

Biomass size-spectra of macrobenthic assemblages along water depth in Antarctica

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ABSTRACT: Several biomass size spectra of benthic assemblages were constructed along a water depth gradient on the southern coast of Livingston Island (South Shetland Islands, Antarctica). The size-spectrum for shallow bottoms (<100 m depth) was bimodal with peaks in the 32–64 and 512–1024 g weight-classes, a feature which was attributable to the existence of large filter-feeders. By contrast, both intermediate (100–200 m) and deep (>200 m) zones showed unimodal spectra with biomass peaks in the 1–2 and 0.5–1 g weight ranges respectively. Filter-feeders also affected the larger size classes at intermediate depths, whereas they were almost absent in deeper waters. The slope of the normalized size-spectrum at shallower bottoms (–0.76) was different from those of intermediate (–1.25) and deeper (–1.31) zones. This clearly indicated 2 contrasting faunal strategies: a biomass increase with size in shallow waters, whereas the biomass decreased with size in deep waters. Estimates of total secondary production were calculated using allometric equations published in the literature. Results indicated a decrease of total secondary production along water depth, with 15 g C m⁻² yr⁻¹ in shallow waters, 9 g C m⁻² yr⁻¹ at intermediate bottoms and 8 g C m⁻² yr⁻¹ at deep bottoms. The pattern of the biomass size spectrum for shallower waters suggested that there was a predictable and regular supply of food, which allowed accumulation of biomass in the larger size classes corresponding to filter-feeder organisms. Conversely, the concentration of biomass in smaller size classes of the spectra for intermediate and deeper waters pointed to more unpredictable and fluctuating food conditions arriving from the overlying layer to the deeper sea floor. Sufficient evidence exists in the literature to indicate that a tight pelagic-benthic coupling was causing biological enhancement of a suspension-feeding macrofauna at shallow bottoms, and that below 100 m depth the effects of the coupling were rather weak.

KEY WORDS: Biomass size spectra · Benthic macrofauna · Total production · Antarctica

INTRODUCTION

Traditional taxon-based approaches to the study of marine benthic assemblages have a procedure which consists basically of identifying, counting and weighing all the specimens collected during faunal surveys. It was originally developed for descriptive ecological studies (Kingston & Riddle 1989) and since then has been applied with little modification to many studies of the marine benthos. However, the taxonomic identification of benthic macrofauna to species is a time-consuming activity and requires considerable expertise

(Ellis 1985, Warwick 1988). Without the cooperation of large teams of taxonomists, it is almost impossible to compile a complete and reliable list of all the invertebrate species collected. This problem is exacerbated in remote areas such as Antarctica, where invertebrate taxonomy is still in its early stages of integration (Picken 1985, Arntz et al. 1997). As a result, benthic studies are often incompletely presented with identifications at higher levels of classification and with few insights (in relation to all the work invested) into the system functioning of the investigated ecosystems.

Non-taxonomic approaches may offer useful and cost-effective alternatives. Allometry, which has been defined (Reiss 1989) as any study of size and its conse-

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quences, has revealed that most biological processes are scaled to the size of organisms. This easily measurable condition of animals is the most extensive and powerful assemblage of generalizations for use in ecology (Peters 1983). Many topical studies in marine benthic research explore similarity among sampling sites by using coefficients such as the Bray-Curtis, which compares samples by their specific composition and abundance (or biomass) values. Alternatively, allometric ecology introduces a major premise, known as 'principle of similitude', whereby body size of organisms can be used as a major criterion of similarity. This indicates that all organisms of the same size, independent of their taxonomical identity, will behave approximately in the same way in bioenergetic terms. Organisms are then aggregated into more or less complex communities, which are, at a global level, even more sensitive to changes in the environment (Diaz 1992). Particularly, benthic assemblages are interesting because they represent a biome where body size varies widely (Strayer 1991). As a result of integration over time, macrobenthic assemblages tend to accumulate biomass in the larger size classes (Sprules & Munawar 1986, Rasmussen 1993). In contrast, standing stocks of biomass remain comparatively low under perturbed conditions. Thus, global measures of community biomass, the most basic parameter in any investigation of community energetics, may provide a new dimension of time, a feature which indicates 2 fundamental aspects of an ecosystem: its stability versus unpredictability.

Spectral methods are useful in separating the total biomass of a given community into major classes of organism size, regardless of its taxonomic composition. This allows visualization of the effects of body size in the plot of total biomass. The technique proposed by Sheldon & Parsons (1967) was suggestive and was applied to many different ecological situations (see for instance Macpherson & Gordoia 1996). A number of authors (from Schwinghamer 1981, 1983 to Thurston et al. 1994) have tested the applicability of the model to marine benthic communities. They identified several peaks and troughs in the size distributions, which represented generally the optimal size categories for the different benthic life-styles. To our knowledge, the only polar applications of the Sheldon model are those of Hardy (1972), Warwick (1984) and Kendall et al. (1997), some of them unfortunately fragmentary. The latter authors speculated the influences of larval biology in the species size spectra, and stressed the necessity of examining new information on Antarctica. The general objective of this study was to investigate the shape and slope of the size distribution of benthic biomass along water depth when applied to an extreme situation such as the polar environment.

MATERIAL AND METHODS

Study area. A total of 73 stations located on the southern coast of Livingston Island (Fig. 1) from depths between 32 and 421 m was investigated. Samples were

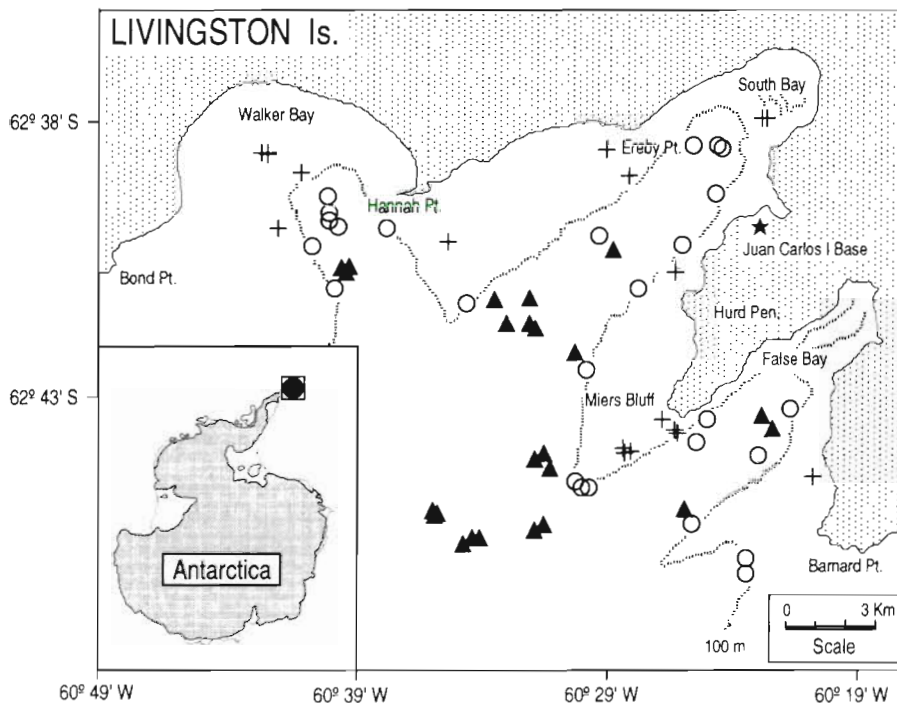


Fig. 1 Location of sampling sites on the southern coast of Livingston Island. (+) Shallow water (<100 m) sampling sites; (O) sites from intermediate depths (100–200 m); (▲) deep water (>200 m) sampling sites. Inset indicates the position of Livingston Island in Antarctica

taken during 2 austral summer cruises in 1994 and 1995 using a van Veen grab of 0.1 m² of sampling area operated from the Spanish RV 'Hesperides'. Benthic organisms were extracted by gently washing the sediment through a 1 mm square aperture sieve. Organisms were sorted by higher taxa and approximate size groups. Their biomasses were calculated on the basis of blotted wet weights (WW), as the material was later preserved in 5% buffered formalin for distribution among taxonomists in Spain.

Data analysis. Biomass size-spectra (BSS) were calculated separately, pooling data from stations over the following depth intervals: <100 m, 100 to 200 m, >200 m. The total BSS for each depth range was determined by summing individual biomasses in each of the log₂-based size classes. To facilitate comparison of the plotted spectra, the biomass in each class was converted to percentage of the total biomass for each depth range (Hanson 1990). Strict filter-feeders (Porifera, Bryozoa and Ascidiacea) were also separately represented in the BSS diagrams as a percentage of the total biomass in each size class range.

The normalized size-spectra were determined by regressing the log₂[(total biomass in size class)/(weight range of the interval)] against the log₂ of the upper limit of the size class following Sprules & Munawar (1986) and Hanson (1990). The slopes of these regression lines can then be used to characterize biomass trends across the size spectrum and simplifies further comparisons between assemblages (Sheldon et al. 1977, Sprules & Munawar 1986). Differences among slopes were tested according to Zar (1984). If significant differences were found ($p < 0.05$), then a Tukey multiple comparison test was used to determine which slope was different from which others.

Estimates of community production by size class were approached following the schemes of Sheldon et al. (1972), Schwinghamer (1981) and Schwinghamer et al. (1986). Calculations were performed using the allometric equation of Tumbiolo & Downing (1994). They improved the empirical relation of Brey (1990), based on population characteristics, by also including effects of water temperature and depth. Therefore, production was calculated by:

$$\log P = 0.18 + 0.97 \log B - 0.22 \log W_m + 0.04 T_b - 0.014 T_b \log(Z + 1)$$

where biomass (B) was given in g DW m⁻², maximum individual body mass (W_m) in mg dry mass, temperature (T_b) at the bottom in °C, and depth (Z) in meters. A wet-to-dry mass conversion factor of 0.1 was applied (Rowe 1983). Production values of all size classes were then summed to estimate total community production.

RESULTS

Size spectra

The total biomass was higher in shallow bottoms (with an overall mean of 2130 g WW m⁻²) than in intermediate (overall mean 680 g WW m⁻²) and deep bottoms (overall mean 520 g WW m⁻²). Biomass in spaced size classes varied substantially among depths (Fig. 2). In the shallow water zone, there was a biomass peak in the 32–64 g weight class, due to the dominance of fil-

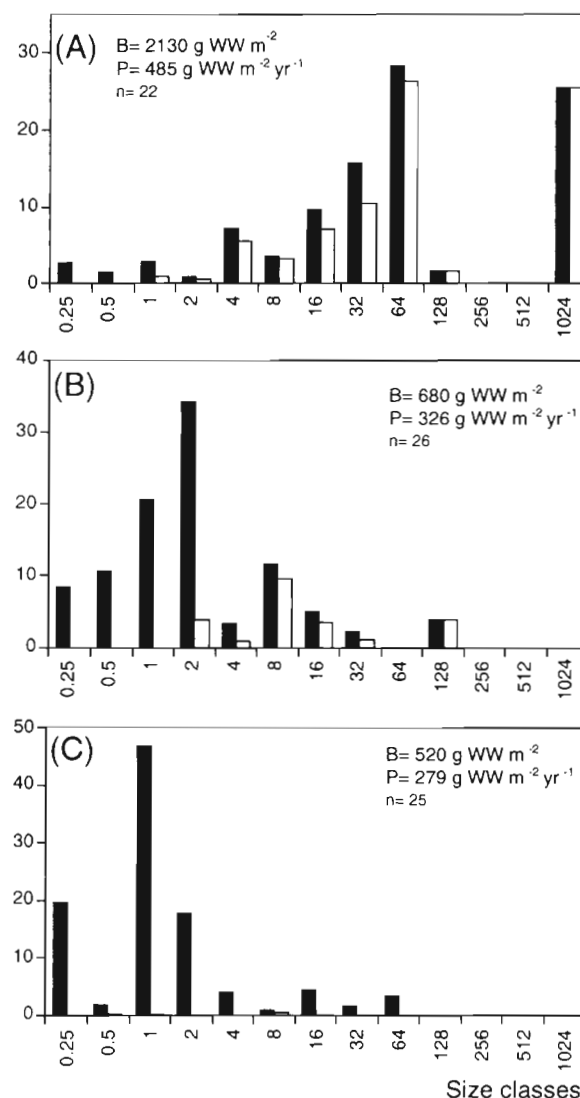


Fig. 2. Mean biomass size-spectra for the macrobenthic assemblages (shaded bars) of Livingston Island: from: (A) shallow water (<100 m) sites; (B) sites from intermediate depths (100–200 m); (C) deep water (>200 m) sites. Filter-feeders (open bars) are shown as a percentage of the shaded bars. Total biomass (B in g m⁻², wet weight) and production (P in g m⁻² yr⁻¹, wet weight) are shown in each plot. Size-classes are in grams, wet weight. n : number of stations sampled

ter-feeders (mainly ascidians) in the larger size classes. In this way, the existence of a few individual sponges introduced a bimodal pattern, with the other biomass peak in the 512–1024 g class. By contrast, both intermediate and deeper zones were characterized by biomass peaks in the 1–2 and 0.5–1 g weight ranges respectively. Filter-feeders were still present in the histograms of the larger size classes at intermediate depths, but almost absent at deeper depths. Clearly, there was a larger portion of the total biomass concentrated in the larger size classes at shallower bottoms (92% between the 5 and 13th size classes) than at both intermediate and deep bottoms, where 74 and 86% of the total biomass belonged to the 1st to 4th size classes respectively.

Normalized size spectra

Normalized spectra (Fig. 3) were computed using base 2 logarithms in both axes. They allowed easier comparisons of biomass distributions among those investigated benthic assemblages along water depth. All the regressions were highly significant ($p < 0.001$) and the residual variations were small ($R^2 = 0.83$ to 0.91). Significant differences among slopes of the normalized size-spectra were found ($F = 4.98$, $p < 0.025$). The slope from shallower waters (-0.76) was different from those of the intermediate (-1.25) and deep (-1.31) zones (Tukey multiple comparison test: $q = 4.71$ and $q = 3.92$, $p < 0.025$, respectively). In contrast, no significant differences were found between slopes from the intermediate and deep zones (Tukey multiple comparison test: $q = 0.51$, $p > 0.5$). Less negative slopes were correlated with increases of biomass to larger sized organisms. This indicated 2 contrasting situations: a biomass increase with size at shallower bottoms, whereas the biomass decreased with size in deeper waters. The shift in slopes along water depth denoted a drastic change in the organization level of the overall benthic system.

Total secondary production of the assemblages

Total production estimates were derived from measures of total biomass and maximum individual body mass in each size class of the spectra. Measures of temperature at the bottom were about 0°C in the investigated area, so the effects of temperature and depth were eliminated in the multiple linear regression. The values of total production showed a decreasing pattern along water depth from $41 \text{ g DW m}^{-2} \text{ yr}^{-1}$ in shallow waters to $22 \text{ g DW m}^{-2} \text{ yr}^{-1}$ at deep bottoms, passing by $25 \text{ g DW m}^{-2} \text{ yr}^{-1}$ at intermediate depths. Most of the

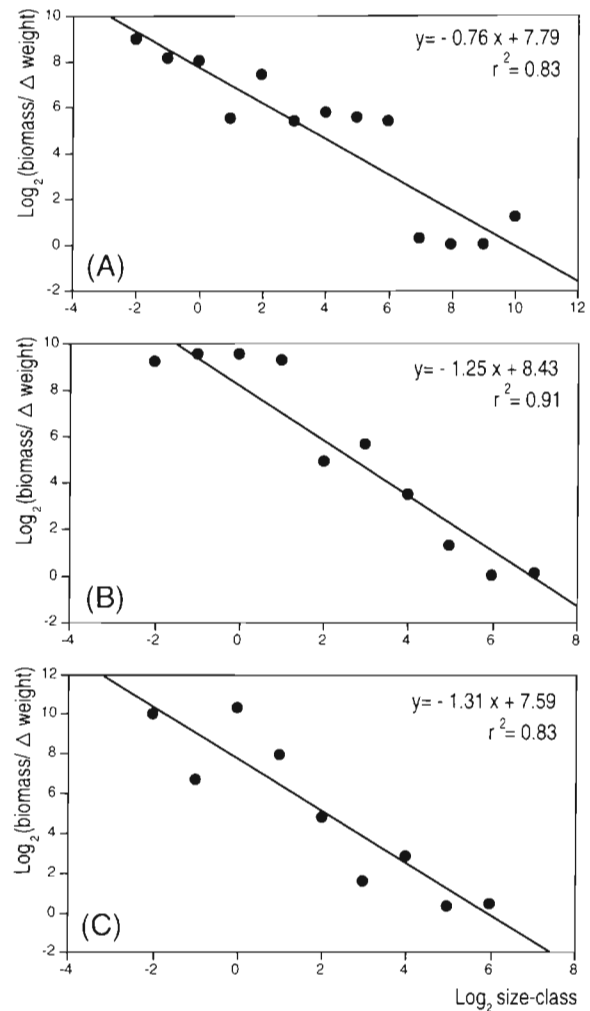


Fig. 3. Normalized size-spectra for the macrobenthic assemblages of Livingston Island from: (A) shallow water (<100 m) sites; (B) sites of intermediate depths (100–200 m); (C) deep water (>200 m) sites. All regressions are highly significant ($p < 0.001$)

total production (63%) on shallow bottoms resulted from larger size classes (from 7 to 13), whereas on intermediate and deep bottoms smaller size classes (from 1 to 4) contributed 83 and 92% of total production, respectively.

P/B ratios were derived from measures of total biomass and production for each size class of the spectra. They varied from 0.57 (1st size class) to 0.08 (13th size class). The P/B ratio, also called turnover rate, gave an indication of temporal stability in the investigated assemblages. Thus, the bimodal pattern detected in the size spectrum (Fig. 2a) on shallower bottoms, with biomass peaks in the 9th and 13th classes, indicated that assemblages are influenced by large body-size individuals which needed at least 6 to 12 yr of food regularity for the renewal of their biomasses. By contrast,

intermediate (Fig. 2b) and deeper (Fig. 2c) bottoms showed the dominance of smaller organisms in the 1st to 4th classes, a feature which indicated a narrower span in the turnover biomass times of 1.5 to 3 yr approximately.

DISCUSSION

The size structure of benthic assemblages and their total annual production varied with water depth at the southern coast of Livingston Island. This produced a vertical depth segregation of 2 major benthic assemblages, with predominance of large filter-feeders in shallow waters, whereas smaller invertebrates colonized the deeper waters. Similar zonal patterns have been reported on shelf waters around South Shetland Islands (Jazdzewski et al. 1986, Saiz-Salinas et al. 1997, Arnaud et al. 1998), although they are less conspicuous in high Antarctic areas, where ice shelves permanently cover shallow bottoms near the coast (Arntz et al. 1994). A relation between body size and food availability was first introduced by Thiel (1975), who found that a limited food supply to the sea floor favoured the predominance of smaller organisms in deeper waters. Other authors corroborated the existence of an overall trend for animal miniaturization with increasing water depth and decreasing food availability (Soltwedel et al. 1996 and references therein). In fact, Richardson & Young (1987) showed benthic biomass concentrations in the larger size classes of the spectra on shallow bottoms, whereas on deep bottoms the biomass peaked in the smaller size classes in the spectra. These varying patterns were also related to different food availabilities and feeding strategies along water depth.

The bimodal nature of the shallow water spectrum and the accumulation of biomass in larger size classes are features which point to a greater regularity and predictability of the food resources. Sufficient evidence exists in the literature to indicate that a tight benthic-pelagic coupling in Antarctic shelf waters (Clarke 1985) creates feeding conditions suitable for the sustenance of large filter-feeder consumers. The loss of metabolic efficiency by benthic assemblages along water depth was well exemplified by unimodal size spectra with biomass dominances in the smaller weight-classes. This indicated the prevalence of more fluctuating and unpredictable trophic conditions for benthic assemblages on deep bottoms, as a result of a progressive weakening of the pelagic-benthic coupling along water depth. In such circumstances, there was a marked decline of filter-feeders, which still influenced the larger size classes at intermediate depths (100–200 m), but were practically absent in deep waters (>200 m). The decrease in size with increasing

depth was attributed to a lower maintenance cost in small organisms (Thiel 1975), since food limitation prevents the high food consumption typical of larger organisms.

Total biomass in pelagic assemblages is often distributed relatively equitably among size classes in aquatic systems (Sheldon et al. 1977), with slopes for normalized size distributions close to -1 . Departures from this condition were related to overall production, after noting a decrease of the regression slopes with an increasing eutrophy in several freshwater ecosystems (Sprules & Munawar 1986). This observation accords well with the regression slopes obtained in this study. More negative slopes are found at intermediate (100–200 m) and deep (>200 m) bottoms, where benthic assemblages are dependent on the sedimentation regime of particulate matter settling from the overlying water column. Once biogenic material reaches the seabed, it contains much skeletal and other refractory substances which are of lower nutritional value for the benthos (Barnes & Hughes 1988). By contrast, on shallow bottoms the regression slope is less negative due to the more eutrophic conditions. A strong interaction between primary producers and benthic consumers, especially filter-feeders, would explain the biomass accumulation in the large size-weight classes of the spectrum. In fact, filter-feeder biomass differences between shallow and intermediate waters were scaled by a factor of 10. The loss of filter-feeder biomass with depth can be related to a decrease in the concentration of chlorophyll *a* in the water column, from higher values at the surface ($1.47 \mu\text{g l}^{-1}$) to lower values at 100 m depth ($0.35 \mu\text{g l}^{-1}$) (Agustí pers. comm.). Apparently, the absence of a productive phytoplankton in deeper waters would explain the reduction of filter-feeders with water depth. It is evident that a benthic assemblage dominated, in terms of biomass, by larger organisms could not be sustained unless the assemblage exploited a resource from outside its own window in the spectrum of biomass; in this case, a higher pelagic production in the water column.

Gaining an understanding of the dynamics of benthic assemblages is difficult in remote areas such as Antarctica. Allometric ecology, which is an interface field between both disciplines, can be used as a cost-effective alternative, developing relations to permit simpler and more rapid estimates of total secondary production scaled with size (Schwinghamer 1981, Schwinghamer et al. 1986). Precisely, this is the principal advantage of the Tumbiolo & Downing (1994) empirical formula, since total production appears as a final numerical value which contains 2 powerful variables of community structure (biomass and body size corrected for water temperature and depth). In this study, the overall production differences between shallow and deep bottoms can be scaled approximately by

a factor of 2. This difference may be explained by different availabilities in food supply to the bottom fauna along water depth. In fact, Brey & Clarke (1993), analysing a large data array of polar and non-polar invertebrates, concluded that the peculiar population parameters exhibited by Antarctic invertebrates were explained both by adaptations to strong seasonal oscillating food levels and by low temperatures.

Most benthic research includes production values such as carbon or ash-free dry weights, which makes direct comparisons of total production difficult. Assuming infauna are approximately 37.5% organic carbon by dry weight (Rowe 1983), the overall mean production of Livingston Island can be converted from 29 g DW m⁻² yr⁻¹ to 11 g C m⁻² yr⁻¹. Compared with the production estimates calculated by Brey & Gerdes (1997) for the high Antarctic latitudes (3.6 g C m⁻² yr⁻¹) and for the Magellan area (5.1 g C m⁻² yr⁻¹), the averaged production estimate for Livingston Island is much higher, but falls within the range of the production estimates (0.3 to 11 g C m⁻² yr⁻¹) compiled by Arntz et al. (1994) for a few Antarctic biotopes. Because our analysis is indirect and involves several approximations, assumptions and conversions, the numerical results are likewise approximate and should be interpreted cautiously. Nonetheless, the results are sufficiently robust to support several broad conclusions about energy flow in the zoobenthos off Livingston Island and they give some perspective on the overall shifts in system-wide secondary production along water depth. Other applications of the BSS derive from the fact there is a relation between the slope of the spectra and the turnover times of organisms of different body sizes (Sheldon et al. 1972, Schwinghamer 1981, Schwinghamer et al. 1986). Estimated *P/B* ratios for larger size classes showed the existence of some biomass maxima, integrated by slow-growing and long-lived organisms, which needed on the order of 12 yr of environmental stability and food regularity to achieve this size. In spite of the limitations and simplicities of the BSS, they allow inferences to be drawn about the general structure and dynamics of benthic assemblages on Livingston Island.

In conclusion, there exists a natural gradient of benthic assemblages from shallow waters to the greatest depths. In all these environments, the distribution of benthic biomass by size revealed 2 contrasting faunal strategies. When the supply of particulate matter to the bottom was high, as in shallow waters, large filter-feeders influenced the large size classes of the spectra. By contrast, the domination of smaller size classes appeared in relation to a limited organic supply on deep bottoms. Both BSS and NBS were useful descriptors for understanding the system function and for estimating difficult parameters such as whole-community production scaled to organism size.

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