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Population dynamics of *Sterechinus antarcticus* (Echinodermata: Echinoidea) on the Weddell Sea shelf and slope, Antarctica

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Abstract: *Sterechinus antarcticus* inhabits the shelf and the slope of the Weddell Sea and is the predominant echinoid between 450 and 1200 m. Growth lines visible in the half pyramids of the Aristotle's lantern were interpreted as annual growth marks. A Von Bertalanffy growth function was fitted to age-diameter data of 217 specimens ($D_\infty = 82.4$ mm, $K = 0.017$ y^{-1}, $t_0 = 1.633$ y). Based on 92 trawl samples, a representative size-frequency distriution of *S. antarcticus* was established. From the growth curve, the size-frequency sample and diameter - weight regressions, mortality and somatic productivity of *S. antarcticus* were calculated by a size-converted catch curve and the weight specific growth rate method. Gonadal productivity was estimated by an average value for reproductive output of cold water echinoderms. Mortality rate Z as well as somatic P/B ratio amounted to 0.07 y^{-1}. Annual somatic production was estimated as 0.3 mg m^{-2} y^{-1}, and annual gonadal production as 0.25 mg m^{-2} y^{-1} between 100 and 1200 m (0.6 and 0.5 mg m^{-2} y^{-1} between 450 and 1200 m).

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Introduction

Population dynamics of marine benthic invertebrates are of particular interest in Antarctic benthic ecology because of the high biomass in various Antarctic benthic habitats (Gallardo & Castillo 1969, George 1977, Hardy 1972, Jazdzewski *et al.* 1986, Platt 1979, White & Robins 1972), and with respect to metabolic or behavioural adaptations to conditions specific to the Antarctic environment (see Clarke 1988, White 1984). Our knowledge of growth and productivity of Antarctic benthic invertebrates is limited to shallow-water sites (Dayton *et al.* 1974, Everson 1977, McClintock *et al.* 1988, Ralph & Maxwell 1977, Stockton 1984), and nothing is known from deeper shelf, slope or abyssal plain areas.

Sterechinus antarcticus inhabits the shelf and slope around the Antarctic continent (Pawson 1969). In the Weddell Sea, two species of the genus, *S. neumayeri* and *S. antarcticus*, occur between 100 and 1200 m water depth. *S. neumayeri* is more frequent in the shallower areas, but *S. antarcticus* is the dominant echinoid below 450 m (Brey & Gutt in press). A motile organism and feeding primarily on superficial sediments and bryozoans, (De Ridder & Lawrence 1982) it may play an important role in the Antarctic benthic interaction web and trophic web (Lawrence & Sammarco 1982).

Methods

Investigation area and sampling

Between 1983 and 1988, 92 trawl samples were taken by RV *Polarstern* on the eastern and southern shelf and slope of the Weddell Sea (Fig.1). An Agassiz trawl (1 x 3 m mouth opening, 20 x 20 mm mesh size in the front parts, 10 x 10 mm in the medium parts and cod end) was employed for collections (Voß 1988). Specimens of *Sterechinus* were collected and stored in 4% buffered formalin. In the laboratory, animals were identified and measured. Linear regressions between diameter and ash free dry weight (AFDW) of the test, gut and gonads were established (Brey & Gutt, in press, for details).

Analysis of age and growth

Based on the methods described by Jensen (1969) and Pearse & Pearse (1975), a modified procedure was employed to visualize the growth zones in the skeletal elements of *S. antarcticus*. The elements were cleaned of organic matter by a 5% solution of NaOCl, washed in 96% ethanol, dried at 60°C and heated in a muffle oven at 300°C for 10 min. Growth zones were more conspicuous on the half pyramids (= jaws) of the Aristotle's lantern than on the genital plates, which are used in most investigations (e.g. Gage & Tyler 1985). The jaws of larger specimens (> 25 mm diameter) were ground smooth to a thickness of about one mm using a fine grained grinding wheel; smaller jaws did not require any further treatment. The growth zones of 217 specimens from stations between 400 and 600 m were examined under a stereo microscope by submerging the jaws in xylene. Von Bertalanffy, Gompertz, and logistic growth curves were fitted to the 217 age-size data pairs by a SIMPLEX algorithm (according to Schnute 1982).

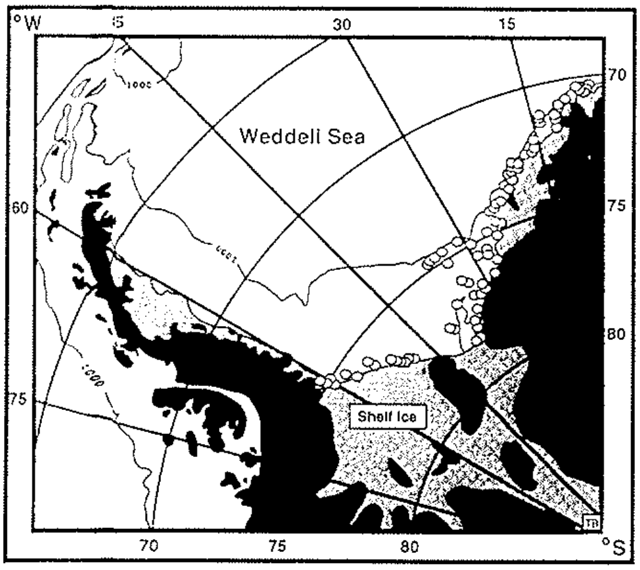

Fig. 1. Distribution of stations on the Weddell Sea shelf and slope. 0 = Trawl samples collected between 1983 and 1988.

Computation of mortality

The mortality rate Z of the single negative exponential mortality model

$$N_t = N_0 * e^{-Z * t}$$

was estimated by a size-converted catch curve (Pauly 1984, Brey *et al.* 1988). This curve was calculated from the size-frequency distribution of the pooled samples (re-arranged in 2 mm size classes) and the Von Bertalanffy growth function:

$$(N_i/\Delta t) = N_0' * e^{-Z * t_i}$$

N_i is the number of animals in size class i, Δt is the time required to grow through this size class and t_i is the relative age of the mid-size of class i. If the plot of $\ln(N_i/\Delta t)$ versus t_i shows a straight descending right arm, total mortality Z can be computed by the linear regression:

$$\ln (N_i/\Delta t) = a + b * t_i \qquad Z = -b$$

The application of this method to benthic invertebrate populations has been described previously by Brey (1986), Brey *et al.* (1988), Brey *et al.* (1990) and others.

Computation of productivity

The size-frequency distribution of the total catch was corrected for sampling errors, (especially for size specific gear selectivity in the smaller size classes) by the values calculated from the regression equation mentioned above substituting the original frequency values. All weight data are expressed as ash free dry weight (AFDW).

From (i) the corrected size-frequency distribution, (ii) the Von Bertalanffy growth function and (iii) the regression of somatic weight (gonads excluded) on diameter, somatic production was calculated by the weight-specific growth rate method according to Crisp (1984):

$P_{W,i} = W_{S,i} * G_i * dt$ (Weight specific individual production)

$P_i = N_i * P_{W,i}$ (Production per size class)

$P_S = \Sigma P_i$ (Production per total catch)

where N_i is the number of animals in size class i, $W_{S,i}$ is the mean individual somatic weight in size class i, dt is the sampling period (1 year) and G_i is the weight-specific growth rate:

$$G_i = b * K * (D_\infty - D_i) / D_i$$

where b is the slope of the size-weight regression (mg mm^{-1}; $r = 0.992$),

$$\log(W_S) = -1.444 + 2.420 * \log(D),$$

K and D_∞ are parameters of the Von Bertalanffy equation and D_i is the mean diameter in size class i. The annual somatic P/B ratio was calculated from production P_S and biomass per total catch B_S:

$$B_S = \Sigma N_i * W_{S,i}$$

Gonadal production (i.e. reproductive output *sensu* Clarke 1987) was computed from the regression of gonad weight on diameter (mg mm^{-1}; $r = 0.927$),

$$\log(W_G) = -4.507 + 3.770 * \log(D),$$

and the size-frequency distribution. Based on data from the Antarctic echinoid *Abatus cordatus* (Magniez 1983), the Antarctic asteroid *Odontaster validus* (McClintock *et al.* 1988) and the deep sea asteroid *Hymenaster membranaceus* (Pain *et al.* 1982), annual gonadal output was estimated to be 50% of individual gonad weight $W_{G,i}$. Gonadal production per total catch P_G was computed by:

$$P_G = \Sigma N_i * W_{G,i} * 0.5$$

Annual production of *S. antarcticus* per square meter was calculated by multiplying the P/B ratio by estimates of average biomass for different depth ranges of the Weddell Sea shelf and slope (Brey & Gutt, in press).

Results

Age and growth

The Von Bertalanffy growth curve shown in Fig. 2 was found to fit the age-size data at best:

$$D_t = 82.4 * (1 - e^{-0.017 * (t - 1.633)})$$

$$n = 217, \text{ Residual Sum of Squares} = 2181.8$$

The oldest animal found was estimated to have an age of 75 years (62.5 mm diameter).

Mortality

The straight descending right arm of the size converted catch curve indicates that mortality in *S. antarcticus* can be described adequately by the single negative exponential model (Fig. 3). Total mortality rate Z was estimated to be 0.07 y^{-1}.

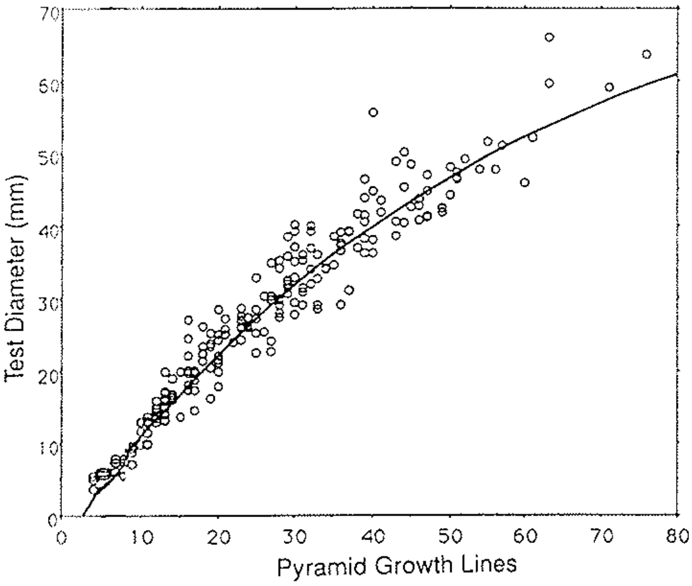

Fig. 2. VonBertalanffy growth curve fitted to 217 data pairs of number of growth lines in the half-pyramids and test diameter of *S. antarcticus*; $D_t = 82.4 * (1 - e^{-0.017*(t - 1.633)})$

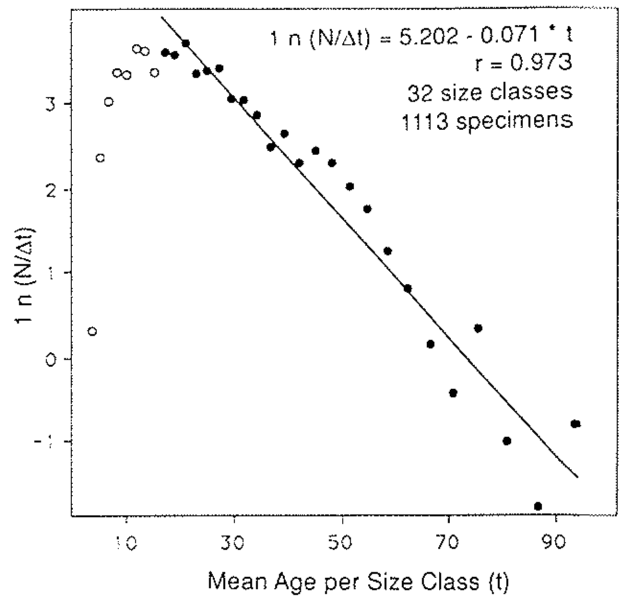

Fig. 3. Size converted catch curve of *S. antarcticus*.
O = Points not included in regression line.

Productivity

Fig. 4 shows the original size-frequency distribution (n = 1113) and the distribution corrected by the catch curve equation (n = 2052), and Table I shows the calculated production values. Annual somatic biomass, production and P/B ratio (values for original data in brackets) were calculated to be 147.6 g/total catch (153.2), 10.6 g/total catch (8.7), and 0.07 (0.06), respectively. Gonadal production was calculated to be 8.5 g/total catch (9.5) by multiplying the biomass of 17.0 g/total catch (19.0) by the P/B ratio of 0.5 y^{-1}.

The biomass of *S. antarcticus* on the Weddell Sea shelf and slope is about 5 mg m^{-2} between 100 and 1200 m and 10 mg m^{-2} between 450 and 1200 m (Brey & Gutt in press). From the total catch, the biomass of the average *S. antarcticus* population consists of 90% somatic tissue and 10% gonadal tissue. Annual production is calculated to be 0.32 mg m^{-2} of somatic tissue and 0.25 mg m^{-2} of gonads between 100 and 1200 m. Below 450 m, somatic production is 0.63 mg m^{-2} and gonadal production 0.50 mg m^{-2}. Total production is about 0.6 mg m^{-2} y^{-1} in the whole depth range and 1.1 mg m^{-2} y^{-1} below 450 m, respectively.

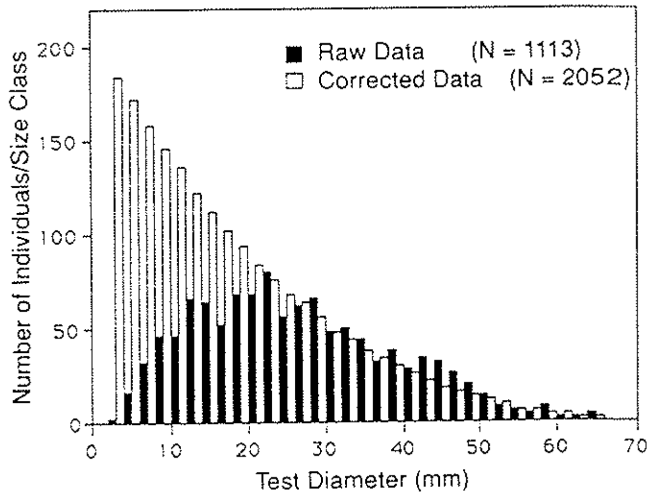

Fig. 4. Size frequency distribution of *S. antarcticus*. Original data and data corrected for gear selection and sampling error by the size converted catch curve.

Table I. Annual somatic and gonadal productivity (g AFDW) of *S. antarcticus* per total catch (92 trawl samples) Raw Data: Original total catch; Corrected Data: Total catch corrected for size dependent gear selectivity [1]: P/B ratio estimated from literature data (gonadal output = 50% of gonad weight)

Number	Raw Data 1113			Corrected Data 2052		
	Somatic	Gonadal	Total	Somatic	Gonadal	Total
Biomass	153.2	19.0	162.2	147.6	17.0	164.6
Production	8.7	9.5	18.2	10.6	8.5	19.1
P/B Ratio	0.06	0.5[1]	0.11	0.07	0.5[1]	0.12

Discussion

Treating growth marks in the jaws of *S. antarcticus* as annual growth lines assumes that there is a distinct annual cycle in the growth of this species on the Weddell Sea shelf, as has been observed in many echinoids from temperate areas (Smith 1980). This assumption can be proven in two ways only, (i) by the comparison of growth zones of specimens sampled in different seasons of the year, or (ii) by a tagging-recapture experiment in the field. Both approaches could not be performed with *S. antarcticus*.

However, investigations on other Antarctic marine invertebrates have shown evidence for a strong seasonal pattern in growth (Bone 1972, Bregazzi 1972, Luxmoore 1982, Picken 1979, 1980, Richardson 1979, Stockton 1984, Thurston 1970). This seasonal pattern in growth is most likely coupled to the strong seasonality in primary production and sedimentation in the Southern Ocean (Fischer *et al.* 1989). Clarke (1988) assumes that metabolic activity of Antarctic ectotherms is primarily limited by food availability. In benthic herbivores and omnivores, growth seems to be limited more or less to the brief summer period of high primary production. The observation of annual growth marks in boreal deep sea echinoids (Gage & Tyler 1985, Gage *et al.* 1986), living under constant temperature and with strong seasonality in food input gives additional support to the hypothesis of annual formation of growth zones in *S. antarcticus*.

If the growth function established for *S. antarcticus*, $D_t = 82.4 * (1 - e^{-0.017 * (t - 1.633)})$, is accurate, this sea urchin grows even slower than related deep sea species such as *Echinus affinus* in the north-east Atlantic at 2200 m depth (Gage & Tyler 1985). However, observations on the growth of sponges and asteroids in McMurdo Sound (Dayton *et al.* 1974, McClintock *et al.* 1988) as well on the growth of the limpet *Nacella concinna* at Anvers Island (Shabica 1976), indicate that several Antarctic macrobenthic species exhibit extremely low growth rates and may reach maximum ages of more than 50 years. Moreover, as pointed out by Ebert (1988), and as indicated by Fig.2, the age of the larger specimens of *S. antarcticus* may still be underestimated due to insufficient resolution of recent growth lines or to resorption of growth lines during years of little food availability.

The relation between the mortality rate Z (0.07 y^{-1}) and the growth constant K (0.017 y^{-1}) found for *S. antarcticus* fits well in the empirical relation between these two parameters in sea urchins by (Ebert 1975), although both values are very low when compared with other echinoids. The similarity of mortality rate Z and P/B ratio (both 0.07 y^{-1}) is a purely mathematical consequence of the combination of the Von Bertalanffy growth function, the single negative exponential mortality model and a steady-state population structure (Allen 1971). The estimate of somatic P/B ratio of *S. antarcticus* 0.07 y^{-1}, is well within the range of the P/B ratios of three species of shallow water asteroids at Cape Armitage, McMurdo Sound, *Odontaster validus*: 0.054 y^{-1}, *Acondontaster conspicuus*: 0.083 y^{-1} and *Perknaster fuscus*: 0.135 y^{-1} (calculated from Dayton *et al.* 1974, Tables V, VI and XI).

In the estimate of gonadal production, three topics are of importance: (i) an annual cycle of reproduction, (ii) the developmental stage of the gonads at sampling, and (iii) the relation of reproductive output to total gonad weight.

(i) There is ample evidence for an annual reproductive cycle in *S. antarcticus* as found in many Antarctic benthic invertebrates (Pearse *et al.* 1990). In Antarctic echinoderms, seasonal reproduction was found in several species, e.g. *Odontaster validus* (Asteroidea, McClintock *et al.* 1988) and *Sterechinus neumayeri* (Echinoidea, Bosch *et al.* 1987, Yakovlev 1983). Also deep sea species such as *Dytaster grandis* (Asteroidea, Tyler *et al.* 1990), *Ophiura ljungmani* (Ophiuroidea, Tyler & Gage 1980) and *Echinus affinis* (Echinoidea, Tyler & Gage 1984) were found to reproduce seasonally.

(ii) The small size of the eggs (0.25 mm, Mortensen 1909) indicates free-swimming feeding larvae in *S. antarcticus* (Pearse *et al.* 1990). Therefore, it is likely that spawning takes place during austral winter and spring, i.e. between May and December as in *S. neumayeri* (Bosch *et al.* 1987, Pease & Giese 1966, Yakovlev 1983), to provide sufficient time for the development of planktotrophic larvae prior to the brief summer period of primary production. The specimens in this investigation were collected primarily during January and February, so gonad weight is assumed to be an underestimate of the maximum weight during the annual cycle.

(iii) Reliable data on the reproductive output of Antarctic and deep sea echinoderms are rare. McClintock (1989) and other authors estimated annual reproductive output to be 100% of gonad weight at sampling, which is likely to be an overestimate (Lawrence & Lane 1982). The ratio of 50% used here for *S. antarcticus* may still be too high. It is based on the annual reproductive cycles of *Abatus cordatus*, *Odontaster validus* and *Hymenaster membranaceus* from different sites. Moreover, echinoids adjust rates of somatic growth and gonad production to the available level of nutrition (Lawrence 1987, Lawrence & Lane 1982). Only a detailed investigation of the annual cycle of gonad development will provide a more precise estimate of gonad production of *S. antarcticus*.

Somatic production per individual (Fig. 5) increases slowly up to a maximum at 42–54 mm diameter (42–63 years of age) and decreases again with increasing size (age). Gonad production is negligible below 20 mm diameter (16 years), if there is any gonad output at all in these small specimens. Above 20 mm diameter, gonad production increases exponentially up to the highest size class (66 mm, theoretically 95 years). Similar patterns of increasing reproductive effort with size have been observed in many echinoderm species (Lawrence 1987). In general, *S. antarcticus* exhibits the typical pattern of slow growth with long lifespan. The older the animals are, the more energy (in absolute terms as well as in relation to total energetic effort) they invest in reproduction. Similar patterns have been described for various long-lived benthic invertebrates such as the bivalves *Aulacomya ater* (Griffiths & King 1979), *Mytilus edulis* (Rodhouse *et al.* 1986) and *Ostrea edulis* (Rodhouse 1978). This strategy, in combination with the mortality within the population, leads to a distinct separation of the peaks of maximum somatic production (18–24 mm diameter, 14–20

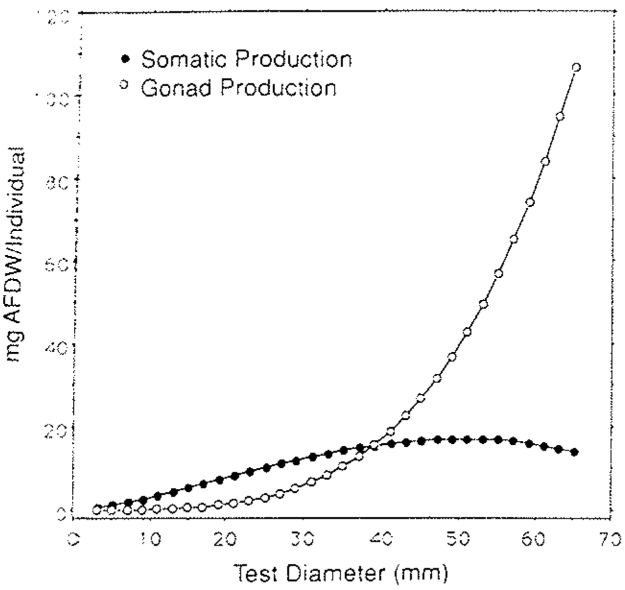

Fig. 5. Size specific distribution of somatic and gonadal production in single individuals of *S antarcticus*. Somatic production calculated by the weight specific growth rate method, gonadal production estimated to be 50% of gonad weight.

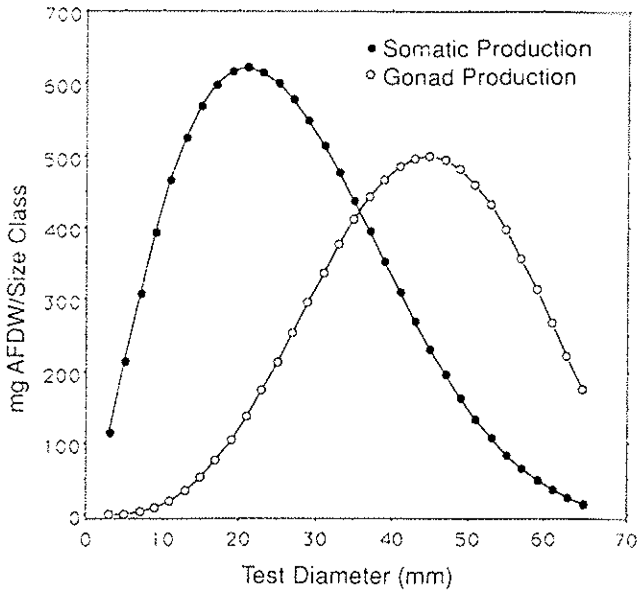

Fig. 6. Size specific distribution of somatic and gonadal production at the population level. Somatic production calculated by the weight specific growth rate method, gonadal production estimated to be 50% of gonad weight.

years) and maximum gonad production (42–48 mm diameter, 42–51 years), as in Fig. 6. This pattern will hold true, even if estimates of gonadal production are only approximate.

The ecological significance of *S. antarcticus* within the benthic community on the Weddell Sea shelf and slope is poorly understood. Almost no data on biomass, productivity and the trophic structure of this community have been published. In shallow water of boreal and tropical regions, feeding activities of echinoids can affect biomass and species composition of algal communities (Lawrence & Sammarco 1982). The feeding of *S. antarcticus* on bryozoans (De Ridder & Lawrence 1982, Brey unpublished data) may have similar effects, especially with respect to competition for space among the various sessile suspension feeding species. In terms of energy flow, *S. antarcticus* seems to play a minor role in the Weddell Sea shelf and slope community. If we assume a growth efficiency (Production/Consumption) of 5% (Lawrence & Lane 1982), then annual food demand is only 60 mg m^{-2}, which is equal to 30 mg C_{org} m^{-2}. The daily sedimentation rates measured by Bodungen *et al.* (1988) during January–February on the eastern shelf, 18–135 mg C_{org} m^{-2} d^{-1}, indicate that annual sedimentation is in the range of several grams (2-10 g C_{org} m^{-2} y^{-1}). On this basis, *S. antarcticus* requires less than one per cent of the annual food input from the pelagic to maintain a steady-state population structure, even if a portion of its diet consists of bryozoans.

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