r^2 = 0.59$ ,  $p < 0.05$ ) between the trophic level and residuals derived from NBSS suggests that these domes might be considered as functional groups comprising organisms from different trophic levels. We suggest that dome-like patterns in the biomass size spectra can provide a robust framework for conceptualizing and statistically modeling trophic levels of macrobenthic communities.

**KEY WORDS:** Macrofauna · Trophic spectrum · Trophic level · Stable isotopes

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## INTRODUCTION

The southeastern Weddell Sea (SEWS) shelf in the high Antarctic is rich and diverse in macrobenthic species which are maintained by high levels of primary production (PP), particularly during the austral summer (e.g. Arntz et al. 1994, Gutt et al. 1998). In addition, this region is affected continuously by iceberg scouring, enhancing the environmental complexity and diversity (e.g. Gutt 2001, 2007, Gerdes et

al. 2008, Gutt et al. 2011). Macrobenthic diversity and distribution patterns as well as environmental conditions have been extensively studied on the SEWS shelf (Arntz et al. 1994, Brey & Gerdes 1998, Clarke & Johnston 2003, Gutt 2007). In general, trophic relationships and food web structure in Antarctic coastal benthic communities are affected by strong coupling of the physical environment and PP (Norkko et al. 2007). The SEWS shelf experiences high sedimentation rates of fresh organic matter

(OM), composed of diatom aggregates and fecal pellets that are accumulated on the sediment as green mats or food banks (Bathmann et al. 1991, Isla et al. 2009, Sañé et al. 2012). Furthermore, tidal currents resuspend and redistribute the OM, which can persist several weeks with a high nutritional value after the spring–summer pulse (Rossi et al. 2013).

Many authors have stressed the importance of body size in benthic marine fauna, but very little is known about the processes that determine size distribution in marine invertebrates (Roy 2002). Studies have focused on bathymetric patterns in relation to the availability of food (Thiel 1975, Gage & Tyler 1991), the physical characteristics of the sediment (Drgas et al. 1998), the gradient of OM (Schwinghamer 1985), the life-history strategies of dominant taxa (Warwick 1984), and oxygen levels (Quiroga et al. 2005). Gage & Tyler (1991) argued that large benthic organisms in deep waters are mainly opportunistic scavengers, although some deposit feeders and suspension feeders are also present, probably associated with the possibility of reducing predation risk or the ability to forage over a wide area. On the SEWS shelf, large sessile and sedentary suspension feeders with associated mobile fauna dominate macrobenthic communities (Gutt 2007). These suspension feeders can feed on a broad spectrum of prey items, which range from bacteria to zooplankton and detrital particulate OM (Gili et al. 2001). For instance, hydrozoans and gorgonians feed on zooplankton, while sponges prefer diatoms, probably due to favorable bottom currents which also support suspension feeders and suspension feeding epibionts by producing an advective food supply in the nepheloid layer (Gaino et al. 1994, Coma et al. 1998, Gili et al. 2001). Few studies have investigated benthic food webs across similar communities from different regions in the Antarctic (Jacob 2005, Mintenbeck et al. 2007, Norkko et al. 2007, Gillies et al. 2013). In the benthic system, the trophic level is expected to increase with increase of body size (see France et al. 1998, Jennings et al. 2002), but empirical evidence describing the relationships between body size and trophic level is limited and also difficult to quantify (France et al. 1998, Jennings et al. 2002).

The stable isotopes of nitrogen ( $\delta^{15}\text{N}$ ) and carbon ( $\delta^{13}\text{C}$ ) are an efficient means for tracing carbon flow and trophic position in food webs (Michener & Lajtha 2007, France 2014). Several studies have used stable isotopes to determine trophic relationships in Antarctic coastal benthic systems (e.g. Nyssen et al. 2002, Jacob 2005, Mintenbeck et al. 2007, Norkko et al. 2007, Gillies et al. 2013). The

nitrogen and carbon isotope compositions of natural samples are given as delta values ( $\delta$ ), representing the isotope ratio of the heavy to the light isotope (‰) relative to an international standard (Michener & Lajtha 2007). The carbon isotope composition ( $\delta^{13}\text{C}$ ) of an organism is used to distinguish isotopically different sources in food webs (DeNiro & Epstein 1978). In contrast, nitrogen isotopes in consumers become enriched in  $\delta^{15}\text{N}$  by 3 to 4 times, which is used to predict an organism's trophic level (Michener & Lajtha 2007).

Normalized biomass size spectra (NBSS) are widely used to describe the structure of marine benthic ecosystems (e.g. Drgas et al. 1998, Saiz-Salinas & Ramos 1999, Quiroga et al. 2005, Akoumianaki et al. 2006, Sellanes et al. 2007, Hua et al. 2013). The NBSS coefficients (slope and intercept) are extracted by performing a least-squares linear regression on the log-transformed values of normalized biomass and body size. These coefficients have been proposed as quantitative indices of aquatic ecosystem structure, which allows a more dynamic interpretation of an ecosystem because the slope of the spectra seems to be related to energy utilization within the whole community (Sprules & Munawar 1986, Kerr & Dickie 2001). In fact, theoretical models regarding the distribution of biomass by size classes have been developed in order to explain ecosystem functioning (Kerr & Dickie 2001). Quintana et al. (2002) suggested an alternative method of studying trophic structure of the aquatic communities based on the distribution of residuals of the NBSS: using this approach, Quintana et al. (2002) described dome-like patterns over particular ranges of body size, which seem to be formed by different trophic groups (Dickie et al. 1987). Each dome in the biomass size spectra represents a trophic position derived from relationships between the body size distribution of the predators in one trophic position and their prey in another, according to predator–prey theory (Kerr & Dickie 2001). Thus, dome-like patterns have been related to trophic organization of organisms living in communities as a consequence of the dependence of the production:biomass ratio (P:B ratio) on body size, and they are used to describe the trophic structure of marine and freshwater communities (e.g. Dickie et al. 1987, Kerr & Dickie 2001, Quintana et al. 2002, Quiñones et al. 2003, Quiroga et al. 2005).

In order to understand the functioning of the benthic ecosystem it is necessary to center our attention not only on community structure analysis, but also on the empirical study of trophic structure of marine communities from an allometric point of view. Here

we explored the relationship between dome-like patterns derived from NBSS and trophic level using  $\delta^{15}\text{N}$  in order to describe the trophic structure of benthic communities. We hypothesized that if these domes of biomass provide a surrogate for trophic level, then analysis of size spectra can be used to describe changes in the trophic structure of marine benthic communities as has been proposed by Jennings et al. (2002). The aims of this study were (1) to analyze the body size distribution of the macrobenthic community on the continental shelf of the SEWS, (2) to describe the trophic structure using stable isotopes, and (3) to determine whether domes of biomass are good descriptors of the trophic structure and trophic level of groups of organisms living in macrobenthic communities on the continental shelf of the SEWS.

## MATERIALS AND METHODS

### Sampling

Macrofaunal samples were collected at 14 stations (88 cores) on the continental shelf of the SEWS during the Benthic Disturbance Experiment (BENDEX) Expedition ANT XXI/2 in 2003 and the Change in Antarctic Marine Biota (CAMBIO) Expedition ANT XXVII/3 in 2011 onboard RV 'Polarstern' (Table 1, Fig. 1). Macrofauna was sampled using a multi-box corer with 9 separate box cores, each with an area of 240 cm<sup>2</sup>. Additionally, the multi-box corer was equipped with a UW digital color camera, which allowed for controlled sampling and provided additional high-quality pictures from the communities sampled at the study sites (Gerdes 1990, Gerdes et al. 2008). The samples were taken from water depths between 261 and 333 m (Table 1). Sediments were sieved through a 500  $\mu\text{m}$  mesh size screen, and the biological material was fixed in a 4% formaldehyde seawater solution buffered with hexamethylenetetramine. In the laboratory, the organisms were assigned to 1 of 28 higher taxonomic groups (e.g. phylum, class). In addition, all organisms were counted (ind. per 240 cm<sup>2</sup>), and biomass (g wet weight per 240 cm<sup>2</sup>) was estimated by weighing the organisms with an analytical balance. Bryozoans and sponges were counted as single individuals. In subsequent calculations, these values were treated as true abundances (see Gerdes et al. 2008).

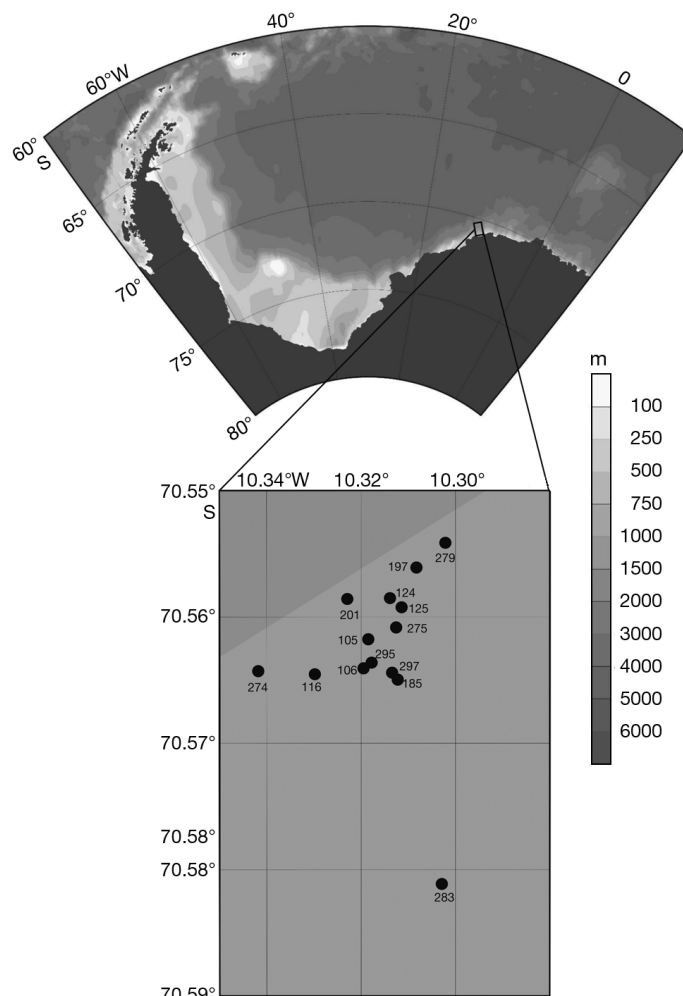


Fig. 1. Locations of the sampling stations on the continental shelf of the south-eastern Weddell Sea

Table 1. Macrobenthos sample information. Samples were collected during the cruises ANT XXI/2 (2003) and ANT XXVII/3 (2011)

Station	Date (d.mo)	Latitude (S)	Longitude (E)	Depth (m)	No. of cores
<b>ANT XXI/2 (2003)</b>					
106	10.12	70° 56.64'	10° 32.03'	304	8
105	10.12	70° 56.50'	10° 32.01'	295	7
116	11.12	70° 56.81'	10° 32.87'	321	6
124	11.12	70° 56.40'	10° 31.74'	290	6
125	11.12	70° 56.40'	10° 31.56'	283	6
185	17.12	70° 56.61'	10° 31.65'	294	6
197	18.12	70° 56.29'	10° 31.32'	253	6
201	18.12	70° 56.26'	10° 33.00'	322	1
<b>ANT XXVII/3 (2011)</b>					
274	25.03	70° 56.58'	10° 34.27'	333	7
275	25.03	70° 56.42'	10° 31.62'	283	8
279	28.03	70° 56.22'	10° 30.33'	250	7
283	29.03	70° 58.00'	10° 30.30'	284	7
295	31.03	70° 56.63'	10° 32.01'	303	6
297	31.03	70° 56.60'	10° 31.63'	276	7

Macrobenthic organisms for stable isotope analyses were collected during the expeditions ANT XIII/3 (1992), ANT XV/3 (1994), ANT XVII/3 (1996), and ANT XXI/2 (1999) with either Agassiz or benthopelagic trawls or traps from water depths between 280 and 322 m. When the trawl reached the deck, each sample was sieved through a 500  $\mu\text{m}$  mesh size screen. Macrofaunal organisms were separated by eye on deck. All samples were immediately freeze-dried and stored until preparation for further analyses. Small organisms were analyzed entirely, whereas in macrofaunal specimens, only body wall pieces or muscle tissue samples were used. In addition, suspended particulate OM (SPOM) was collected with an *in situ* seawater pumping system from below the ship's hull (12 m water depth). All samples (macrofauna and SPOM) were kept frozen at  $-30^\circ\text{C}$  until further analysis. Samples were lyophilized for 24 h in a Finn-Aqua Lyovac GT2E and then ground to a fine powder. Each sample was split in half: 1 part was acidified to remove  $\text{CaCO}_3$  in accordance with Fry (1988) and Cloern et al. (2002) by adding 1 mol  $\text{l}^{-1}$  hydrochloric acid (HCl) drop by drop until no more  $\text{CO}_2$  was released, re-dried at  $60^\circ\text{C}$  without rinsing to minimize loss of dissolved OM, and ground again; the other half did not receive any further treatment. Stable isotope analysis was conducted with an isotope-ratio mass spectrometer Thermo/Finnigan Delta plus from the GeoBioCenter in Munich, Germany (Mintenbeck et al. 2007). In order to avoid potential effects of seasonality on the isotopic compositions of organisms from different sampling periods, a *t*-test was used to determine the significance of the slopes of regressions between carbon and nitrogen stable isotope data sets (Zar 1999).

### Data analysis

The density and biomass data from each box-corer replicate was considered a pseudo-replicate, and then standardized by area in order to determine the means and standard deviations per station. Additionally, mean individual weight ( $W$ ) was estimated as total macrofaunal community biomass divided by total macrofaunal density. Biomass size-spectra were normalized as described by Platt & Denman (1978). This normalization is required, since the width of the size classes varies through the size spectra. In brief, the procedure consists of dividing the variable of interest  $m(s)$  in the size class characterized by the weight or volume ( $s$ ) by the width of the size class,  $\Delta s$ .

Thus, the normalized version of the variable  $M$  is equal to:

$$M(s) = m(s)/\Delta s \quad (1)$$

The parameters of the NBSS were determined by regressing the  $\log_2(\text{normalized biomass})$  against  $\log_2(\text{individual weight})$ . Domes of biomasses were determined using the distribution of residuals in single samples derived from NBSS (Quintana et al. 2002, Quiroga et al. 2005). We used linear regressions to explore cross-species relationships between body size ( $\log_2$  individual mass) and trophic level ( $\delta^{15}\text{N}$ ). Results were considered significant at  $p < 0.05$  in all tests. In addition, although  $\delta^{15}\text{N}$  values are often sampled at the level of individuals, food web and stable isotope models are assumed as groups of individuals, independent of body size. We conducted an analysis of covariance (ANCOVA) in which feeding mode, body size, and their interactions were included as predictor variables. This analysis was proposed in order to distinguish the effect of feeding modes (i.e. suspension feeders, deposit feeders, predators, and omnivores) on the relationship between body size and trophic level (Reum & Marshall 2013). The ANCOVA was carried out using Statistica 7.0 software (StatSoft) for combined data sets (i.e. ANT XIII/3, ANT XV/3, ANT XVII/3, and ANT XXI/2).

In order to describe the relationships between body size and trophic level in the macrobenthic community of the study area, we collected macrobenthic organisms using a multi-box corer with the purpose of identifying the domes of biomasses. Additionally, we also collected macrobenthic organisms with trawls (i.e. Agassiz or benthopelagic) for the isotopic composition determinations. Additional taxonomic information for all species included in the analysis is provided in Table A1 in the Appendix. These data are comparable, because due to the lack of taxonomical resolution, the SEWS shelf macrobenthic communities are not truly determined by species composition, as pointed out by Gutt (2007). In fact, that author proposed a new classification based on the dominance of either sessile suspension feeders or infauna and mobile deposit feeders, which might be more applicable than the sediment-community concept. In this sense, macrobenthic species on the continental shelf of the SEWS (200–450 m) are dominated by large sessile suspension feeders with an associated mobile fauna (Fig. 2), which have been extensively studied through quantitative sampling techniques (Gerdes et al. 2008, Arntz et al. 1994, Brey & Gerdes 1998).

## RESULTS

In total, we recorded 28 major taxa of macrobenthos, with a mean total abundance of  $65 \pm 32$  ind. per  $240 \text{ cm}^2$  and biomass of  $17.45 \pm 31.54$  g wet wt per  $240 \text{ cm}^2$  (Fig. 3a,b). In terms of biomass, sponges ( $14.94 \pm 31.32$  g wet wt per  $240 \text{ cm}^2$ ; 82.67%), tunicates ( $0.65 \pm 1.54$  g wet wt per  $240 \text{ cm}^2$ ; 5.29%), errant polychaetes ( $0.64 \pm 0.66$  g wet wt per  $240 \text{ cm}^2$ ; 3.51%) and holothurians ( $0.29 \pm 0.44$  g wet wt per  $240 \text{ cm}^2$ ; 1.73%) accounted for more than 93% of the overall total biomass in the study area (Fig. 3b,c). The contribution to total biomass of different taxa, without sponges, is shown in Fig. 3d. None of the remaining taxa exceeded 1% contribution, and all together, they made up  $<7\%$  of the overall biomass (Fig. 3d).

In relation to the isotope compositions, 25 taxa of benthic macrofauna from trawls were analyzed for stable carbon and nitrogen isotopes, covering almost the whole range of taxonomic groups and feeding guilds (Table 2). We found no significant differences in the isotope compositions among sampling periods ( $p < 0.05$ ). The carbon stable isotope composition ( $\delta^{13}\text{C}$ ) in the macrobenthic organisms varied between  $-20.1\text{‰}$  (asteroids) and  $-26.7\text{‰}$  (sedentary polychaetes). The nitrogen stable isotope composition ( $\delta^{15}\text{N}$ ) in the samples varied between  $5.2\text{‰}$  (sedentary polychaetes) and  $9.8\text{‰}$  (errant polychaetes; Table 2, Fig. 4). Nitrogen values among all consumers spanned a  $\delta^{15}\text{N}$  range of  $4.6\text{‰}$  (Table 2, Fig. 4). Among suspension feeders,  $\delta^{15}\text{N}$  values ranged from  $5.3\text{‰}$  (bryozoans) to  $6.7\text{‰}$  (sponges) and  $7.6\text{‰}$  (anthozoans). In contrast, predator  $\delta^{15}\text{N}$  values ranged from  $9.8\text{‰}$  (errant polychaetes) to  $9.6\text{‰}$  (asteroids, nemerteans, and cephalopods; Table 2, Fig. 4). Based on findings of Nyssen et al. (2002), the trophic level was estimated as  $(D - 3.2)/3.0 + 1$ , where  $D$  is the  $\delta^{15}\text{N}$  value of the organism and 3.2 refers to the mean value of SPOM ( $\pm 1.1\text{‰}$ ) in the study area. SPOM isotope ratios ( $n = 7$ ) were  $-29.3 \pm 1.0\text{‰}$  for  $\delta^{13}\text{C}$  and  $3.2 \pm 1.1\text{‰}$  for  $\delta^{15}\text{N}$  (Table 2, Fig. 4). In general, the difference between  $\delta^{15}\text{N}$  of 2 organisms is a measure of the distance between their trophic levels. Based on the assumed 3‰ enrichment per trophic level (Nyssen et al. 2002, Gillies et al. 2013), the suspension feeders ( $6.4 \pm 0.81\text{‰}$ ) and deposit feeders were restricted to a second trophic level with a mean value of  $7.9 \pm 0.68\text{‰}$  of  $\delta^{15}\text{N}$  (Fig. 4), and differed from omnivores ( $8.4 \pm 0.42\text{‰}$ ). Predators occupied a third trophic level with a mean of  $9.5 \pm 0.22\text{‰}$   $\delta^{15}\text{N}$  (Fig. 4).

The relationship between  $\delta^{15}\text{N}$  and body size for the whole macrobenthic community (i.e. interspecific relationship) in the study area was  $y =$

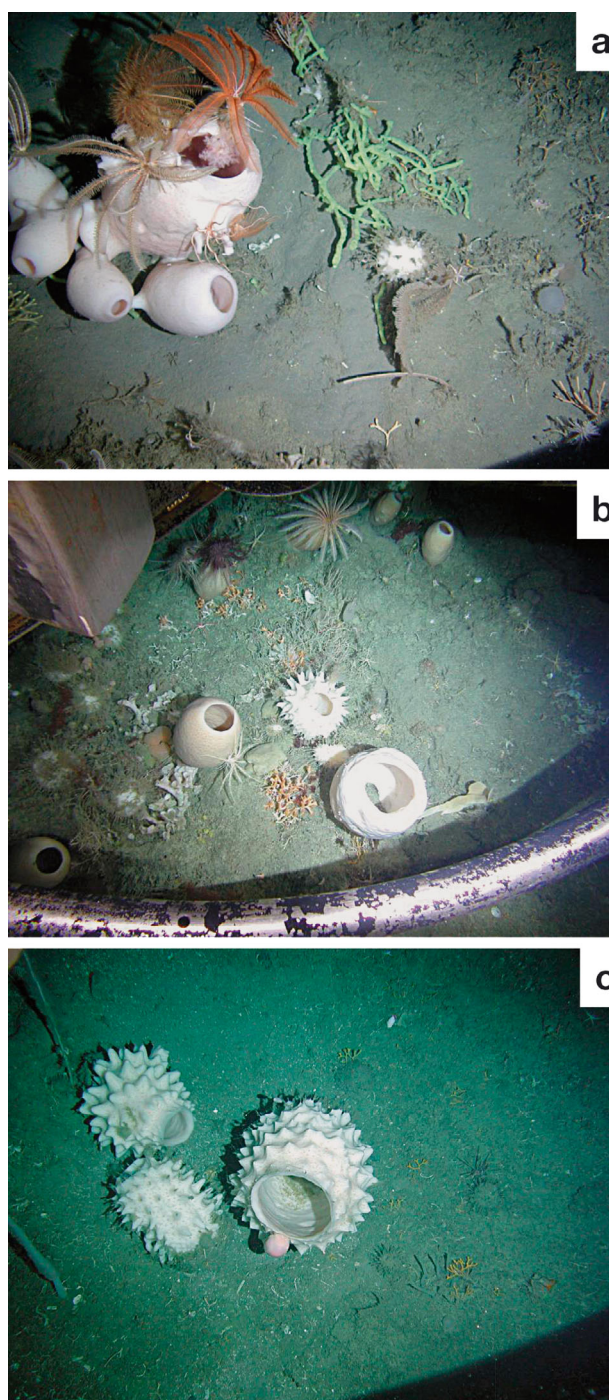


Fig. 2. Selected images of the seabed during the ANT XXVII/3 cruise. (a) Station 274: sponges with associated mobile fauna such as crinoids and ophiuroids. (b) Station 279: sponges, bryozoans, ascidians, crinoids and ophiuroids. (c) Station 283: sponges (sponge with a large ascidia), bryozoans and echinoids (photographs by D. Gerdes)

$-0.11x + 8.51$  and was not significant ( $r^2 = 0.08$ ,  $p > 0.05$ ; Fig. 5). This result can be associated with the high contribution (in terms of individual biomass) of

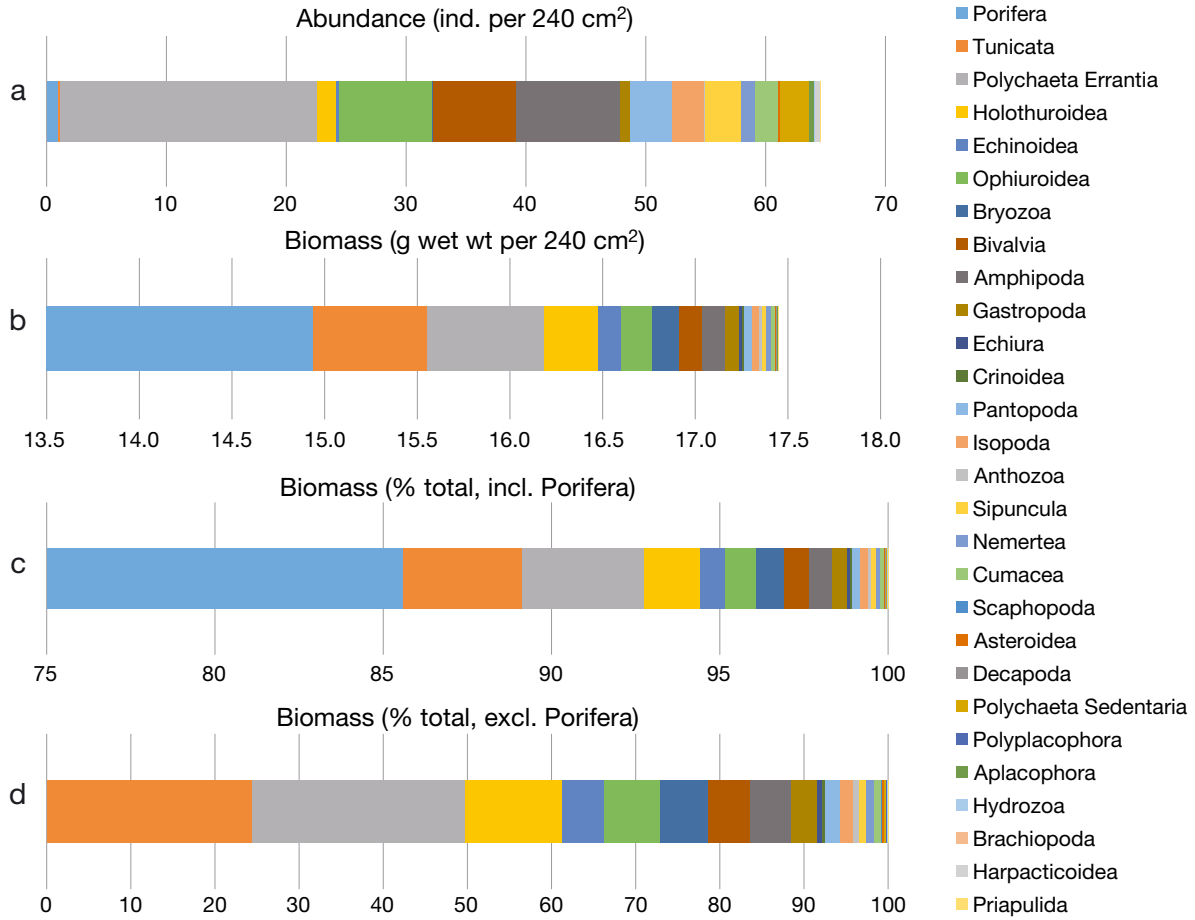


Fig. 3. Composition of macrobenthos in terms of (a) abundance, (b) biomass, (c) contribution to total biomass with Porifera, and (d) contribution to total biomass in percentage, without Porifera

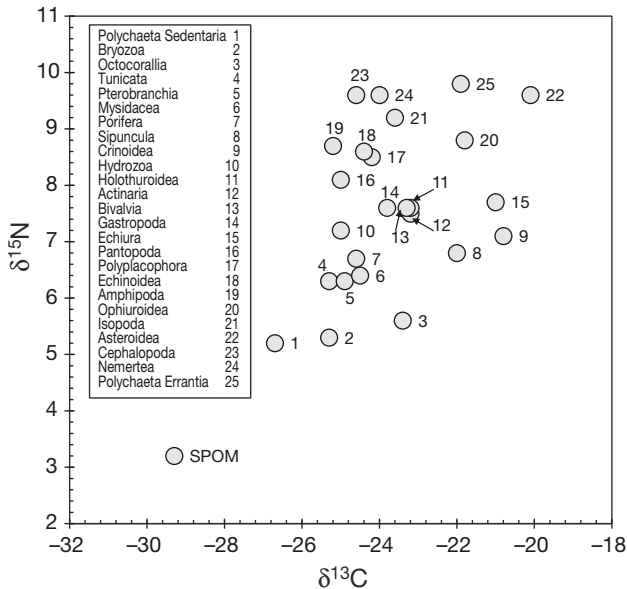


Fig. 4.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  stable isotope values in suspended particulate organic matter and macrobenthic taxa from the southeastern Weddell Sea shelf

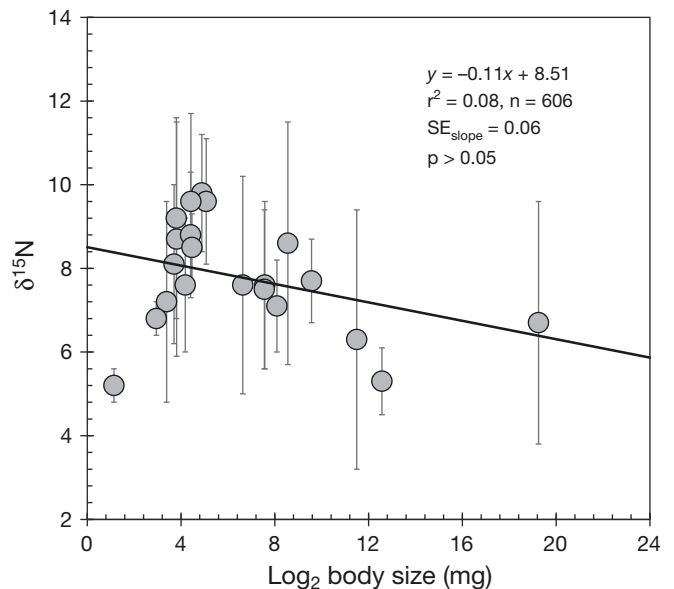


Fig. 5. Fitted linear regression between the  $\delta^{15}\text{N}$  (mean  $\pm$  SD) of macrobenthic taxa from the southeastern Weddell Sea shelf and their  $\log_2$  body size

sponges, bryozoans, holothurians, anthozoans, crinoids, echiurids, echinoids, and gastropods to larger size classes, which were classified to both suspension feeders and deposit feeders. In general, the increase in trophic level with increasing body size within a community has been described for a shallow benthic system in the North Sea (Jennings et al. 2002), although those authors focused on fishes and the epibenthic community as a whole. In our study area, the relationship between body size and trophic level ( $\delta^{15}\text{N}$ ) did not fit a linear model, indicating that body mass is not a good predictor of trophic level. It is clear that large suspension feeders did not belong to higher trophic levels. Hence, the relationship between body size and trophic level needs to be analyzed in a different way in order to examine predictions made by theoretical and empirical data. In this context, we used the data on residuals derived from the regression between normalized biomass and body size in order to relate the body size with the trophic level. Based on our results from shelf stations in the depth range of 261 to 333 m, no significant differences ( $p < 0.05$ ) were found among the slopes of the NBSS, and we hence constructed an NBSS pooling together spectra of all stations, disregarding the water depth. The spectra fit with a  $\log_2$ - $\log_2$  linear model having a slope of  $-0.43$  ( $y = -0.43x - 1.32$ ,  $r^2 = 0.53$ ,  $p < 0.05$ ; Fig. 6a). Residual distribution of regression analysis shows the formation of domes of biomass (Fig. 6b), which might be related to trophic organizational/functional groups of organisms living in the communities. We found important positive biomass residuals, which were pooled in 4 groups: size classes 5, 8, 12, and 20 (Fig. 6b). Size class 5 consists of bivalves, ophiuroids, nemerteans, polyplacophors, and errant polychaetes, size class 8 is composed of holothurians and anthozoans (Table 3, Fig. 6b). Size classes 12 and 20 are composed of tunicates and sponges, respectively, which are important faunistic components of Antarctic macrobenthos over extensive areas on the continental shelf (see Gutt 2007, Gerdes et al. 2008, and references cited therein).

In order to relate the trophic level with body size of the benthic organisms in the study area, we constructed a trophic spectrum using mean  $\delta^{15}\text{N}$  of species from almost all benthic taxa in the study area (Fig. 6c). The relationship between mean  $\delta^{15}\text{N}$  and body size showed a similar shape as the residual distribution derived from the NBSS. Mean  $\delta^{15}\text{N}$  stable isotope values for all macrobenthic organisms were also pooled in 4 groups belonging to size classes 5, 8, 12, and 20 (Table 3, Fig. 6c), and the relationship between  $\delta^{15}\text{N}$  and residuals for the whole

Table 2.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values (mean  $\pm$  SD) of taxa collected on the southeastern Weddell Sea shelf. SPOM: suspended particulate organic matter; n: number of samples; TL: trophic level; SF: suspension feeder; DF: deposit feeder; Om: omnivore; Pr: predator

Taxon	n	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	TL	Feeding mode
Bryozoa	13	$-25.3 \pm 2.3$	$5.3 \pm 0.8$	1.7	SF
Polychaeta	6	$-26.7 \pm 0.6$	$5.2 \pm 0.4$	1.7	SF
Sedentaria					
Octocorallia	11	$-23.4 \pm 1.9$	$5.6 \pm 1.6$	1.8	SF
Tunicata	30	$-25.3 \pm 0.9$	$6.3 \pm 3.1$	2.0	SF
Pterobranchia	11	$-24.9 \pm 0.8$	$6.3 \pm 1.1$	2.0	SF
Mysidacea	3	$-24.5 \pm 0.9$	$6.4 \pm 0.4$	2.1	SF
Porifera	56	$-24.6 \pm 1.5$	$6.7 \pm 2.9$	2.2	SF
Sipuncula	3	$-22.0 \pm 1.7$	$6.8 \pm 0.4$	2.2	SF
Crinoidea	20	$-20.8 \pm 2.5$	$7.1 \pm 1.1$	2.3	SF
Hydrozoa	29	$-25.0 \pm 1.6$	$7.2 \pm 2.4$	2.3	SF
Actinaria	35	$-23.2 \pm 3.4$	$7.6 \pm 2.0$	2.4	SF
Holothuroidea	61	$-23.2 \pm 2.8$	$7.5 \pm 11.9$	2.4	SF
Bivalvia	12	$-23.3 \pm 1.9$	$7.6 \pm 1.6$	2.5	SF
Gastropoda	29	$-23.8 \pm 1.5$	$7.6 \pm 2.6$	2.5	DF
Echiura	19	$-21.0 \pm 1.6$	$7.7 \pm 1.0$	2.5	DF
Pantopoda	21	$-25.0 \pm 0.8$	$8.1 \pm 1.9$	2.6	Om
Polyplacophora	24	$-24.2 \pm 1.2$	$8.5 \pm 0.8$	2.8	DF
Echinoidea	7	$-24.4 \pm 1.7$	$8.6 \pm 2.9$	2.8	DF
Amphipoda	77	$-25.2 \pm 2.7$	$8.7 \pm 2.8$	2.8	Om
Ophiuroidea	21	$-21.8 \pm 2.3$	$8.8 \pm 1.5$	2.9	DF
Isopoda	41	$-23.6 \pm 1.7$	$9.2 \pm 2.4$	3.0	DF
Asteroidea	42	$-20.1 \pm 2.0$	$9.6 \pm 1.5$	3.1	Pr
Cephalopoda	12	$-24.6 \pm 3.0$	$9.6 \pm 1.9$	3.1	Pr
Nemertea	25	$-24.0 \pm 2.8$	$9.6 \pm 2.1$	3.1	Pr
Polychaeta	26	$-21.9 \pm 1.5$	$9.8 \pm 1.4$	3.2	Pr
Errantia					
SPOM	7	$-29.3 \pm 1.0$	$3.2 \pm 1.1$		

Table 3.  $\log_2$  size class normalized biomass (NB) and standardized residuals (SR) for each taxon collected on the southeastern Weddell Sea shelf

$\log_2$ size class	NB	SR	Taxa
-1	-4.34	-1.48	Harpacticoida
1	-2.98	-9.65	Priapulida
2	-2.90	-0.41	Polychaeta Sedentaria
3	-1.34	0.50	Sipuncula
4	0.39	1.48	Aplacophora, Brachiopoda, Hydrozoa, Cumacea, Pantopoda, Isopoda, Amphipoda
5	1.34	2.11	Bivalvia, Ophiuroidea, Nemertea, Polyplacophora, Polychaeta Errantia
6	-5.74	-0.92	Asteroidea, Decapoda
7	-3.72	0.20	Scaphopoda, Gastropoda
8	-3.15	0.66	Holothuroidea, Anthozoa
9	-4.79	0.10	Crinoidea, Echinoidea
10	-6.92	-0.67	Echiura
12	-5.68	0.28	Tunicata
13	-9.39	-1.21	Bryozoa
20	-9.72	0.01	Porifera

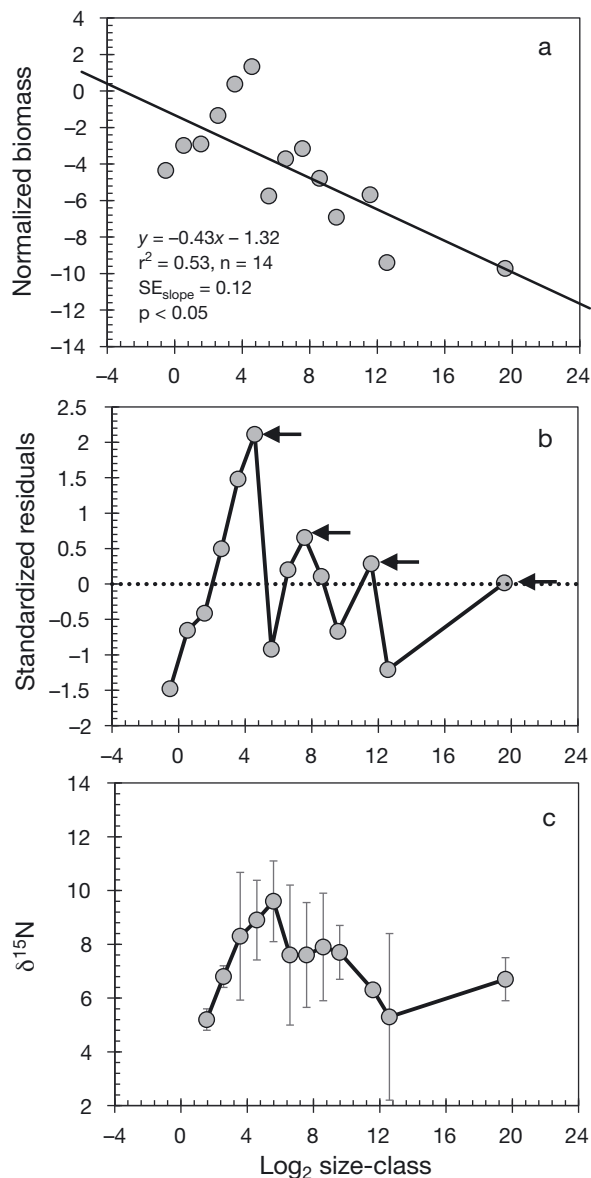


Fig. 6. (a) Integrated normalized biomass size spectrum, (b) residual distribution of the macrofauna in the study area (arrows indicate domes of biomass), and (c) relation between  $\delta^{15}\text{N}$  (mean  $\pm$  SD) and  $\log_2$  body size for all taxa

macrobenthic community in the study area was  $y = 0.90x + 6.91$ , and was significant at  $p < 0.05$  ( $r^2 = 0.59$ ; Fig. 7). ANCOVA revealed that the relationship between trophic level and body size was significant ( $p < 0.001$ ), indicating that the trophic level may be related to feeding modes (Table 4).

## DISCUSSION

The analysis of body-size distribution constitutes an important tool for describing and comparing the

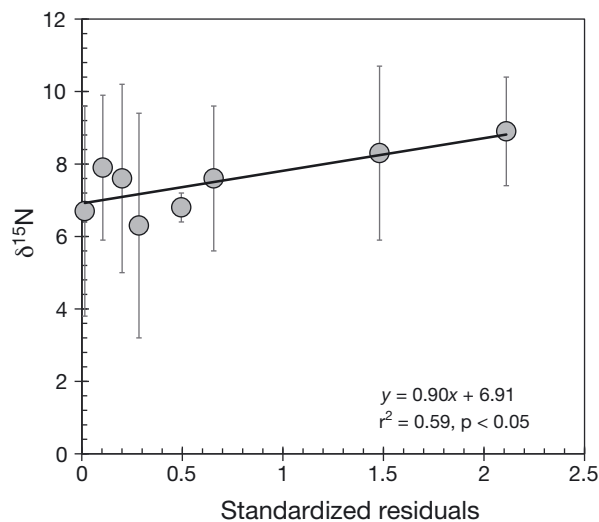


Fig. 7. Fitted linear regression between the  $\delta^{15}\text{N}$  (mean  $\pm$  SD) and standardized residuals derived from normalized biomass size spectra of macrobenthic taxa from the southeastern Weddell Sea shelf

Table 4. Results of the analysis of covariance with feeding modes as a covariate variable

Effect	SS	df	MS	F	p
Intercept	991.701	1	991.701	1719.969	<0.001
Body size	0.002	1	0.002	0.004	0.949
Feeding mode	23.460	3	7.823	13.568	<0.001
Error	9.220	16	0.576		

structure and function of marine ecosystems (Kerr & Dickie 2001). In fact, community size structure is one of the most important characteristics of an ecosystem and is essentially an indicator of ecosystem functioning (Sprules & Munawar 1986). Theoretical models regarding the distribution of biomass by size classes have been mostly developed for pelagic ecosystems (e.g. Kerr & Dickie 2001, Quiñones et al. 2003). In the benthic ecosystem, organisms are more strongly affected by the physical habitats afforded or imposed by the sediment (e.g. Drgas et al. 1998). However, on the SEWS shelf, sea ice dynamics in combination with hydrographic conditions exert a strong influence on environmental conditions, which may shape the size structure of the macrobenthos. NBSS of the macrobenthic communities in the study area were similar to those from other benthic ecosystems (e.g. Drgas et al. 1998, Saiz-Salinas & Ramos 1999, Quiroga et al. 2005, 2012, Hua et al. 2013). In our study area, we calculated an integrated NBSS (Fig. 6a), whose slope fell within the range ( $b = -0.43$ ,  $r^2 = 0.53$ ) of those reported for the Antarctic Peninsula by Saiz-Salinas & Ramos (1999), which ranged from  $-0.76$  to



Table 5. Slopes of the normalized biomass size spectra from different locations

Location	Geographic position	Environment	Slope	Reference
Livingston Island, Antarctic Peninsula	62° 43' S, 60° 29' W	Continental shelf	-0.71, -1.31	Saiz-Salinas & Ramos (1999)
Baltic Sea	54° 40' N, 19° 00' E	Continental shelf	-0.30, -0.60	Drgas et al. (1998)
Mississippi, USA	30° 30' N, 88° 30' W	Estuary	-0.25, -1.35	Rakocinski & Zapfe (2005)
Eastern South Pacific, Chile	22° 49' S, 70° 28' W	Oxygen minimum zone	-0.82	Quiroga et al. (2005)
Eastern South Pacific, Chile	42° 05' S, 74° 33' W	Continental shelf	-0.46	Quiroga et al. (2005)
Gulf of Maliakos, Mediterranean Sea	38° 52' N, 22° 30' E	Estuary	-0.47, -1, 03	Akoumianaki et al. (2006)
Eastern South Pacific, Chile	36° 25' S, 73° 07' W	Continental shelf	-0.63, -1.06	Sellanes et al. (2007)
Yangtze Estuary, China	31° 30' N, 121° 30' E	Estuary	-0.98, -1.17	Wang et al. (2010)
Baker Estuary, Chile	47° 74' S, 73° 35' W	Estuary-fjord	-0.17, -0.78	Quiroga et al. (2012)
East China Sea	38° 27' N, 118° 94' E	Continental shelf	-0.68, -0.71	Hua et al. (2013)
South Eastern Weddell Sea	70° 34' S, 10° 34' W	Continental shelf	-0.43	This study

-1.31 (Table 5). The slope value in our study area may indicate differences in the energy utilization within the macrobenthic communities among different Antarctic regions. It is important to note that these slopes of the normalized biomass spectra show an overall trend of increasing biomass with body size, which can be seen when the spectra are properly normalized. In other words, slopes of NBSS more positive than -1.2 imply increasing biomass with body size in the size range analyzed. Therefore, the body size of the macrobenthic community on the SEWS shelf (0.25 to 786 431 mg wet weight) is larger than those reported for the Antarctic Peninsula (0.25 to 768 mg wet weight: Saiz-Salinas & Ramos 1999). There are relationships between such biological and physical processes in the water column and the benthos (e.g. Gutt et al. 1998, Smith et al. 2006, Isla et al. 2009, Sañé et al. 2012). In the SEWS, a seasonal cycle of PP with high levels in spring ( $>400 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) and low levels in winter ( $<300 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) has been described (Bathmann et al. 1991, Arrigo et al. 2008). However, very low PP ( $15.6\text{--}41.5 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) was also reported in the study area during autumn. The higher macrobenthic standing stock in the study area suggests that benthic organisms rapidly utilize a large fraction of the OM derived from the PP (Isla et al. 2006). In addition, the rapid particle sinking with high nutritional values in combination with lateral advection by tidal forcing may provide fresh OM from a potential food bank that maintains the high biomass of the local macrobenthic communities (Sañé et al. 2012, Rossi et al. 2013). At the level of individuals or colonies, Antarctic benthic suspension feeders are efficient in organic carbon recycling (Gili et al. 2001). In fact, these suspension feeders are often the primary consumers and may influence other feeding guilds such as secondary consumers and

detritivores, and they therefore play an important role in the structuring and functioning of this high Antarctic benthic ecosystem (Gili et al. 2001).

The slope of the NBSS in our study indicated the prevalence of high biomass of suspension feeders (i.e. in particular the demosponges and tunicates) in the larger size classes of the spectrum. These results confirm that productivity might determine the shape and the taxonomic composition of the biomass size spectra on the SEWS shelf. The slope of the NBSS is an important index in evaluating marine pelagic ecosystem structure and its productivity (Sprules & Munawar 1986, Kerr & Dickie 2001, Quiñones et al. 2003). In fact, slopes higher than -1.0 indicate an ecosystem with high productivity (Sprules & Munawar 1986, Kerr & Dickie 2001). In the benthic system, Saiz-Salinas & Ramos (1999) pointed out that the slopes of the NBSS in the Antarctic Peninsula tend to be more negative with increasing depth as a response to a decreasing food supply from PP in the water column. This decrease is probably the result of a progressive weakening of the pelagic-benthic coupling along water depth profiles. It is known that the quantity and quality of exported OM flux from the euphotic zone through pelagic-benthic coupling may influence the structure and function of Antarctic shelf benthic ecosystems (e.g. Gutt et al. 1998, Mincks et al. 2005, Smith et al. 2006). The slope of the NBSS also indicates that in our study area, large suspension feeders dominate the macrobenthic communities. In contrast, macrobenthic communities living in deeper water seem to be dominated by other feeding guilds such as deposit feeders and omnivores, probably associated with a decrease in the concentration of chlorophyll *a* in the water column as has been observed in the Antarctic Peninsula region (Saiz-Salinas & Ramos 1999, Gutt et al. 2011). Indeed,

the low standing stock (i.e. abundance and biomass) in the macrobenthic communities along the eastern coast of the Antarctic Peninsula have been associated with a limitation in food supply due to ice coverage (Gutt et al. 2011, Sañé et al. 2012).

In the study area, the  $\delta^{13}\text{C}$  values of suspension feeders ( $-20.8 \pm 2.5$  and  $-26.7 \pm 0.6$ ) were lower than those of SPOM ( $-29.3 \pm 1.0$ ) in comparison to those reported by Gillies et al. (2013) for the Vestfold Hills. These results suggest that other carbon sources are incorporated by at least some of the suspension feeders. There are high temporal and spatial variabilities in primary food sources in other Antarctic regions (Norkko et al. 2007, Gillies et al. 2013). Norkko et al. (2007) showed that some bivalves could have variable diets in response to environmental gradients in food supply. In contrast, predator  $\delta^{13}\text{C}$  values were similar to other Antarctic shallow-water communities, showing that consumers occupy similar trophic levels. According to the  $\delta^{15}\text{N}$  signal, the trophic structure of the macrobenthic community in the study area shows 3 levels in the food web structure. This trophic structure is similar to that reported for the study area by Nyssen et al. (2002) and for other regions in Antarctica (e.g. Jacob 2005, Gillies et al. 2013), displaying a continuum of  $\delta^{15}\text{N}$  values from suspension feeders to predators. This pattern in the  $\delta^{15}\text{N}$  values suggests that few feeding guilds are coupled with specific food sources as has been proposed by Gillies et al. (2013). Sponges, tunicates, bryozoans, sedentary polychaetes, octocorals, and hydrozoans are the dominant macrobenthic groups in terms of biomass in the study area (Gerdes et al. 2008). All taxa mentioned above are suspension feeders and are considered to be closely coupled to the seasonal input of OM from the water column. In contrast, cephalopods, isopods, asteroids, nemerteans, and errant polychaetes were identified as predators, characterized by higher  $\delta^{15}\text{N}$  content ( $>9.2\%$ ). However, we found an overlap between  $\delta^{15}\text{N}$  values in omnivores and deposit feeding organisms, which might be associated with the amphipods. This group displays a continuum of guilds from suspension feeders to scavengers (Nyssen et al. 2002). In addition, omnivores and deposit feeders appear separate on the  $\delta^{13}\text{C}$  axis, which might be related to different food sources, or deposit feeders assimilate specific fractions of OM (e.g. resuspended by bottom near currents) as has been suggested by Gillies et al. (2013).

Size-based nitrogen stable isotope analysis has been used to quantify intra- and inter-specific variation in trophic levels in many marine ecosystems (e.g. Fry & Quiñones 1994, Kerr & Dickie 2001, Jen-

nings et al. 2002). In the pelagic system, the first empirical study using nitrogen stable isotopes in size-fractionated plankton samples was realized by Fry & Quiñones (1994). The results of that study indicated a large degree of trophic level overlap among various zooplankton size classes and an increase in trophic level with increasing size in the mesozooplankton community. This trophic organization is related to many energetic processes, which can be used to predict slopes of size spectra in complete food webs and subsets of those webs (Kerr & Dickie 2001, France 2014). In relation to benthic size spectra, there are limited studies on the role of inter-specific relationships between body size and trophic level in a benthic community (France et al. 1998, Jennings et al. 2002). We found that the relationship between the trophic position and body size for benthic organisms from different taxonomic groups can be used to describe the trophic structure of the community. Jennings et al. (2002) demonstrated that body mass was positively and significantly related to trophic levels as a consequence of intra-specific increases in trophic levels with body mass rather than the higher trophic levels of species (inter-specific levels) with larger body mass. This pattern is similar to those reported for tropical (Layman et al. 2005) and temperate estuarine food webs (Akin & Winemiller 2008), indicating that trophic position may positively covary with predator body size (France 2014). However, in our study area, the linear relationship between trophic level and body mass was not significant ( $r^2 = 0.08$ ,  $p > 0.05$ ) due to the presence of large suspension feeders, in particular demosponges and tunicates. In this sense, the residual distribution (i.e. domes of biomass) might be very useful to describe the community trophic structure (Dickie et al. 1987, Quintana et al. 2002). In our study area, we found 4 well-defined domes of biomass (i.e. ascending residuals), which belonged to different functional groups (sensu Dickie et al. 1987). These domes of biomass appear when large benthic species are abundant in an ecosystem (Quiroga et al. 2005). Sponges and tunicates dominated suspension feeders with maximal positive residuals, which are especially favored in an environment with high OM fluxes in the study area (Gili et al. 2001). The  $\delta^{15}\text{N}$  values of these suspension feeders are typical and resemble those reported in other studies (e.g. Gillies et al. 2013). The same situation occurs with anthozoans and holothurians, which constituted another dome of biomass, characterized by  $\delta^{15}\text{N}$  values ranging from 7.5 to 7.6‰. In contrast, size class 5 is composed mainly of ophiuroids, nemerteans, and errant polychaetes, exhibit-

ing a wide range of  $\delta^{15}\text{N}$  values (7.6–9.8‰), which could be associated with the high contribution of deposit feeders and predators to intermediate size classes of the benthic community. Bivalves exhibited similar  $\delta^{15}\text{N}$  values to those observed in holothurians and anthozoans (see Table 2), but the individual growth rates and annual P:B ratios in bivalves seem to be influenced more by temperature than by food supply (Brey & Hain 1992).

In the pelagic system, dome-like patterns in the biomass size spectra have been observed in several ecosystems (e.g. Sprules & Munawar 1986, Quiñones et al. 2003). According to Dickie et al. (1987), 2 kinds of slopes in the relationships between log-specific production and log-body size can be identified: a primary slope, which reflects the size dependence of metabolism, and a secondary slope, which represents an ecological scaling of production related to rapid changes of log(annual specific production) with log(body size) within groups of organisms with similar production efficiencies (Quiñones et al. 2003). In fact, this secondary slope would produce dome-like patterns in the biomass size spectra (Kerr & Dickie 2001). In this sense, Quintana et al. (2002) described the presence of domes in aquatic communities where positive biomass residuals were related to high densities of large species. In the benthic system, there are limited studies on the dome-like patterns. Quiroga et al. (2005) identified dome-like patterns, which were related to functional groups of organisms living in the oxygen minimum zone off central Chile. These functional groups were identified as positive biomass residuals, which are composed of a few polychaete species of small body size such as *Aricidea pigmentata* and *Mediomastus branchiferus*. These species have been previously described as highly abundant in habitats associated with low oxygen environments and high concentration of OM (Quiroga et al. 2005). In the study area, the observed relationship between  $\delta^{15}\text{N}$  and standardized residuals for the whole benthic community suggests that domes of biomass represent functional groups comprising organisms with different trophic levels. Suspension feeders are expected to account for the largest proportion of total biomass, but this is not consistent with the increase in trophic level with body size (France et al. 1998, Jennings et al. 2002). However, the role of sponges, tunicates, and many others organisms in the size-based epibenthic food webs we studied is far from clear.

In view of climate change, environmental alterations detected so far in the Southern Ocean resemble many of those observed on a worldwide scale. In

this sense, glacier retreat, currently observed both in the Arctic and in the Antarctic, is accompanied by an increase in meltwater outflow with high levels of particulate mineral material (e.g. Gorlich et al. 1987, Włodarska-Kowalczyk et al. 2005, Sicinski et al. 2012). Arctic tidal glaciers are among the most studied ecosystems in the northern hemisphere (e.g. Gorlich et al. 1987, Włodarska-Kowalczyk et al. 2005, Węśławski et al. 2011). Macrobenthic communities in Arctic tidal glaciers are exposed to chronic physical disturbance, which are also often accompanied by changes in macrobenthic biomass, feeding modes, mean size of organisms, and diversity patterns along the gradient of glacier-induced disturbance (e.g. Włodarska-Kowalczyk et al. 2005). However, the trends observed in the diversity patterns are difficult to generalize and depend on the nature of the stress-generating factors, as has been recorded by Włodarska-Kowalczyk et al. (2005). For instance, those authors described a clear pattern for macrobenthic fauna along the gradient of glacial disturbance by the Kongsbreen glacier: small-bodied bivalves and polychaetes appeared to dominate in the glacial front, but in the central area, macrobenthic associations were characterized by the dominance of large tube-dwelling polychaetes such as maldanids and spionids. In contrast, in the Baker Fjord (Chilean Patagonia), small-bodied polychaetes, characterized by continuous year-round breeding, short life spans, and fast turnover rates, were observed probably associated with the Baker River, which is characterized by frequent deposition and resuspension of phytodetritus, vascular plant fragments, and other suspended particles in the near-bottom water layer (Quiroga et al. 2012). For this reason, a simplification of the functional structure of these disturbed communities may be more useful in order to obtain an ecological indicator estimated in a straightforward manner from standing macrobenthic samples. Within the Antarctic ecosystems, the macrobenthos with its unique species and biomass rich communities might be directly modified by human activities, climate change, and/or natural variability induced by grounding of icebergs (Ingels et al. 2012). In this scenario, more knowledge on Antarctic benthic ecology is needed for the development and application of appropriate conservation measures in Antarctica (Griffiths 2010). The relationship between trophic levels and domes of biomass might be used to identify changes in the trophic structure of disturbed macrobenthic communities and to assess the environmental impact of disturbance associated with natural variability or climate change in marine ecosystems.

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## Appendix

Table A1. Species collected with either Agassiz or benthopelagic trawls or traps during this study

Phylum Class Family	Species	Phylum Class Family	Species
Porifera		Annelida	
Demospongiae		Polychaeta	
Hymedesmiidae	<i>Kirkpatrickia variolosa</i>	Ampharetidae	<i>Phyllocomus crocea</i>
Stylocordylidae	<i>Stylocordyla borealis</i>	Aphroditidae	<i>Laetmonice producta</i>
Tetillidae	<i>Cinachyra antarctica</i> <i>Cinachyra barbata</i>	Maldanidae	<i>Maldane</i> sp.
Hexactinellida		Nephtyidae	<i>Aglaophamus</i> sp.
Rossellidae	<i>Rossella antarctica</i> <i>Rossella nuda</i> <i>Rossella racovitzae</i>	Polynoidae	<i>Barrukia cristata</i> <i>Eulagisca gigantea</i> <i>Eunoe gigantea</i> <i>Eunoe</i> sp. <i>Harmothoe spinosa</i> <i>Polyeunoa laevis</i> <i>Polynoe</i> sp. Unidentified
Cnidaria		Terebellidae	
Anthozoa		Arthropoda	
Actiniidae	<i>Isosicyonis alba</i>	Malacostraca	
Actinostolidae	<i>Hormosoma</i> spp.	Aegidae	<i>Aega antarctica</i>
Isididae	<i>Primnoisis</i> sp.	Ampeliscidae	<i>Ampelisca richardsoni</i> Unidentified
Primnoidae	<i>Ainigmaptilon antarcticum</i> <i>Armadillogorgia cyathella</i> <i>Fannyella (Fannyella) rossii</i> <i>Primnoella</i> sp. <i>Thouarella</i> sp.	Calliopiidae	<i>Oradarea</i> sp. <i>Oradarea tridentata</i> <i>Glyptonotus antarcticus</i> <i>Natatolana obtusata</i> <i>Colossendeis</i> sp.
Umbellulidae	<i>Umbellula pallida</i> <i>Umbellula</i> sp.	Chaetiliidae	<i>Notocrangon antarcticus</i>
Nemertea		Cirolanidae	<i>Epimeria similis</i>
Anopla		Colossendeidae	<i>Euphausia crystallorophias</i>
Lineidae	<i>Lineus longifissus</i> <i>Parborlasia corrugatus</i>	Crangonidae	<i>Eusirus perdentatus</i> Unidentified
Valenciiniidae	<i>Baseodiscus antarcticus</i>	Epimeriidae	<i>Monoculodes scabriculosus</i>
Mollusca		Euphausiidae	<i>Chorismus antarcticus</i>
Bivalvia		Eusiridae	<i>Themisto gaudichaudii</i> <i>Iphimediella</i> sp. Unidentified Unidentified
Carditidae	<i>Cyclocardia astartoides</i>	Lysianassidae	<i>Orchomenella</i> sp. <i>Pseudorchomene plebs</i> <i>Pseudorchomene rossi</i> <i>Tryphosella</i> sp. <i>Waldeckia obesa</i> <i>Paraceradocus</i> sp.
Limopsidae	<i>Limopsis marionensis</i>	Maeridae	<i>Antarctomysis maxima</i>
Philobryidae	<i>Lissarca notorcadensis</i>	Mysidae	<i>Nematocarcinus lanceopes</i> <i>Nematocarcinus longirostris</i>
Cephalopoda		Nematocarcinidae	<i>Prostebbingia brevicornis</i> <i>Ceratoserolis meridionalis</i> <i>Frontoserolis bouvieri</i>
Psychroteuthidae	<i>Psychroteuthis glacialis</i>	Pycnogonida	
Vampiroteuthidae	Unidentified	Nymphonidae	<i>Nymphon hiemale</i> <i>Pentanympion antarcticum</i>
Gastropoda		Echinodermata	
Capulidae	<i>Torellia mirabilis</i>	Asteroidea	
Cochlespiridae	<i>Aforia magnifica</i>	Asteroidea	
Fissurellidae	<i>Parmaphorella mawsoni</i>	Asteriidae	<i>Diplasterias</i> sp.
Velutinidae	<i>Marseniopsis conica</i> <i>Marseniopsis mollis</i> <i>Harpovoluta charcoti</i>	Astropectinidae	<i>Bathybiaster loripes</i> <i>Macroptychaster accrescens</i>
Volutidae		Ganeriidae	<i>Cuenotaster involutus</i> <i>Cuenotaster</i> sp.
Polyplacophora			
Ischnochitonidae	<i>Tonicina zschau</i>		
Mopaliidae	<i>Nuttallochiton mirandus</i>		
Echiura			
Echiuroidea			
Bonelliidae	<i>Alomasoma belyaevi</i> <i>Hamingia</i> sp. <i>Maxmuelleria faex</i> <i>Echiurus antarcticus</i>		
Echiuridae			
Priapulida			
Unidentified			
Unidentified	Unidentified		
Sipuncula			
Sipunculidea			
Golfingiidae	<i>Golfingia</i> sp.		

Table A1 (continued)

Phylum Class Family	Species	Phylum Class Family	Species
Heliasteridae	<i>Labidiaster annulatus</i>		<i>Psolidium poriferum</i>
Odontasteridae	<i>Acodontaster conspicuus</i>		<i>Psolus antarcticus</i>
	<i>Acodontaster hodgsoni</i>		<i>Psolus dubiosus</i>
Poraniidae	<i>Porania antarctica glabra</i>		<i>Psolus</i> sp.
Solasteridae	<i>Lophaster</i> sp.	Synallactidae	<i>Bathyplores bongraini</i>
	Unidentified		<i>Bathyplores</i> spp.
Crinoidea		Ophiuroidea	
Antedonidae	<i>Anthometrina adriani</i>	Gorgonocephalidae	<i>Astrotoma agassizii</i>
	<i>Promachocrinus kerguelensis</i>	Ophiolepididae	<i>Ophioceres incipiens</i>
Unidentified	Unidentified	Ophiuridae	<i>Ophionotus victoriae</i>
Echinoidea			<i>Ophioplithus brevissima</i>
Echinidae	<i>Sterechinus antarcticus</i>		<i>Ophioparte gigas</i>
	<i>Sterechinus neumayeri</i>		
Schizasteridae	<i>Abatus curvidens</i>	Bryozoa	
Unidentified	Unidentified	Gymnolaemata	
Holothuroidea		Alcyonidiidae	<i>Alcyonidium</i> sp.
Chiridotidae	<i>Sigmodota contorta</i>	Bugulidae	<i>Camptoplites tricornis</i>
Cucumariidae	<i>Heterocucumis steineni</i>	Eminoeciidae	<i>Isoschizoporella tricuspis</i>
	<i>Staurocucumis</i> sp.	Flustridae	Unidentified
Elpidiidae	<i>Rhipidothuria racovitzai</i>	Chordata	
Paracucumidae	<i>Paracucumis turricata</i>	Asciacea	
Psolidae	<i>Echinopsolus acanthocola</i>	Polyclinidae	<i>Synoicum</i> sp.
		Styelidae	<i>Cnemidocarpa</i> spp.

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