PUBLICATION III

The Antarctic lollypop sponge *Stylocordyla borealis* (Lovén, 1868): 2. Energetics and growth rates

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Abstract

At present it is impossible to assess growth or age of slow-growing Antarctic sponges with traditional methods. We introduce a new approach (AMIGO: Advanced Modelling of Invertebrate Growth from Oxygen consumption data) to model growth and age at size from oxygen consumption data. The model showed good agreement with field and laboratory data of the temperate *Halichondria panicea* except in very young individuals. AMIGO was then applied to estimate growth and age of the lollypop sponge *Stylocordyla borealis*, a known early settler in iceberg scour marks on the Antarctic shelf. Metabolic activity was inferred from mass specific respiration rates and the activity of the electron transport system (ETS) for individuals of 0.03-2.9 g $AFDM_{tot}$. Bodies of *S. borealis* showed a markedly higher ETS activity than did stalk parts. According to our model average sized *S. borealis* ($AFDM_{tot}$ = 0.8 g) were 10 years old while the largest individual ($AFDM_{tot}$ = 7.7 g) was 151 years old. Using data on abundance and size frequency distributions we calculated a P_s/B ratio of 0.106 for *S. borealis* on the eastern Weddell Sea shelf.

Introduction

The lollypop sponge *Stylocordyla borealis* (Lovén, 1868) (Demospongiae, Hadromerida) is a very conspicuous member of the Antarctic sponge fauna occurring in sometimes dense aggregations (≤ 48 ind m^{-2} Gatti et al. subm). In spite of their abundance and their known significance for resettlement processes after iceberg scouring (Gutt 1996, Gutt & Starmans 2001), data about growth rates and population dynamic parameters of lollypop sponges are hitherto lacking. The main reason for this lack of such data on Antarctic sponges in general is the fundamental difficulty of measuring the very slow growth rates directly. Dayton (1979) found that only two sponge species (*Mycale acerata* and *Homaxinella sp.*) were growing comparatively fast. Nine species near McMurdo (Ross Sea, Antarctica), however, showed no measurable increase in size in 10 years. Sponges lack such structures that may serve as 'growth recorders' such as skeleton parts of molluscs, echinoderms or fish (Campana & Neilson 1985, Gage 1990a, b, Rodhouse 1991). Aging by the naturally occurring radionuclide ^{32}Si is not possible as single sponge spicules contain insufficient activity and larger samples would be a mixture of old and recent spicule material (pers. comm. M. Rutgers van der Loeff, AWI). Carbon content of spicules is too low (<0.2% of spicule mass Schwab & Shore 1971) to facilitate analysis of carbon isotope ratios.

In this study we determined mass specific respiration data and ETS data (activity of the electron transport system) for lollypop sponges and modelled growth rates from those data. Based on our modelling results, we calculated population dynamic

parameters of *S. borealis* and evaluated this species' contribution to energy flow patterns on the eastern Weddell Sea shelf. Our modelling results are the first estimate of growth rates of the Antarctic lollypop sponge and contribute to answering the following questions: (1) Is *S. borealis* only of structural importance for the resettlement process after iceberg scouring or does also play an important role in carbon and silicon cycling on the eastern Weddell Sea shelf? (2) Sponges are presently one of the main targets in the intensified search for bio-active compounds (Müller et al. 2000). Could *S. borealis* support a managed sustainable exploitation if e.g. it was of commercial interest owing to bio-active compounds?

Materials and methods

Study area: Samples were taken within the framework of the EASIZ II program (Ecology of the Antarctic Shelf Ice Zone) in austral summer 1998 during RV "Polarstern" cruise ANT XV/3 to the eastern Weddell Sea. A complete list of stations, water depths, and deployed gear is given in Arntz & Gutt (1999). Experiments (respiration and ETS assays) were performed during ANT XV/3 and XV/4 (Jan. - May 1998). Life maintenance of sponges at 0°C in natural unfiltered seawater was successful for the entire period of five month throughout which sponges appeared to be in a healthy physiological state (visual inspection).

1. Metabolic rate

Respiration rates were determined form decrease of oxygen saturation in an intermittent flow system, using unfiltered seawater. Oxygen saturation data were recorded continuously by oxygen microoptodes and recorded online by a laptop computer. Details of the experimental system are given in Gatti et al. (2002). Microoptodes do not consume oxygen and show hardly any drift at low temperatures (Gatti et al. 2002). They are thus a very suitable tool for measurements of low respiration rates in cold water. Oxygen consumption rates were calculated by

Equation III-1

$$V'_{O_2} = \frac{\frac{sat_{t=0} - sat_{t=60}}{100} \times O_{2sat} \times V - O_{2contr}}{M}$$

Where: V'_{O2} = mass specific oxygen consumption rate [cm^3 O_2 h^{-1} g^{-1} AFDM], O_{2sat} = oxygen content of seawater saturated with oxygen [cm^3O_2 dm^{-3}seawater], $sat_{t=0}$ = oxygen saturation [%] at beginning of experiment, $sat_{t=60}$ = oxygen saturation [%] after 60 minutes as calculated from linear regressions of each cycle, V = true water volume of respiration chamber and tubing [dm^3] (i. e. corrected for animal volume), M = body

mass of animal [g AFDM], O_{2contr} = oxygen consumption attributed to bacteria and microheterotrophs inside experimental chamber, AFDM = ash free dry mass (after 24 hours of igniting at 500°C).

We used individuals of 0.03 g - 2.7 g AFDM in our respiration experiments. Influence of body mass on respiration rates was assessed by weighted least square linear regression (Draper & Smith 1980). Each group of data points (same body mass, different respiration rates) represents repeated measurements of the respiration of one individual. Variance between the repeated measurements is used as a measure of data reliability. Inverted variances are applied as weights to the regression thus assigning more weight to data with less variance. Using this technique we were able to compensate for the bias in data introduced by different quality of measurements. The upper and lower 95% confidence limits for the slope of the weighted regression were calculated according to Sachs (1999).

The activity of the electron transport system (ETS) was determined by the tetrazolium (INT) reduction technique introduced by Packard (1971). ETS data give an estimate of the maximum amount of oxygen that can be processed at the mitochondrial and microsomal membranes of an organism (Lampert 1984). Handling of samples and concentrations of the added chemicals followed the procedures given in Owens & King (1975) with the exception of the quenching solution. Because of its toxicity the quenching solution of Owens & King (50% formalin and 50% 1M H_3PO_4, pH 2.5) was substituted by fuming hydrochloric acid. A set of pilot studies had shown that this chemical stopped the reaction as quickly and completely as the Owens & King (1975) quenching solution. Marked differences in organic content of body and stalk part of an individual (Gatti et al. subm.) motivated determination of ETS activity for body and stalk parts, separately. Samples of approx. 0.2 mg WM were routinely taken from: (1) a quarter section of the stalk (approx. 1 cm long) and (2) the inner tissue of the body (i. e. excluding material from the dermal membrane). Absorbance of the sample and measurement of turbidity control were determined in separate readings as suggested by Packard & Williams (1981). Two abiotic controls (i. e. without sponge tissue) were run in parallel with every set of 10 assays to control for bacterial contamination of the chemicals. To calculate maximum oxygen consumption from ETS data we modified the equation given by Packard & Williams (1981) into

Equation III-2

$$ETS' = \frac{60 \times Q \times H \times (A_{assay} - A_{contr} - A_{turb})}{1.42 \times S \times M_{sample} \times T}$$

where: ETS' = mass specific activity of the electron transport system [$mm^3O_2\ h^{-1}\ g^{-1}$AFDM] or [$mm^3O_2\ h^{-1}\ g^{-1}$WM], H = crude homogenate volume (here: 3 cm^3 + sponge volume [cm^3]), Q = volume of quenched assay (here: 5 cm^3), A_{assay} = assay absorbance at 490nm, A_{contr} = absorbance of abiotic control at 490 nm, A_{turb} =

absorbance of turbidity control at 760 nm, S = volume of supernatant added (here: 1 cm^3), M_{sample} = mass of the sample [g AFDM] or [g WM], and T = incubation time [min].

ETS' data were corrected for differences between incubation temperature and *in situ* temperature following the Arrhenius equation. ETS_{tot} of an individual was calculated with

Equation III-3 $$ETS_{tot}=ETS_{stalk}+ETS_{body}=ETS'_{stalk}\times M_{stalk}+ETS'_{body}\times M_{body}$$

where: ETS_{tot} = ETS of the whole individual [cm^3O_2 h^{-1} ind^{-1}], ETS_{stalk} = ETS of the stalk part of an individual [cm^3O_2 h^{-1} ind^{-1}], ETS_{body} = ETS of the body part of an individual [$cm^3O_2 h^{-1}$ ind^{-1}], ETS'_{body} = mass specific ETS activity of the body [cm^3O_2 h^{-1} g^{-1}AFDM] or [cm^3O_2 h^{-1} g^{-1}WM], ETS'_{stalk} = mass specific ETS activity of the stalk [cm^3O_2 h^{-1} g^{-1}AFDM] or [cm^3O_2 h^{-1} g^{-1}WM], M_{body} = mass of the body [g AFDM] or [g WM], and M_{stalk} = mass of the stalk [g AFDM] or [g WM].

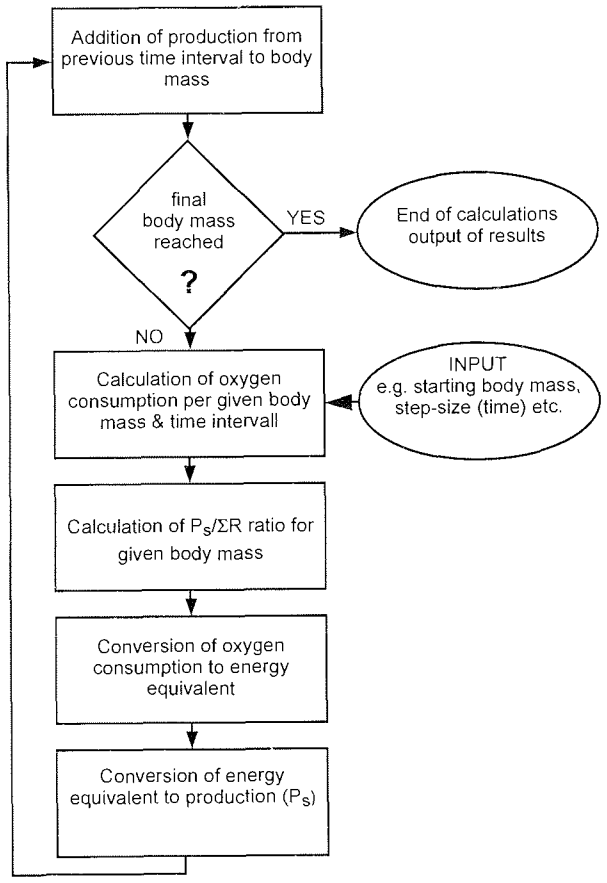
2. Modelling

Clarke (1987) formulated the energy budget equation as

Equation III-4 $$A=P_s+P_g+\Sigma R+U$$

where A = assimilation, P_s = somatic production, P_g = production of gonad tissue, ΣR = sum of all respiratory costs (including basal metabolism, cost of locomotion, and costs of somatic and gonadic reproduction), and U is excretion. The sum of all respiratory costs (ΣR) is an equivalent of oxygen consumption (V_{O2}) and it is not possible to determine its different components by experiment (Clarke 1987). Nevertheless, if reliable measurements of oxygen consumption rates are available, accumulated production can be calculated from such data (Lampert 1984). One problem arises from these considerations: ΣR as well as the ratio $P_s/\Sigma R$ depend on the age and/or size of an individual. From data given by Thomassen & Riisgård (1995) it was possible to relate the $P_s/\Sigma R$ ratio to body mass of a sponge individual (demosponge *Halichondria panicea* from the Baltic Sea). As our knowledge about reproduction patterns of Antarctic sponges in general and *S. borealis* specifically is presently limited (Burton 1928, Gatti et al. subm., Sarà et al. in press), and we do not know how often this species reproduces, we did not explicitly include a term describing reproductive effort into our modelling approach. Neglecting reproduction events leads to an overestimation of somatic growth. Hence all growth rates ($G_t = \delta M \times \delta t^{-1}$, where M is body mass and t is time) derived from our model are maximum growth rate estimates and thus minimum age estimates.

The modelling routine AMIGO (Advanced Modelling of Invertebrate Growth from Oxygen consumption) was written for the software ME10 (Hewlett & Packard: Student



Version 7.1). Computations of this study were performed with AMIGO 4.04. The model calculates somatic production from oxygen consumption data. Figure III-1 shows a flow chart of the modelling routine.

Figure III-1 Flow chart of the AMIGO modelling routine. Conversions between units of mass and oxygen consumption follow: C_{org} [mg] = 0.44 × O_2 [cm^3] (Lampert 1984), M_e [kJ] = 45.7 × C_{org} [g] (Salonen et al. 1976), C_{org} [g] = AFDM [g] × 0.5 (Barthel 1986).

Relationship of individual body mass and oxygen consumption was calculated with

Equation III-5 $$\log V'_{O2} = a' + b' \times \log M$$

where V'_{O2} = mass specific oxygen consumption [$cm^3O_2\ g^{-1}$AFDM h^{-1}] and M = body mass [g AFDM] as determined in our respiration experiments.

The relationship between body mass and the ratio $P_s/\Sigma R$ was calculated with

Equation III-6 $$\frac{P_s}{\Sigma R} = a'' + b'' \times \ln M_e$$

where: P_s = somatic production, ΣR is oxygen consumption and M_e is the energy equivalent of body mass [kJ]. The boundary value for this function is given as $P_s/\Sigma R = 0$ at $M_e = M_{emax}$, where M_{emax} is defined as the energy equivalent of maximum body mass observed in the field increased by 10% to account for incomplete sampling of the population. To test the model we used oxygen consumption data and the $P_s/\Sigma R$ ratio of *Halichondria panicea* as derived from Thomassen & Riisgård (1995).

For estimation of growth rates of *Stylocordyla borealis* we performed three modelling runs: (1) with oxygen consumption data as described by the weighted least square linear regression, (2) and (3) with oxygen consumption data as described by the upper and lower 95% confidence limit for the estimation of slope of the weighted linear regression line, respectively.

3. Calculation of population energy budget

A von Bertalanffy growth function (VBGF) $M_t=M_\infty (1-e^{-k (t-t0)})^D$, where M_t is the body mass at given time t, M_∞ is the infinite body mass, k and D are constants defining shape of the growth curve, and t_0 is the theoretical age at which $M_t=0$, was fitted iteratively to mass at age data as obtained from the modelling output. Infinite body mass (M_∞) was set equal to M_{max} from the AMIGO model (= 4.38 gC) Using the average assimilation efficiency of 188 herbivorous suspension feeding species (36.3%, SD: 25.9 - 44.2%, Brey unpubl. data compilation) and model output data, we calculated carbon requirements of individual lollypop sponges. Applying a mean body mass of 0.414 gC, carbon requirements were calculated for average and high density patches of *S. borealis* (3.02 ind m^{-2} and 48 ind m^{-2}, respectively, Gatti et al. subm). Annual production to biomass ratio (P_s/B) was then calculated by the mass specific growth rate method (MSGRM) following Brey et al. (1996) and Brey (1999) using the automated spreadsheet computations for mass frequency distributions given in Brey (2001) and the mass frequency distribution for *S. borealis* shown in Figure III-2.

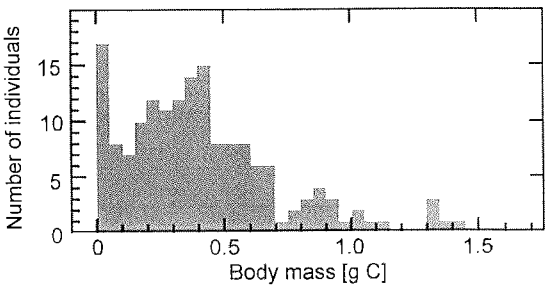


Figure III-2 *Stylocordyla borealis*. Mass frequency distribution (gC) of individuals (N=165) collected at station PS 48-222 during ANT XV/3. Graph is modified from Gatti et al. (subm).

Results

1. Metabolic rate

Relationship between body mass (AFDM) and oxygen consumption rates of *Stylocordyla borealis* is shown in Figure III-3AB. Individual oxygen consumption rate increased exponentially with body mass (Figure III-3A): $\log V_{O2} = -0.855+0.479\times\log M$ (R^2_{adj} = 0.690, N= 70, $p\leq0.001$), whereas mass specific oxygen consumption rate decreased exponentially with increasing body mass (Figure III-3B): $\log V_{O2} = -0.855-0.521\times\log M$ (R^2_{adj} = 0.724, N= 70, $p\leq0.001$).

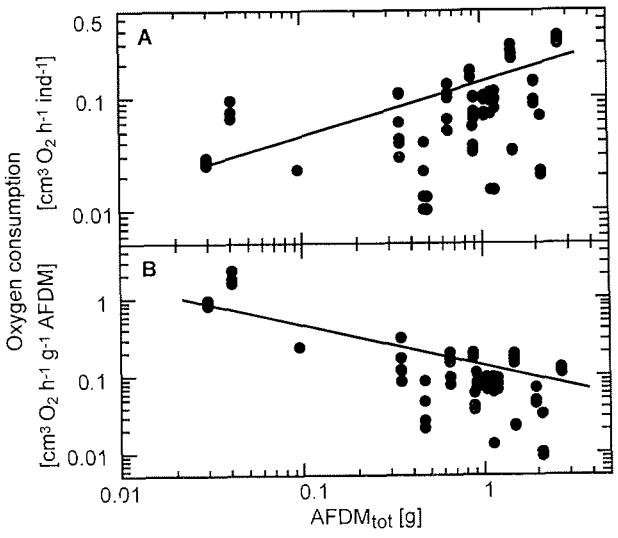


Figure III-3AB *Stylocordyla borealis*. Total individual (A) and mass specific (B) respiration rates. Regressions shown are weighted least square linear regressions: (A): log V_{O2} = -0.855+0.479×log M (R^2_{adj} = 0.690, N= 70, p≤0.001); (B): log V_{O2} = -0.855-0.521×log M (R^2_{adj} = 0.724, N= 70, p≤0.001). For discussion of regression technique see text.

Table III-1 *Stylocordyla borealis*. Comparison of ETS_{body} and ETS_{stalk} in terms of WM and AFDM. N=40 for all analyses; * indicates significantly higher values (p<0.001).

ETS'	$cm^3\ h^{-1}\ g^{-1}$ WM		$cm^3\ h^{-1}\ g^{-1}$ AFDM	
	Mean	SE	Mean	SE
Body	0.202*	0.010	1.965	0.098
Stalk	0.061	0.004	2.900*	0.190

Based on wet mass ETS'_{body} was significantly higher than ETS'_{stalk} (p<0.001), whereas based on AFDM ETS'_{body} was significantly lower than ETS'_{stalk} (p<0.001) (Table III-1). Individual ETS activity increased exponentially with body mass (Figure III-4A) but there was no significant relation between either one of the mass specific ETS' parameters and body mass (Figure III-4B). Oxygen consumption rate to individual ETS activity ratio (V_{O2}/ETS) decreased exponentially with body mass (Figure III-5). It decreased from 0.47 for small sponges (AFDM = 18 mg) to 0.043 for large individuals (AFDM = 2.9 g).

2. Modelling

A test run of our model with *Halichondria panicea* data of Thomassen & Riisgård (1995) showed good agreement between predicted and observed value of body mass (M_t) and growth rate (G_t) at time t (Figure III-6). The fit is almost perfect for M>2.36 g C (age ≥5.6 years), whereas systematic deviations are present in smaller and younger individuals.

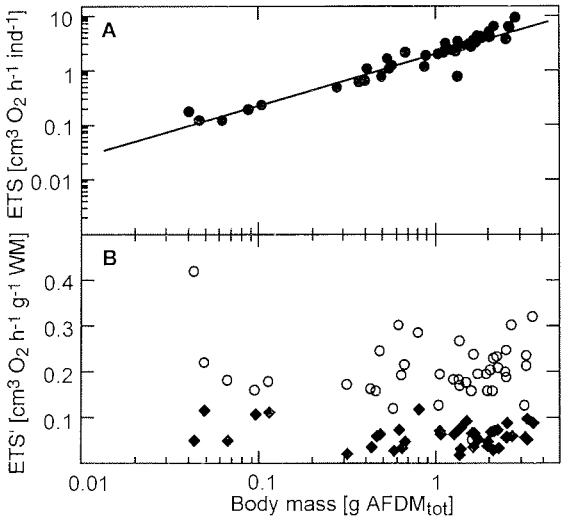


Figure III-4AB *Stylocordyla borealis*. Increasing individual ETS_{tot} activity (A): log ETS_{tot} = 0.289 + 0.948 × log M (N=70, r^2= 0.926) and mass specific ETS' activity (B) separated for body (circles) and stalk (diamonds) parts of an individual showing no trend with increasing body mass.

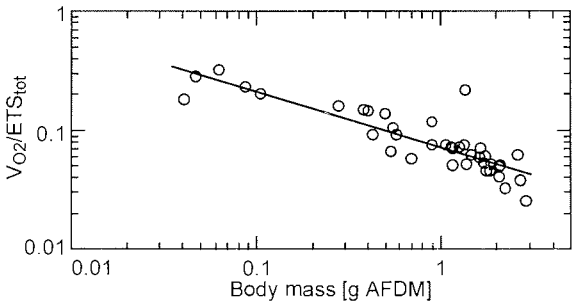


Figure III-5 *Stylocordyla borealis*. Exponentially decreasing ratio V_{O2} over ETS_{tot} activity vs. $AFDM_{tot}$. log VO2/ETS_{tot} = -1.143-0.469 × log $AFDM_{tot}$ (n=70, r^2=0.753).

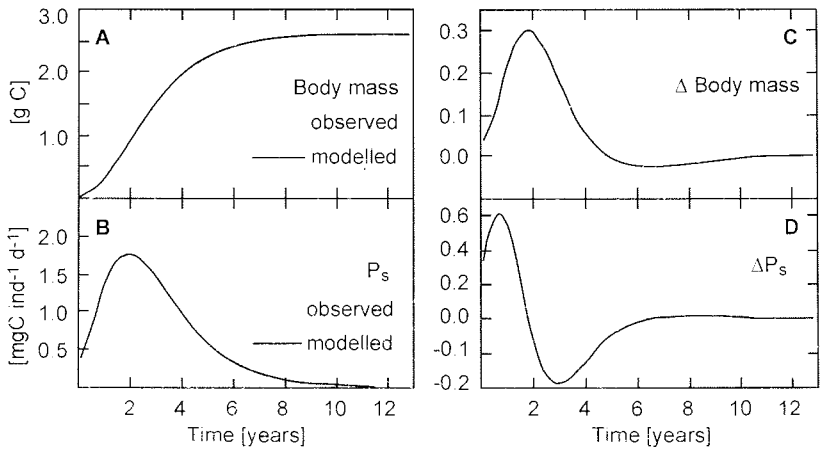


Figure III-6 *Halichondria panicea*. Comparison of model output with observed data for: body mass at time t (A), P_s at time t (B), difference between observed and modelled body mass at time t (C), and difference between observed and modelled P_s values at time t (D) (data points for each curve: N=202). The model was initialized with the following parameters: log V'_{O2}= 0.232-0.073×log M, log(P_s/ΣR)= 0.213-0.044×log M_e, stepsize SS=1 day, and initial body mass iniBM=0.03 gC.

According to the growth curve for *Stylocordyla borealis* as derived from the AMIGO model (Figure III-7) the smallest individual of our experiments ($AFDM_{tot}$ = 0.018 g) was 188 days (95% confidence interval:128-273 days) old, an averaged sized individual ($AFDM_{tot}$ = 0.828 g) was 10.4 (9.3-11.6) years old and the largest individual of this study ($AFDM_{tot}$ = 2.9 g) was 32.9 (32.9-33.2) years old. The largest individual found during ANT XIII/3 in 1996, weighted 7.7 g ($AFDM_{tot}$) corresponding to an age of 152.3 (137.6-169.5) years.

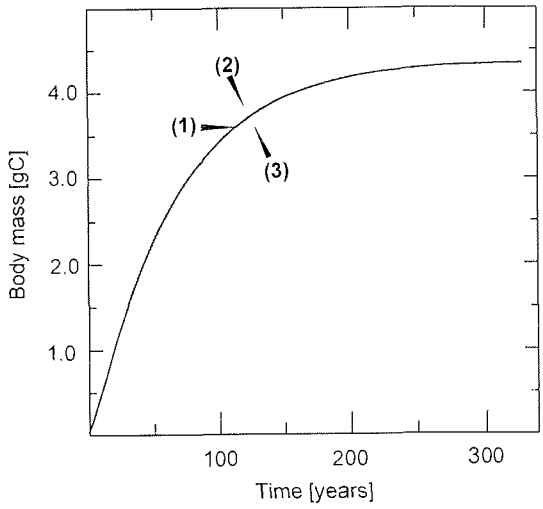


Figure III-7 *Stylocordyla borealis*. Results of model output for weighted linear least square regression (1) (log V_{O2} = -0.855 -0.521 × log M), upper 95% confidence limit of slope of weighted regression (2) (log V_{O2} = -0.855 - 0.444 × log M), lower 95% confidence limit of slope of weighted regression (3) (log V_{O2} =-0.855-0.597×log M). Data points for each curve: N=1201. The model was initialized with log($P_s/\Sigma R$)=0.219-0.041×log M_e, step-size SS=1 day, initial body mass iniBM=0.0001 gC. Parameters of the VBGF for curve (1) are: M_∞ = 4.38 gC, k=0.015, D=1.185, t_0=0.0, r^2=1.0.

3. Population energy budget

The parameters of the computed general VBGF are M_∞ = 4.38 gC, k = 0.015, t_0 = 0.0 and D = 1.185. Somatic production of the population shown in Figure III-2 amounted to 0.133 gC y^{-1} m^{-2} in patches of average abundance (3.02 ind m^{-2}, Gatti et al. subm.). All results of the calculations regarding carbon requirements of lollypop sponges are summarized in Table III-2. Mean annual productivity calculated with the MSGRM was P_s/B = 0.106.

	Patch	Mean density	Max. density
Abundance (ind m^{-2})		3.02	48
Biomass (gC m^{-2} y^{-1})		1.25	19.9
Consumption (gC m^{-2} y^{-1})		4.46	70.8
Assimilation (gC m^{-2} y^{-1})		1.62	25.7
Production (gC m^{-2} y^{-1})		0.133	2.11
Opal production (gSiO_2 m^{-2} y^{-1})		1.19	18.9
Respiration (gC m^{-2} y^{-1})		1.48	23.57

Table III-2 *Stylocordyla borealis*. Energy budget for patches with average and maximum abundance. Calculations are based on model results for weighted linear least square regression of respiration data, mean sponge biomass of 0.414 gC and a mean assimilation efficiency of 36.3% (see text for reference)

Discussion

1. Metabolic rate

Oxygen consumption rates of *Stylocordyla borealis* are low when compared with tropical or boreal invertebrates but within the range of oxygen consumption rates known for Antarctic invertebrates (Figure III-8).

During the respiration experiments we had to use unfiltered seawater as the sponges had tightly closed oscula when exposed to filtered seawater (Gatti et al. 2002). We conclude that sponges were feeding during our experiments and, since we were not able to measure true resting metabolism (i. e. that of fasting individuals) which should be somewhat lower than our data. Ideally the oxygen consumption measurements used for our AMIGO model should include year-round measurements. By measuring summer-metabolism only we possibly overestimate the annual oxygen consumption.

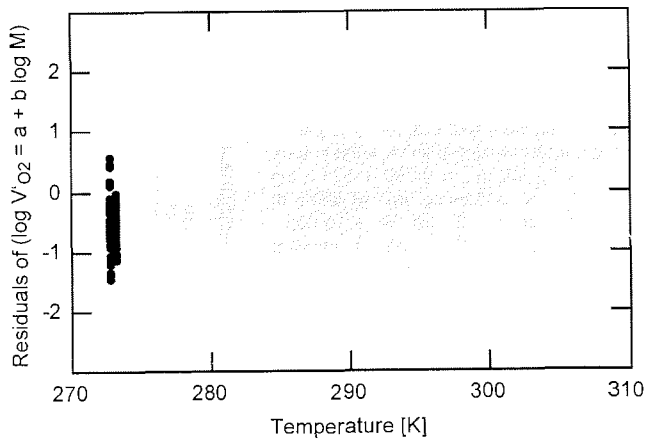


Figure III-8 Comparison of invertebrate oxygen consumption data worldwide. Data shown are residuals of the regression of mass specific oxygen consumption data vs. body mass. Grey dots: 19834 data points, 771 invertebrate species including 13 sponge species (unpublished data compilation T. Brey); black dots, oxygen consumption of *S. borealis* (N=70 data points).

Our study is the first to determine ETS activities of a sponge species. Our results are in general agreement with data from other taxa (e.g. Båmstedt 1980). However, we found ETS'_{body} g^{-1}WM > ETS'_{stalk} g^{-1}WM (Figure III-4B) whereas ETS'_{body} g^{-1}AFDM < ETS'_{stalk} g^{-1}AFDM (Table III-1). Stalks contained very little organic matter (2.3±0.7% of WM_{stalk}, mean ± SE) and a rather large proportion of spicules (51.6±1.1% of WM_{stalk}) (Gatti et al. subm.). The higher ETS'_{stalk} activity per gram AFDM indicates that the few living cells of a stalk are potentially metabolically very active (pers comm. Packard). As spicule synthesis is an energy consuming process (Simpson 1984, Jones & Pearson 1990, Frøhlich & Barthel 1997) a high level of ETS activity in spicule making stalk-cells is necessary, particularly as only a small number of cells participate in the process.

ETS_{tot} increased linearly with body mass (Figure III-4A), whereas V_{O2} increased exponentially but with an exponent < 1 (Figure III-3A). Thus the ratio V_{O2}/ETS_{tot} decreased with increasing body mass (Figure III-5). From this regression we can calculate a theoretical minimum body mass of $AFDM_{tot}$ = 3.62 mg at which V_{O2}/ETS_{tot} = 1. For smaller individuals oxygen consumption rates would exceed ETS_{tot} values, which is theoretically impossible. The smallest individual Gatti et al. (subm.) found had an $AFDM_{tot}$ of 18 mg. Body length of that individual [~2mm] was comparable to the biggest embryos that were found in the specimens (Gatti et al. subm). Thus it is very likely that body mass even of the smallest free-living lollypop sponge is well above the theoretical minimum of 3.62 g AFDM.

In the sponge *Stylocordyla borealis* V_{O2}/ETS_{tot} declined exponentially with increasing body mass (Figure III-5). This observation is contradictory to results of Madon et al. (1998) and Ikeda (1989). Both found constant V_{O2}/ETS ratio spanning body masses of several orders of magnitude (Madon et al.: 0.06-0.07 for zebra mussels, Ikeda: 0.62 - 0.71 for different species of myctophid fish). The highest ratio (0.47) we measured in young *S. borealis* may indicate that these juveniles may be somewhat overexploiting their electron transport system, almost reaching ratios documented for fish. This may be one reason for the rapid growth of juvenile lollypop sponges (Figure III-7), which is typical for early colonizers.

2. Modelling

Growth rates of most Antarctic sponges are too slow to be measured directly (Dayton 1979). Hitherto inferring growth rate from metabolic rate seems to be the only feasible approach to growth of Antarctic sponges. Empirical data about the $P_s/\Sigma R$ ratio are summarized in Humphreys (1979) and in Banse & Mosher (1980). These data collections comprise a wide variety of invertebrate species (marine and terrestrial) but do not include any sponge species. The discussion of fundamental differences between sponges and other invertebrates regarding their metabolism (Thomassen & Riisgård 1995) makes the use of existing empirical data problematical. Consequently, we based our model on findings of the latter paper. Nevertheless our model based on oxygen consumption data provokes some problems. As stated before, our respiration data are likely to overestimate true resting metabolism as well as annual oxygen consumption rate. Together these overestimations lead to a possible overestimation of growth rates thus making our age-at-size data somewhat conservative.

The trial run with *Halichondria panicea* data (Figure III-6) indicates that the fit of our model is less than ideal regarding the smaller individuals. Hence our model results for young *Stylocordyla borealis* are also likely to be biased to some extend. Initial trial runs with different $P_s/\Sigma R$ fittings had shown that there is a trade-off between bias in results for small individuals on one hand and bias in results for large individuals on the

other hand. For our purposes of assessing the sponges' contribution to carbon and silicon cycling in the eastern Weddell Sea we used model settings providing the better fit in older and larger individuals.

3. Population energy budget

Based on our findings we can estimate components of the energy budget: C = P + R + E, where C is consumption, P is production, R is respiration and E is excretion (Table 2). Carbon requirements of *Stylocordyla borealis* were calculated with 4.5 gC m^{-2} y^{-1} and 71.5 gC m^{-2} y^{-1} for patches with average and maximum abundance, respectively. These calculations need to be interpreted in the light of two aspects: Firstly, at present our knowledge about feeding strategies of Antarctic sponges is less than fragmentary. Secondly, also our knowledge about the dynamics heterotrophic pico- and nanoplankton of the food web is limited.

On the basis of initial feeding experiments (Orejas, unpubl. data) it can be hypothesized that *S. borealis* may be feeding year round on microheterotrophs and nanoflagellats - the smaller planktonic fraction. Carbon from this fraction of the plankton is available in Antarctic waters throughout the whole year, albeit at lower levels when compared with microplankton summer blooms (Kang et al. 1997). Direct and indirect evidence points toward the utilization of this fraction by some filter-feeding taxa, such as cnidarians on the eastern Weddell Sea shelf (Orejas 2001) and the bryozoan *Arachnopusia inchoata* at Signy Island (Barnes & Clarke 1995). Additionally, sponges have been observed to take up dissolved nutrients in other latitudes (Reiswig 1981, Pile et al. 1996, Ribes et al. 1999). Primary production (PP) in Antarctic waters ranges from 16-100 gC m^{-2} y^{-1} (Grebmeier & Barry 1991). On the eastern Weddell Sea shelf PP in summer 1983 was 674 mgC m^{-2} d^{-1} (v. Bröckel 1985) corresponding to 81 gC m^{-2} y^{-1} (120 d y^{-1} of PP). Even though *S. borealis* does most probably not utilize PP directly, the above PP-figures indicate that carbon flow towards the heterotrophic planktonic food web and subsequently to the benthos is principally sufficient for *S. borealis*' requirements. This conclusion is also correct for patches of densest aggregations (48 ind m^{-2}), as hardly any other species can be found inside such dense patches of *S. borealis*.

Annual production of the *Stylocordyla borealis* population shown in our mass frequency distribution (Figure III-2) with a mean abundance of 3.02 ind m^{-2} (Gatti et al. subm.) amounts to 0.133 gC m^{-2} y^{-1}. This value is in the same order of magnitude as that of seastars near McMurdo Station (e.g. *Acodontaster conspicuus*: 0.187 gC m^{-2} y^{-1}, *Odontaster validus* 0.104 gC m^{-2} y^{-1}, Dayton et al. 1974), but distinctly lower than that of the pectinid *Adamussium colbecki* near McMurdo Sound (5.0-6.5 gC m^{-2} y^{-1}, Stockton 1984, Berkman 1990).

Lollypop sponges showed low annual P_s/B values (~0.106 y^{-1}) albeit not as low as was expected prior to this study (P_{tot}/B=0.03, Jarre-Teichmann et al. 1997). Our results are in the same range as those for the bivalve *Yoldia eightsi* at Signy Island: 0.117 (Rabarts 1970 fidem Brey & Clarke 1993), the seastars at McMurdo Station: *Odontaster validus*: 0.036 - 0.045 (Dayton et al. 1974, McClintock et al. 1988) and *Acodontaster conspicuus*: 0.069 (Dayton et al. 1974) and the sea urchin *Sterechinus antarcticus* on the Southern Weddell Sea shelf: 0.065 (Brey1991) (all data compiled in Brey & Clarke 1993). Lollypop sponges are thus most likely not contributing substantially to carbon flow patterns on the eastern Weddell Sea shelf. Somatic production of 0.133 gC m^{-2} y^{-1} corresponds to a deposition of 1.19 g m^{-2} y^{-1} of opal (biogenic SiO_2) in the form of spicules within the lollypop sponges (Gatti et al., subm.). Opal from PP that reaches the sea floor has not yet been determined with certainty for the eastern Weddell Sea shelf (Ragueneau et al. 2000). In the seasonal ice zone of the Weddell Sea it amounts to few mg SiO_2 m^{-2} y^{-1} (Tréguer & Jacques 1992). Compared with these existing figures it can be concluded, that lollypop sponges can locally be the predominant pathway of silicate to opal. Sponge spicules of Antarctic sponges may not dissolve *in situ* (Kabir 1996) and the accumulated spicule mass is deposited in the sediment after the death of the individual creating spicule mats up to 1.5 m thick (Koltun 1970, Barthel 1992). Spicule depositions can be up to 9000 years old (Conway et al. 1991), indicating that once opal is deposited in the form of sponge spicules it leaves biological cycling in the ocean.

Interest in population dynamic parameters of sponges has hitherto been limited, as sponges rarely contribute substantially to benthic biomass and have not, apart from bath sponge species (e. g. *Hippospongia lachne*), been used commercially. Thus production and productivity data for sponges are scarce. Hitherto commercial exploitation of Antarctic sponges has not been a topic of any interest. However, the intense search for bio-active compounds has also reached Antarctic waters. Based on the rather low annual estimates of P_s/B ratio (0.106) the low standing stock (1.3 gC m^{-2} y^{-1}) of *S. borealis* we conclude that there is an extremely low potential for extra mortality and commercial exploitation of this sponge species would be ecologically and economically unsustainable.

Conclusions

Stylocordyla borealis is a slow-growing Antarctic sponge reaching a maximum age of 150 years. Production and growth rates of this species as calculated by our model are possible on the basis of the known carbon input to the benthic system. From the low annual P_s/B ratio (0.106) and production (0.133 gC m^{-2} y^{-1}) we must conclude, that *S. borealis* does not contribute substantially to carbon flow on the Antarctic shelf. Nevertheless it is an important mediator in permanent burial of opal.

Based on AMIGO this is the first estimate of growth rates of a slow-growing sponge species. AMIGO is a valuable tool in assessing growth rates and age of species which can otherwise not be dated. In ongoing studies we will establish growth rates also for the large hexactinellid sponge species which characterize undisturbed areas on the Antarctic shelf.