PUBLICATION II

The Antarctic Iollypop sponge *Stylocordyla borealis* (Lovén, 1868): 1. Morphometrics and reproduction

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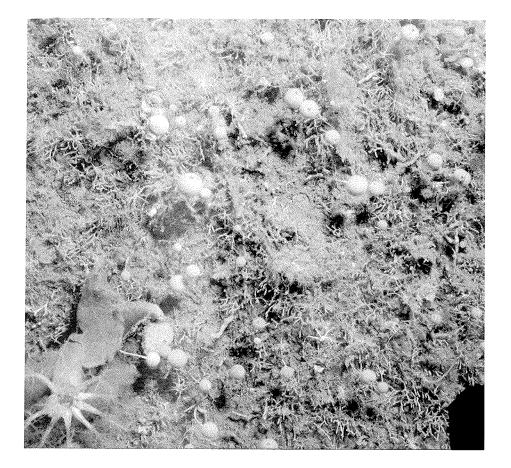
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Abstract

Parts of the Weddell Sea shelf (Antarctica) are characterized by dense aggregations of the lollypop sponge Stylocordyla borealis. Regardless of its distinct appearance and its known importance for recolonisation processes after iceberg scouring S. borealis has not yet been the subject of detailed ecological research. Mean abundance of S. borealis as documented in this study was 3 ind $m^{\text{-2}}$ (SE $\pm\,0.2),$ densest aggregations were inhabited by 48 ind m⁻². We determined basic morphometric relationships and presence or absence of embryos relative to size and mass of individuals. Bodies and stalks showed marked differences in their composition with bodies containing 9.2 % organic matter (% of wet mass) while stalks showed the lowest organic matter content documented for sponges (2.3 % of wet mass). Bodies contained 88.5 % ± 0.8 (mean ± 1SE) of the organic matter of the individual and can thus be assumed to be the metabolically active part, whereas stalks are of structural importance. Of the examined individuals 29% carried macroscopically visible embryos. At present it is not known how the embryos are released from the adult sponge. Based on size frequency distributions we hypothesize that the bodies of some individuals can be completely lost upon release of large numbers of embryos and may be regenerated thereafter.

Introduction

The lollypop sponge Stylocordyla borealis (Lovén, 1868) (Demospongiae, Hadromerida) is a very conspicuous member of the Antarctic sponge fauna. From underwater video and photographic studies we know that this species usually occurs in patches of sometimes dense aggregations (Figure II-1) on the shelf of the eastern Weddell Sea (Barthel & Gutt 1992, Gutt et al. 1996). Single individuals of lollypop sponges have been encountered in the Ross Sea near the stations McMurdo and Terra Nova Bay (pers. comm. McClintock). According to Burton (1928) S. borealis also occurs throughout the northern and southern Atlantic Ocean. Research on the family Stylocordylidae hitherto comprises histological studies (e. g. Sarà et al. in press), evaluation of its taxonomic status (e. g. Bergquist 1972) and biogeographical descriptions (e. g. Koltun 1976). Ecological data of lollypop sponges and Antarctic sponges in general are scarce. From extensive underwater imaging studies Gutt et al. (1996) concluded that S. borealis plays an important role in early recolonisation processes in iceberg scour marks. Despite their abundance and known structural importance on the eastern Weddell Sea shelf we know next to nothing about basic morphometric relationships or life cycle strategies of lollypop sponges. Sarà et al. (in press) recently clarified the reproduction mode of S. borealis.



According to their study lollypop sponges reproduce sexually by generating embryos. The authors concluded that embryos fall from the adult sponge and settle in close vicinity of it, as they did not find any larvae. We established basic morphometric relationships, and assessed reproductive effort of individuals of different size. These data will serve as a basis for further modelling of the growth and energy budget of *S. borealis* (Gatti & Brey subm.).

Materials and methods

Samples were taken in 1998 during RV "Polarstern" cruise ANT XV/3 (EASIZ II) in the eastern Weddell Sea. A complete list of stations, water depths, and deployed gear is given in Arntz & Gutt (1999). To assess abundance of *Stylocordyla borealis* a 70-mm underwater camera (Photosea 70) was used at 12 stations (depth range: 159 - 279 m) on the continental shelf off Kapp Norvegia. At each station sequences of 80-100 perpendicular colour slides (Kodak Ektachrome 64), each covering approximately 1m² of the seabed, were taken at evenly spaced time intervals along a transect. The optical resolution was around 0.3 mm. A total of 1131 seafloor photographs was analysed representing an area of 1131 m². A detailed description of the camera system is given in Arntz and Gutt (1999). In each picture all specimens of *S. borealis* were counted and were related to one of the two categories of benthic structure according to Gutt & Starmans (2001): (i) recolonisation stage or (ii) undisturbed scenario.

Conversion factors of different units of mass and volume, as well as relationships between mass of stalk and mass of body were determined from all intact specimens sampled during the entire cruise. One station (PS 48-222) yielded a catch of approximately 400 individuals of *S. borealis* (120ft bottom trawl, water depth about 250m, trawling distance 931.3m) of which about 180 specimens were in a sufficiently good condition for morphometric examination. These specimens were also used to establish a mass frequency distribution.

Length (L) and diameter (D) measurements taken are illustrated in Figure II-2. Volume (V), wet mass (WM), dry mass (DM) and ash free dry mass (AFDM) were determined following common procedures (e. g. Gatti et al. in press). AFDM was corrected for water loss of spicule mass during ignition (Dayton et al. 1974).

Figure II-1 *Stylocordyla borealis*. Dense aggregation of individuals on the shelf of the eastern Weddell Sea (station: PS 48-242, depth: ~166m). Photo: Julian Gutt, AWI.

All measurements were recorded for body and stalk separately. The indices 'body', 'stalk', 'tot' indicate that the value refers to body or stalk only or to the complete individual. Indices 'Smax', 'Smin' and 'S10' refer to maximum, minimum of stalk diameter and to stalk diameter 10 cm from the top, respectively (see also Figure II-2).

Inside a number of individuals we found spherical corpuscles of approximately 0.2 - 2 mm diameter which were identified as embryos by Sarà et al. (in press).

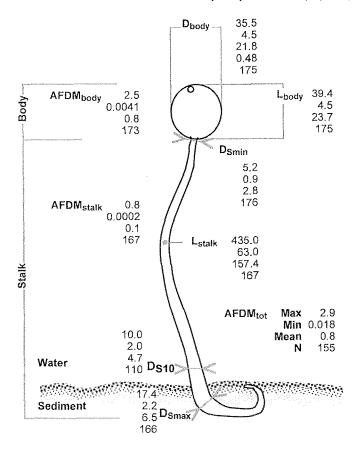


Figure II-2 *Stylocordyla borealis.* Average sized individual schematically drawn to scale. Measurements taken for morphometric analysis: L_{body} = body length (measured along stalk - osculum axis), D_{body} = body diameter (measured at a 90° angle to stalk-osculum axis), L_{stalk} = stalk length, D_{Smin} = stalk minimum diameter (usually directly below the body), D_{S10} stalk diameter 10 cm below the body (if applicable), and D_{Smax} = stalk maximum diameter (usually at a typical 90° sharp bend near basis of stalk). The column of data beside each measurement give maximum, minimum, mean values and number of individuals included in measurements in this order.

73 N/KN 185 KN	rdi (0)	Long (W)		orada	N photos [n]	[ind m ⁻²]	MIN [ind m ⁻²]	Max. [ind m ⁻²]	I otal [ind m ⁻²]
	«N 71° 07.2'	011°28.3′	276-278	Ο	56	1.9±0.2	0	7	104
	N 71° 31.7'	014°22.9'	162-160	D	88	4.46 ± 0.4	0	17	393
				٩	12	10.2 ± 1.4	9	20	122
				AII	100	5.2 ± 0.4	0	20	515
192 KN	N 71° 13.6'	012°25.4'	253-244	Ο	31	0	0	0	0
				٩	69	0.014±0.01	0	-	~-
				AII	100	0.01 ± 0.01	0	~	~
200 KN	N 71° 15.4'	013°08.7'	154-157	D	83	1.6±0.2	0	6	130
215 KN	N 71° 06.4'	011°31.9'	167-154	Π	85	3.1 ± 0.5	0	21	266
				٩	7	4.8 ± 2.7	0	21	34
				Scour	ø	0	0	0	0
				١١	100	3 ± 0.5	0	21	300
221 KN	N 70° 50.1'	010°35.6'	167-154		თ	5.4 ± 1.7	0	16	49
				٩	91	0.7 ± 0.2	0	თ	64
				١	100	1.1 ± 0.3	0	16	133
226 KN	N 70° 50.4'	010°34.8'	249-259	٩	62	1.2 ± 0.37	0	20	74
				Scour	37	0	0	0	0
				١	66	0.74 ± 0.24	0	20	74
229 KN	N 70° 50.7'	010°30.8'	223-228	П	97	0.04 ± 0.02	0	2	4
232 KN	N 70° 49.3'	010°29.0'	271-273	D	100	1.7 ± 0.2	0	6	174
239 KN	N 71° 06.2'	011°31.9'	190-227		42	3.2 ± 0.8	0	20	133
				Ъ	55	3.6 ± 0.8	0	36	197
				١N	97	3.4 ± 0.5	0	36	330
242 KN	N 71° 16.2'	012°19.8'	159-158	Γ	86	19.2 ± 1.4	0	48	1648
				٩	13	2.6 ± 0.8	0	ω	34
				١I	66	17.0 ± 1.38	0	48	1682
278 N/KN	<pre><n 53.4'<="" 70°="" pre=""></n></pre>	010°41.7'	279-273	С	100	0	0	0	0
; IIA	All Stations				1131	3 ± 0.2	0	48	3427

Table II-1 *Stylocordyla borealis*. Abundance in the eastern Weddell Sea during "Polarstern" cruise ANT XV/3. Data include mean \pm SE, minimum, and maximum number of individuals per photo for each recolonisation stage and station. 'Total sum' refers the specimens counted within the photo sequences (n). Each photo covers an area of approximately 1 m².

As embryos could not be separated quantitatively from somatic tissue, counting of exact numbers of embryos per individual was impossible. Abundance of embryos within an individual was noted semi-quantitatively on a three-step scale (none, few, many) and was then correlated with parent size and mass.

Results

Table II-1 shows the abundance of *S. borealis* calculated from 1131 photos belonging to 12 stations. Abundance was highly variable among stations and indicates a patchy distribution pattern. Four photographic transects were selected to illustrate the spatial dispersion of *S. borealis* (Figure II-3).

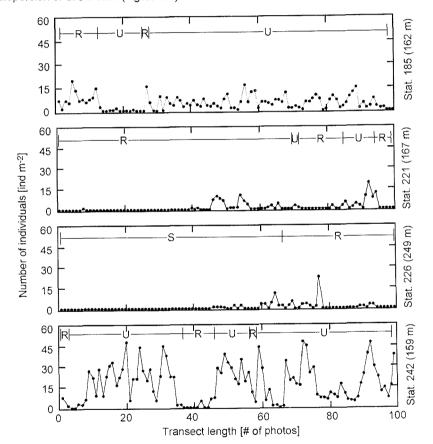


Figure II-3 *Stylocordyla borealis*. Spatial dispersion of along 4 photographic transects in Kapp Norvegia (Weddell Sea). Each point represents one photo analyzed. Different recolonisation stages are indicated by: R recolonisation stage (composed by initial recolonizing sessile species), U undisturbed, mature stage (consisting mainly of sessile suspension feeders), S scour mark (devoid of benthic fauna).

Mean abundance for all the stations was 3 ± 0.2 ind m⁻² (mean \pm SE). Three stations were characterized by the absence of *S. borealis* (279 photos). Five stations showed intermediate values (from 1.7 ± 0.2 to 5.2 ± 0.4 ind m⁻², 453 photos). Station 242 exhibited the highest mean value (17.0 ± 1.38 , 99 photos) with a maximum of 48 ind m⁻². In undisturbed areas abundance of *S. borealis* was generally higher than within recolonization stages. Comparative abundance of this species revealed differences in densities within small spatial scale and benthic structure.

Most of the mass of an individual was found within the body rather than the stalk. Specifically, body mass was $67.4\% \pm 1.1$ of WM_{tot}, $55.1\% \pm 1.0$ of DM_{tot} and $88.5\% \pm 0.8$ of AFDM_{tot} (all values mean ± 1 SE). Bodies consisted of $68.6\% \pm 0.62$ water, $21.8\% \pm 0.65$ spicule mass and $9.6\% \pm 0.18$ organic matter. Stalks consisted of $46.1\% \pm 0.63$ water, $51.6\% \pm 1.06$ spicule mass, and $2.3\% \pm 0.07$ organic matter. Maximum, minimum, and mean values of all length parameters and AFDM parameters are given

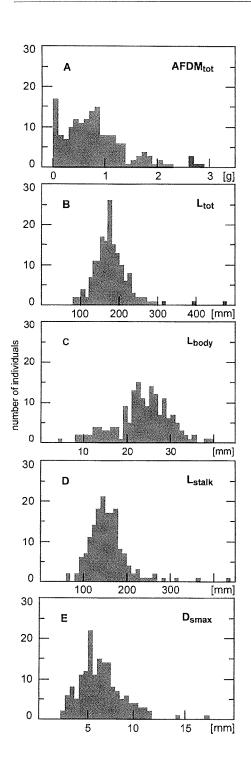
Table II-2 *Stylocordyla borealis.* Relationship between the different mass and volume measurements given as slope (b) and intercept (a) of linear regression. Units: mass [g], volume [cm³], length [mm].

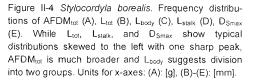
Х	Y	а	b	r ²
Vol	WM			
Voltot	WM _{tot}	0.9613	0.9749	0.926
Vol _{staik}	WM _{stalk}	0.9240	0.7828	0.853
Vol _{body}	WM _{body}	0.9446	0.8675	0.898
Vol	DM			
Voltot	DM _{tot}	0.3395	0.2139	0.932
Vol _{stalk}	DM _{stalk}	0.4930	0.5633	0.866
Vol _{body}	DM _{body}	0.2616	0.2436	0.873
Vol	AFDM			
Vol _{tot}	AFDM _{tot}	0.0813	0.0655	0.932
Volstalk	AFDM _{stalk}	0.0281	0.0100	0.745
Vol _{body}	AFDMbody	0.1008	0.0942	0.879
WM	DM			
WM _{tot}	DM _{tot}	0.3509	0 3661	0.938
WM_{stalk}	DM _{stalk}	0.4554	0.2818	0.970
WM_{body}	DM _{body}	0.2740	0.2886	0.863
WM	AFDM			
WM tot	AFDM _{tot}	0.0737	-0.0081	0.899
WM _{stalk}	AFDM _{stalk}	0.0252	-0.0052	0.869
WM_{body}	$AFDM_{body}$	0.1028	-0.0427	0.915
DM	AFDM			
DM _{tot}	AFDM _{tot}	0.1897	-0.0010	0.800
DM _{stalk}	AFDM _{stalk}	0.0547	-0.0191	0.872
DM_{body}	AFDM _{bady}	0.3089	0.0077	0.719

and AFDM parameters are given in Figure II-2. Conversions between all mass and volume measurements are summarised in Table II-2.

Frequency distributions of AFDM_{tot} and L_{tot} (Figure II-4 A and B, respectively) taken from the same set of individuals differed distinctly. No modes are distinguishable in L_{tot} frequency distribution while the AFDM_{tot} distribution seems to comprise 5-6 modes.

Bodies were spherical or near spherical in shape $(L_{body}/D_{body} = 1.1\pm0.01)$. Some individuals had disproportional small bodies resulting in high L_{stalk}/L_{body} ratios (Figure II-5, circles). There were no disproportional large bodies, which would have caused much smaller L_{stalk}/L_{body} ratios (i. e. far below the regression line).





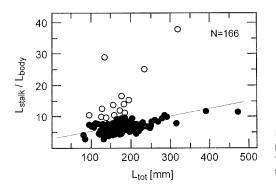
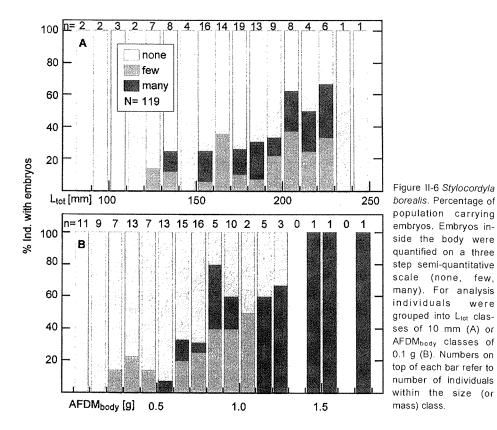


Figure II-5 Stylocordyla borealis. Regression plot of Lstalk/Lbody vs. Ltot. Dots: typical individuals, circles: individuals with extraordinarily small body (large Lstalk/Lbody ratio).

We found embryos in 29% of the individuals. All embryos were inside the body, none in the stalk of S. borealis. Within the body embryos appeared to be evenly distributed. Individuals of $L_{tot} \ge 120$ mm or AFDM_{tot} ≥ 0.2 g carried embryos (Figure II-6). About half of the embryo carrying individuals had few embryos while the other half carried many embryos.



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Discussion

Evaluation of the photographic material (Table II-1, Figure II-3) revealed the variable abundance of *Stylocordyla borealis* within a small spatial scale (m²) in different benthic assemblages over a relative large sampling area (1131 m²). The low mean abundance of the photographic station 221 (identified mainly as a recolonization stage) contrasted with the bottom trawl at the nearby station 222, where around 400 specimens were found. An explanation of this difference is the patchy distribution of Antarctic fauna. Also other typical pioneer species (the gorgonians *Primnoisis antarctica, Primnoella sp.*) occurred in high densities dominated along the transect at station 221. Nevertheless, we can conclude that *S. borealis* is one of the most dominant species in the Kapp Norvegia area. Spatial distribution of Antarctic sponges is influenced by a number of biotic and abiotic factors (e. g. Barthel & Gutt 1992). The influence of reproduction on distribution patterns is discussed below.

Table II-3 Organic content of Antarctic sponges. Minimum value (Min), maximum value (Max), average value (Mean), standard error (SE) for AFDM as % of DM as found by the respective study as well as number of specimens (N) and number of species (Species) included in the study.

Min	Max	Mean	SE	Ν	Species	Study
13.8	72.0	30.4	3.7	66	16	Dayton et al. 1974
20.4	68.1	38.6	3.1	51	17	McClintock 1987
7.4	60.1	21.9	1.9	403	37	Barthel 1995
3.3	31.3	17.8	0.5	155	1 (total)	this study
0.04	8.4	4.0	0.1	167	1 (stalks)	this study
9.1	49.7	30.5	0.7	173	1 (bodies)	this study

Morphologically individuals of S. borealis are clearly divided into two parts: A spherical body on top of an elongated rather thin stalk. Bodies of S. borealis showed organic content values typical of Antarctic sponges (30.5 ± 0.7 AFDM_{body} [% DM_{body}]) while stalks showed the lowest organic content values

(AFDM_{stalk} 4.0% \pm 0.1 of DM_{stalk}) ever measured for sponges (Table II-3).

For the first time we documented a marked difference in organic content of different morphological parts of one sponge individual. Furthermore, the body contributed the largest portion of an individual (67.4 % of WM_{tot}, 55.1 % of DM_{tot}, 88.5 % of AFDM_{tot}). The high spicule content of the stalk (51.6 % of WM_{stalk}), its very low organic content (2.3 % of WM_{stalk}) and its comparatively low water content (46.1 % of WM_{stalk}) cause the stalk to be a rather dense and rigid structure. The body on the other hand consists of only 21.8 % (of WM_{body}) spicules, much more water (68.6 % of WM_{body}) and organic matter (9.6 % of WM_{body}). The body is thus less dense, much more porous and consequently more permeable for water. Such a clear division into morphologically, structurally and compositionally different parts suggests an equally clear division with regards to functional purposes. From the studies of Koehl et al. (2001) and Patterson et al. (1991) we know that nutrient availability, gas exchange and consequently metabolic activity of sessile invertebrates are positively correlated with

water flow speed. Moreover, the steepest gradient in increase of flow velocity is found within the first few centimetres above the bottom (Jumars & Nowell 1984). Principally sessile organisms can utilise various strategies to access more favourable higher layers of water: (1) Organs for prey capture as well as nutrient and gas exchange can be extended into higher water layers. Captured nutrients and exchanged gases need to be actively transported from the capture site down to the metabolically active body part (e. g. Crinoidea). (2) Assimilation can be performed in apical body parts and acquired energy equivalents serve as an energetic reservoir for maintenance of lower body parts (e, g. Sedentaria). In this case transportation of energy equivalents is necessary. And (3) the whole metabolically active part of an individual can be raised into the water column by a 'self-made' carrier which in itself does not cause high energetic costs for building or maintenance (e. g. Pennatulacea). Our results strongly suggest that Stylocordyla borealis belongs to the third group. A separation into a structural part (the stalk) lifting the complete metabolically active part of the individual (the body) up into more favourable water layers may even be energetically more efficient than transportation of energy equivalents or food particles. The general scarcity or absence of thinly encrusting sponge species from the Antarctic benthos (Barthel et al. 1997) may be related to the overall iow food particle availability (Arntz et al. 1994). A separation into morphologically, structurally and compositionally different parts has hitherto not been documented for sponges and can be considered a special adaptation of a filter feeding organism to general food scarcity in the Antarctic environment.

Sponges, contrary to other metazoans, lack distinct tissues and have often been considered to be simple lumps of cells with little or no co-ordination between cells. This perception of sponges as simple organisms even led to explicit restriction in research (Schupp et al. 1999). While other erect sessile marine organisms were regularly examined for intra-individual gradients of secondary metabolites, sponges were subjected to such research only recently (Becerro et al. 1998). Physiological evidence is accumulating supporting the observed morphological and compositional differences. (1) Becerro et al. (1998) and Schupp et al. (1999) documented a gradient of levels of secondary metabolites within one individual. (2) A marked difference in organic content of stalks and bodies of *S. borealis* was found (this study). (3) Metabolic activity within individuals *S. borealis* differs strongly between stalk and body (Gatti & Brey, subm). (4) Reproduction products were concentrated within certain body parts and were absent from other body parts of *R. topsenti* (Ayling 1980) and for *S. borealis* in this study (see below). These results indicate that sponge biology may be a little more elaborate than has hitherto been assumed.

The smallest individual carrying embryos had a L_{tot} of 123 mm (i.e. 26% of maximum L_{tot}). Larger individuals tended to carry more embryos and also a larger proportion of individuals participated in reproduction (Figure II-6). Fell (1993) reviews that reproduction in sponges starts once a minimum size (or age) is attained. Jamaican

Mycale sp. produce eggs only when specimens have reached a volume of at least 8% of maximum individual volume (Reiswig 1973). Raspailia topsenti in northern New Zealand did not reproduce when an individual had less than 5% of maximum number of finger-like protrusions from the base (Ayling 1980). On the other hand do all individuals (i. e. also very small ones) of the Macedonian freshwater sponge Ochridaspongia rotunda and the Caribbean Clathrina contribute to reproduction (Gilbert & Hadzisce 1977, Johnson 1978, respectively). Also, all but the very small postlarval individuals of Haliclona loosanoffi (from the Cape Hatteras region) initiate gametes (Fell 1976). This evidence suggests that reproduction can start very early in the life history of many sponges. However, Witte (1995) found that individuals of Thenea abyssorum from the Greenland deep sea started reproducing only at a minimum diameter of 8 mm (i. e. 32% of maximum diameter). S. borealis in our study carried at least some embryos when they had reached 26% of maximum Ltot. Reproduction in the two studied species of polar sponges thus started comparatively late i. e. at a larger size than in tropical or temperate sponge species. Such a comparatively late onset of reproduction can also be observed in other polar marine invertebrates (e. g. Clarke 1982).

The body part is the sole site of reproduction, as we never found embryos in the stalk part of an individual. It has hitherto been assumed that reproductive products (eggs, sperm, embryos or developing larvae) were distributed evenly in all parts of a sponge individual (Simpson 1984). The only other report of a strict limitation of reproductive products to certain parts of a sponge refers to *Raspailia topsenti* where larvae are found in apical parts only (Ayling 1980). Upper parts of a sponge are usually exposed to a more favourable current regime supplying more food particles (see above). As oogenesis is a particularly energy consuming process (Fell 1983) an alignment of the sites of oogenesis and of enhanced food supply within one individual is plausible. Also, from a larvae, embryos, or gametes point of view it is advantageous to start dispersal from an elevated point utilizing stronger currents rather than starting close to the sediment surface where flow velocity is generally smaller (Jumars & Nowell 1984).

Approximately 8.4 % of the collected individuals carried a disproportional small body (Figure II-5 circles). For the majority of the individuals (91.6 %) AFDM_{tot} depended to more than 82% on AFDM_{body}. As AFDM_{body} has such a large influence on AFDM_{tot} the frequency distribution of AFDM_{tot} (Figure II-4A) reflects variations in body mass rather than consecutive age groups as typically caused by subsequent reproductive events. The conclusion that the modes do not represent age classes is substantiated by the fact that comparable modes could not be found in the frequency distributions of L_{tot}, L_{stalk}, or D_{Smax} (Figure II-4B-D).

To explain the presence of disproportional small bodies we propose the following hypothesis: an individual may loose its body and subsequently the body can be regrown on top of the stalk material left after body loss. If indeed only the body would

be affected by a mechanism of loss we would find a 'too small' body on top of a 'too large' stalk during the period of regrowth. Neither Lstalk nor Dsmax would be affected by such a loss of body and the described difference in frequency distribution plots would be plausible. Reasons for such a body loss could be (1) predation, (2) physical damage or (3) reproductive events. As lollypop sponges often occur in dense aggregations, predation (because of easy access to prey) and physical damage (e. g. iceberg scouring) should affect a larger number of individuals (i. e. more than 8.4 % of the population). To us the most likely explanation for loss of a body is a reproductive event. The body of some of the individuals containing 'many' embryos was densely packed with several hundred embryos and with very little tissue in between. Some of the larger embryos were more than 1.5 mm in diameter. If a large proportion or all of those embryos were released within a short period of time the body would virtually be an empty sphere. Furthermore the body wall would be ruptured several times to release many embryos at once. Release of reproductive products through the dermis has previously been reported for Hemectyon ferox (Fell 1983). Additionally, Maldonado & Uriz (1999) report that chances of establishing new populations are enhanced by the dispersal of larger fragments of sponge containing embryos. While according to Sara (pers. com.) and Maldonado and Uriz (1999) embryos alone are limited in their dispersal ability, larger sponge fragments containing embryos can travel rapidly over several kilometres (Maldonado & Uriz 1999). Following that argument, embryos of S. borealis could reach open patches some distance away when incorporated in body fragments but would stay within the same patch when released from the body without fragmentation. One body rupturing from its stalk and containing several hundred embryos would be able to initiate a new dense aggregation of lollypop sponges at considerable distance downstream. Even though we were never able to directly observe release of embryos, we hypothesise that occasional massive embryonic release and/or fragmentation from single individuals with subsequent regrowth of body material is the mechanism underlying the observed difference Lstalk/Lbody ratios (Figure II-4). In the extremely fire-resistant and shade intolerant giant sequoia (Stephenson 1992) the simultaneous release of several million seeds (Hickman 1996) is event driven by fires around the tree trunk. At present it is unknown whether release of embryos in S. borealis is also event driven by some hitherto unknown mechanism or whether it follows an internal rhythm. A detailed study of genetic variation within and between aggregations of Stylocordyla borealis would further our knowledge about dispersal patterns of this species.

The findings of this paper will serve as a basis for a detailed study of metabolic activity of the different parts of *S. borealis.* Based on respiration rates we will model growth rates of this species and assess its contribution to carbon flow patterns on the Antarctic shelf.