

Population dynamics and production of *Scolelepis gaucha* (Polychaeta: Spionidae) on the sandy beaches of Southern Brazil

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ABSTRACT: *Scolelepis gaucha* (Orensanz & Gianuca, 1974) is the most abundant polychaete species on subtropical and temperate intertidal beaches along the Atlantic coast of South America. The population and production dynamics of this species were described from samples taken between May 1988 and July 1989 at each of 4 intertidal beach transects near Patos Lagoon in Southern Brazil. *S. gaucha* presented a multiannual life cycle (with 2 cohorts each year) which was related to the diffusion pattern necessary to maintain its endemic distribution on a coast with strong seasonal processes. The spatial differences observed in mortality rates (Z varying from 3.24 to 11.35 yr⁻¹) were associated with variations in intertidal stability as expressed by the different sedimentological zones found between transects. Differences in growth and mortality were observed between the cohorts, caused by the temporal modification of beach profile which benefitted the food uptake of the first cohort. Compared with other spionid species on sandy beaches, high values of mean annual biomass (between 2 and 31 g AFDW m⁻²) and production (between 6 and 113 g AFDW m⁻² yr⁻¹) were found. Beach morphodynamics was the major factor controlling both the mortality and growth patterns of *S. gaucha* and thus its production on the Southern Brazil sandy beaches.

KEY WORDS: Population dynamics · Secondary production · Polychaeta · Brazil · Sandy beaches

INTRODUCTION

Although spionids are one of the most common benthic community species in shallow marine ecosystems (Blake 1983), data on their population dynamics and production are comparatively few (Buchanan & Warwick 1974, Warwick et al. 1978, Vázquez & Rojas 1980, Warwick & George 1980, Rees 1983, Tamai 1985, Lambek & Valentijn 1987, Ambrogi 1990, Steinle et al. 1990). To a great extent, this scarcity of numerical data reflects the methodological difficulties in sampling and measuring small, soft-bodied infaunal species with a short life-span. These characteristics, which are generally associated with high fecundity rate and large temporal fluctuations in abundance, depend on high turnover rates that make such species likely to play an important role in the benthic energy flow.

This study focuses attention on the population dynamics and production of *Scolelepis gaucha* (Orensanz & Gianuca, 1974), an endemic polychaete species in Southern Brazil, Uruguay and Northern Argentina. In this regions *S. gaucha* is the most abundant polychaete species in the intertidal, with densities up to 100 000 ind. m⁻² in spring and early summer (Santos 1991). The presence of 2 cohorts was suggested by Gianuca (1985), based on the presence of very young individuals in both late autumn and early spring. Santos (1991) described the influence of a temporary freshwater stream on the recruitment and growth of this species and suggested that beach morphodynamics was a major factor acting on its population dynamics.

MATERIALS AND METHODS

Four transects (A, B, C and D) were located at 2, 8, 26 and 76 km respectively south of the outlet of Patos Lagoon, Southern Brazil (Fig. 1). In this area the

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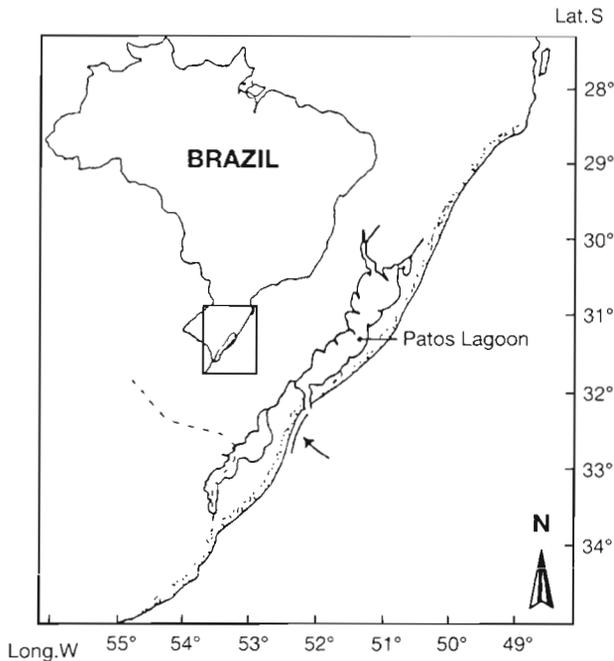


Fig. 1. Location of the study site in southern Brazil. Arrow indicates transects area

mean grain size of the beach varies between 0.100 and 0.250 mm with an intertidal slope of 0.7 to 3.8° (Santos 1990). Gianuca (1985) described it as 'exposed' using the McLachlan (1980) rating system. Using granulometric characteristics, slope and wave energy (Fleming & Fricke 1983) it can also be classified as a dissipative beach (Short & Wright 1983). Tides are usually very small, the range rarely exceeding 0.5 m (Motta 1969). Therefore, the water level variation is strongly controlled by winds (Gianuca 1985). Sea water temperature and salinity vary from 11 to 27°C and 17 to 35‰, respectively, demonstrating a clear seasonal pattern (Gianuca 1985).

At each transect, 5 stations (I to V) were fixed at 10 m intervals from low tide mark upwards and surveyed fortnightly or monthly (Transect B) or at 3 mo intervals (other transects) between May 1988 and July 1989. During this period data were obtained from both the intertidal benthos and the surf-zone zooplankton.

At each station ten 0.0018 m² × 0.3 m cores were taken. Sediment samples were sieved through 0.3 mm screens after preservation in 10% formalin. After counting the animals, the width of the 5th setiger of a minimum of 100 individuals, chosen haphazardly, was measured to determine the population size structure. Population densities were expressed as individuals per linear meter of beach front (ind. m⁻¹) (Brown & McLachlan 1990), where transect length was 40 m.

Zooplankton samples were taken with a 0.3 m diameter, 0.2 mm mesh size, cylindrical net. The volume

of water filtered varied from 500 to 1500 l and was measured by a flow meter placed within the net mouth. Samples were taken on the surface of the water column facing each transect.

The programme Compleat ELEFAN (version 1.10) was used to estimate growth parameters, mortality rate and recruitment pattern (Gayaniilo et al. 1989). The routine ELEFAN I was used to fit a von Bertalanffy growth curve modified for seasonal oscillations in growth (Pauly & Gaschutz 1979) to the set of restructured length-frequency samples. This curve has the form:

$$Wd_t = Wd_\infty \{1 - \exp[-K((t-t_0) + C/2\pi \cdot \sin(2\pi(t-t_5)))]\}$$

where Wd_t is the width at time t , Wd_∞ the asymptotic width, K the von Bertalanffy growth constant, C a constant expressing the amplitude of growth oscillation, t_5 the starting point of oscillation with respect to $t = 0$, and t_0 the origin of the growth curve.

The routine ELEFAN II provided preliminary values for both Wd_∞ (asymptotic width) and Z/K , using the Wetherall method as modified by Pauly (1986). The annual mortality rate coefficient Z (from the single negative exponential model: $N_t = N_0 e^{-Zt}$, with t in yr) using a length-converted catch curve (Pauly 1984), and the recruitment pattern determined through the projection of the size frequency data backward onto the time axis, were also estimated by this routine. One or two normal distributions were fitted to the restructured data when these were sufficient to explain 80 to 110% of the observed recruitment.

Production was estimated using both Crisp's method 3A (production for stocks with recruitment, age classes not separable; Crisp 1984), and Allen's relationship for populations with mortality expressed by a simple exponential and growth expressed by a von Bertalanffy model. In the latter case, production to biomass ratio (P/B) equals the mortality rate (Allen 1971).

For the production calculation the relationship between body ash-free dry weight (AFDW in mg) and the width of the 5th setiger (Wd in mm) was used as: $\ln AFDW = -19.984 + 3.881 \ln Wd$ ($r = 0.991$ and $n = 18$ groups of different size-class individuals) (Santos 1990).

Data on simultaneously obtained environmental factors (such as salinity, temperature, midlittoral profile, granulometric parameters and others) were taken from Santos (1990).

RESULTS

Planktonic larvae

Stages from 5-setiger larvae to juvenile forms similar to early benthic recruits were recorded in zooplankton samples. No adults were observed.

Table 1 *Scolecipis gaucha*. Planktonic density values (ind. m⁻³) for larvae at each transect with time

Date	Transects			
	A	B	C	D
02 May 1988	20	-	35	3
20 May	-	23	-	-
17 Jun	-	6	-	-
15 Jul	-	6	-	-
27 Jul	0	0	0	0
17 Aug	-	5	-	-
01 Sep	-	99	-	-
21 Sep	-	38	-	-
28 Sep	-	1718	-	-
12 Oct	-	43	-	-
27 Oct	17	9	46	455
25 Nov	-	0	-	-
16 Dec	-	0	-	-
15 Feb 1989	0	1	0	0
15 Mar	-	0	-	-

Plankton densities of *Scolecipis gaucha* were highly variable in time and space (Table 1) but 2 density peaks could be observed, the first with lower values (probably registered only in part) on 20 May 1988 and the second with higher values (maximum 1718 ind. m⁻³) on 28 September 1988.

Benthic stages

With a maximum density of 1106250 ind. m⁻³ (25 November 1988 at Transect B), the abundance of *Scolecipis gaucha* in the benthos also displayed high spatial and temporal variability (Table 2). On the other transects the same trend was observed, though with different average densities (Table 2). Values of variance to mean ratio between core samples for single stations were not different from those expected for a Poisson distribution (Santos 1990).

Growth

The length frequency data used to model *Scolecipis gaucha* growth were taken only from transect B and are presented in Fig. 2. Wetherall's method provided the values of 0.87 mm and 3.929 as first estimates of Wd_{∞} and Z/K respectively. Examination of the length frequency data suggested the existence of at least 2 cohorts. Thus, growth curves were fitted to the data with different

Table 2. *Scolecipis gaucha*. Benthic density values (ind. m⁻³) for each transect (40 m long) with time

Date	Transects			
	A	B	C	D
04 May 1988	7 185	5 790	4 420	3 320
03 Jun	-	98 585	-	-
17 Jun	-	52 475	-	-
01 Jul	-	54 135	-	-
15 Jul	-	50 810	-	-
26 Jul	7 170	47 500	16 580	57 990
17 Aug	-	63 940	-	-
01 Sep	-	103 275	-	-
14 Sep	-	103 285	-	-
28 Sep	-	584 340	-	-
12 Oct	-	548 565	-	-
27 Oct	272 390	792 000	42 530	945 050
25 Nov	-	1 106 250	-	-
16 Dec	-	88 420	-	-
18 Jan 1989	-	14 910	-	-
15 Feb	0	3 310	3 865	22 925
15 Mar	-	1 100	-	-
10 Apr	-	1 840	-	-
08 May	0	0	4 000	-
09 Jun	-	920	-	43 520
14 Jul	-	6 620	-	-

starting points in order to determine the parameters for each cohort. This procedure, run with ELEFAN I, provided 2 growth curves differing especially in the parameter K (Fig. 2). Rn goodness of fit values (roughly corresponding to the parameter r^2 in correlation analysis; $Rn = 10^{(\text{Explained sum of peaks}/\text{Available sum of peaks})/10}$) of 0.62 and 0.88 were obtained for the first and second cohorts respectively (fitted separately to individual cohort data; width class interval 0.06 mm).

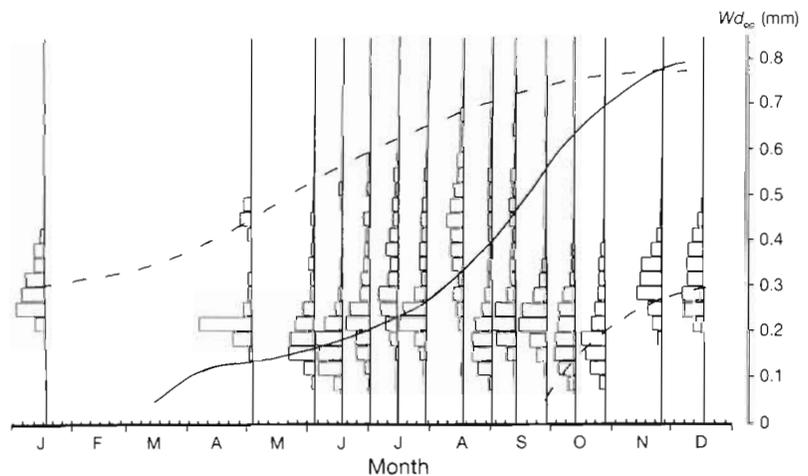


Fig. 2. *Scolecipis gaucha* growth curves plotted over size-frequency data of Transect B (2 years combined). The growth parameters are: for the first cohort (solid line), $Wd_{\infty} = 0.89$ mm, $K = 3.4$, $C = 0.85$, and $t_s = 0.90$; and for the second cohort (dotted line), $Wd_{\infty} = 0.83$ mm, $K = 2.5$, $C = 1.0$, and $t_s = 0.55$

Recruitment

Fig. 3 presents the recruitment pattern obtained with ELEFAN II, using the average of the 2 cohort growth curve parameters and the length frequency data of Transect B. Two normal distributions were fitted to the data, explaining 97% of the observed recruitment; the peaks of the 2 distributions were separated by a period of approximately 5 mo.

Mortality

The length-converted catch curve for Transect B data (using average growth parameters) provided a high mortality rate coefficient ($Z = 11.354 \text{ yr}^{-1}$) (Fig. 4). A similar value ($Z = 11.787 \text{ yr}^{-1}$) was obtained using the Z/K value of 3.929 from Wetherall's method and the mean growth parameter K . Mortality rate coefficients calculated on individual cohort data were 10.084 and 16.435 yr^{-1} for the first and second cohorts respectively.

The length frequency data from seasonal sampling provided the following values of Z : 10.429 yr^{-1} for Transect A; 17.310 for Transect B; 4.937 for Transect C and 5.522 for Transect D.

Production

With a mean annual biomass of 5.71 g m^{-1} and a production of $73.8 \text{ g m}^{-1} \text{ yr}^{-1}$ (calculated with Crisp's method for Transect B data), *Scolecipis gaucha* presented a high value of production to biomass ratio ($P/B = 12.92$) at Transect B. The temporal production pattern (Fig. 5) shows clearly that most of this production is attained in 3 mo.

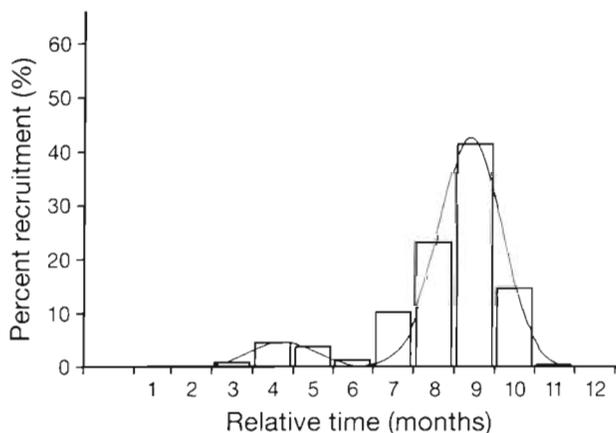


Fig. 3. *Scolecipis gaucha* recruitment pattern at Transect B. First and second pulses responsible for 10.68 and 86.36% of the total recruitment

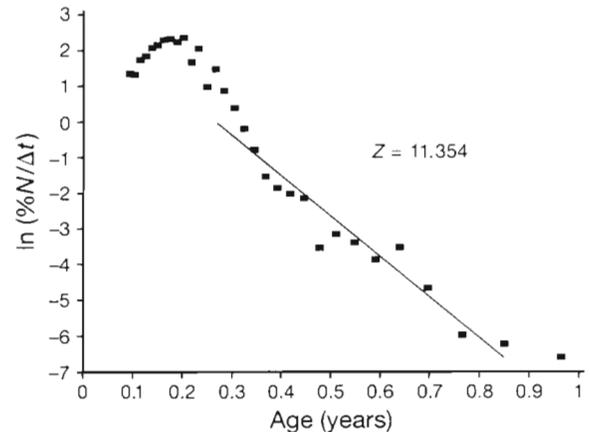


Fig. 4. *Scolecipis gaucha*. Length-converted catch curve at Transect B ($Z = 11.354 \text{ yr}^{-1}$)

Considering $Z = P/B$ (Allen's method), the estimated value of $64.8 \text{ g m}^{-1} \text{ yr}^{-1}$ obtained for the production at Transect B is not very different from that obtained using Crisp's method. By correcting the mortality rates and the biomass values (Table 3) for the seasonal sampling interval effect (using the values obtained for Transect B) values of 19.9, 5.7 and $113.4 \text{ g m}^{-1} \text{ yr}^{-1}$ were obtained for the production at Transects A, C and D respectively.

DISCUSSION

The existence of 2 generations every year of *Scolecipis gaucha* (as is suggested by the density data, where 2 peaks could be observed with time intervals of 4.3 and 5.7 mo for zooplankton and benthos respectively; Tables 1 & 2) was supported by the clearly bimodal recruitment pattern with modes separated by 4.6 mo (Fig. 3).

According to the classification proposed by Fauchald (1983), *Scolecipis gaucha* exhibiting 2 annual generations and a partly benthic development, may be classified as multi-annual. The capacity for great dispersion or diffusion (sensu Pielou 1977) during the planktonic development (mean velocities of 1.3 km h^{-1} for the coastal currents (Motta 1969)) seems however to make the multiannual life diagram pattern inapplicable for this species.

The high velocities of the coastal current speeds (Motta 1969) and the high turbulence of the surf-zone suggests, in according with Hannan (1984), that *Scolecipis gaucha* larvae act as passive particles when dispersing along the coast. Wind is the main factor driving coastal currents in the shallow waters along the beaches of Southern Brazil. A sustained wind from one direction during the period of planktonic development

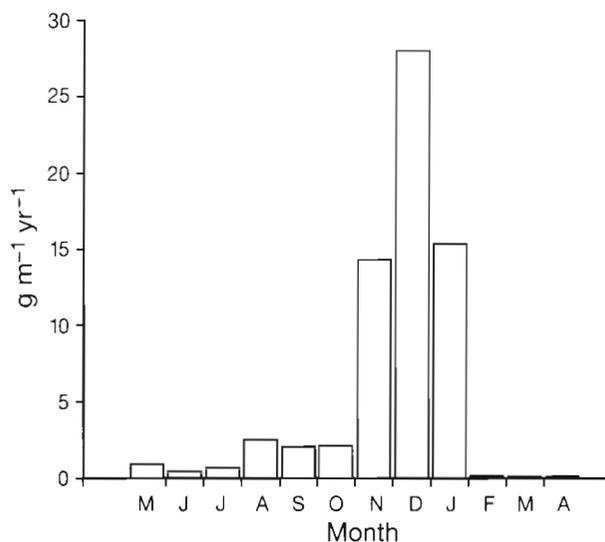


Fig. 5. *Scolecipis gaucha*. Time distribution of production

Table 3. Mean annual biomass (g AFDW m⁻¹) and production (g AFDW m⁻¹ yr⁻¹) values for the different sampled transects (40 m long) (values for Transects A, C and D corrected for the sampling interval effect)

	Transects			
	A	B	C	D
Biomass	2.91	5.71	1.77	31.32
Production	20	74	6	113

would tend to displace the population from its area of origin and probably cause competition with the ecological equivalents: *Scolecipis squamata* in the north (Bolivar & Lana 1988) and *Spio* sp. (Escofet et al. 1979; probably *Spio quadrisetosa* Blake, 1983) in the south.

During late autumn the higher frequency of winds from NE and N, associated with the lower energetic level waves from SE to S (Santos 1990), probably carries the first cohort larvae to the south. This tendency is, however, reversed by the higher frequency of SW to S winds in late winter that probably carry the second cohort larvae to the north. The bivoltine pattern in this population of *Scolecipis gaucha* may be a mechanism that helps to maintain this species along a coastline with seasonally strong long-shore currents (Santos 1990).

The von Bertalanffy model described well the growth of *Scolecipis gaucha* specimens and allowed each cohort growth to be distinguished (Fig. 2). The seasonal growth pattern was clear for the first cohort with a winter point (equal to $t_s + 0.5$ and corresponding to the moment of lowest growth rate during the year cycle) occurring in May. This was a period with low

water temperature (mean 14 °C) (Santos 1990), and probably reflects the influence of temperature on the growth of this species (see also Rice & Simon 1980, Levin & Creed 1986 and Yokoyama 1988 for other spionids).

Thus, the difference between the growth curves of the 2 cohorts at Transect B (Fig. 2), the winter point and the higher mortality rate found for the second cohort are all probably the result of seasonal morphological variations of the beach profile or beach morphodynamics. The first cohort settled at a time of high wave energy during the annual cycle (i.e. when the beach presents a swell- or winter-profile characterized by slight declivity). These dissipative conditions enable the swash to extend further and thus allowed a greater area/time with optimum water velocity for feeding, for the same vertical variation of water level.

According to Gianuca (1985) this period is also characterized by a higher frequency of bloom occurrence of the diatom *Asterionella glacialis*, which is ingested by *Scolecipis gaucha* and could also be responsible for higher growth rate and lower mortality. The second cohort settled during a period of lower wave energy and, during its growth, the intertidal zone presented greater declivity (mean values of 1.33° between 27 October and 9 December 1988 as compared with 1.15° between 3 June and 8 September 1988; data from Santos 1990).

Correction of the mortality rates for the seasonal sampling interval effect provided values of $Z = 6.84$, 3.24 and 3.62 yr⁻¹ for Transects A, C and D respectively. The lower mortality rates estimated for Transects C and D are probably related to the greater stability of their sediment deposits on the intertidal zone during the recruitment periods. The standard variations ($n = 7$) of intertidal declivity were 0.290, 0.376, 0.187 and 0.232° for Transects A, B, C and D respectively (data from Santos 1990). An exponential regression between these values and the mortality rates is significant ($T = 7.91$, $p < 0.05$). The sedimentological statistical parameters for the different intertidal groups of stations (Table 4; data from Santos 1990) were also more stable on Transects C and D as compared with parameters for A and B during this period.

Allen & Moore (1987) showed that environmental stability is the main factor structuring sandy beach communities. Studying the impact of a temporary freshwater stream on the population dynamics of *Scolecipis gaucha*, Santos (1991) suggested that beach morphodynamics was a major factor affecting the survival of the different cohorts. This hypothesis is supported in the present study on a larger scale, and the influence of beach morphodynamics can be regarded

Table 4. Sedimentological statistical parameters for 3 areas in the midlittoral through time (values in phi units)

Date	Parameter	Group: Transects:	Lower midlittoral		Upper midlittoral		Runnel C & D
			A & B	C & D	A & B	C & D	
Jul 1988	Mean		2.70	2.25	2.85	2.46	–
	Median		2.72	2.25	2.80	2.54	–
	SD		0.41	0.49	0.32	0.46	–
	Skewness		–0.11	0.03	0.19	–0.26	–
	Kurtosis		1.31	0.77	1.07	0.99	–
Oct 1988	Mean		2.49	2.33	2.85	2.55	–
	Median		2.48	2.35	2.83	2.60	–
	SD		0.35	0.50	0.35	0.39	–
	Skewness		0.10	–0.04	0.09	–0.27	–
	Kurtosis		1.30	0.80	1.19	1.11	–
Feb 1988	Mean		2.92	2.23	2.87	2.41	2.29
	Median		2.90	2.21	2.83	2.49	2.30
	SD		0.36	0.51	0.34	0.45	0.47
	Skewness		0.02	0.11	0.11	–0.24	–0.02
	Kurtosis		0.90	0.92	1.02	1.01	0.76
May 1988	Mean		2.83	2.40	2.87	2.52	2.37
	Median		2.81	2.46	2.81	2.60	2.42
	SD		0.38	0.53	0.32	0.44	0.48
	Skewness		0.02	–0.11	0.20	–0.28	–0.13
	Kurtosis		1.25	0.87	1.00	1.14	0.83

as a factor extending to the control of growth rates for different cohorts.

The mean biomass values were high (Table 3); transformed from AFDW to dry weight (to enable comparison with other published data), they varied from 3.40 g m⁻¹ on Transect C to 63.4 g m⁻¹ on Transect D. McLachlan et al. (1981) estimated, for the congeneric *Scolelepis squamata* on South African sandy beaches, a value below 1 g m⁻¹ for a beach width of 40 to 80 m and a total biomass of 1503 g m⁻¹. McDermott (1983) calculated a value of 50 g m⁻¹, also for *S. squamata*, on the Atlantic coast of the United States for a 'Scolelepis zone' of 20 m. In the latter study, the spionid was the dominant species in the community and also the principal food (on a dry weight basis) for the surf zone fish community. Since biomass, and thus production, are negatively influenced by formal preservation (Howmiller 1972, Lambeck & Valentijn 1987), the calculated values are probably underestimated by a factor of 25%. Considering especially the temporal distribution of production (Fig. 5), the values calculated for *S. gaucha* indicate that this small species can play an important role in the southern Brazil sandy beach community.

The production value obtained by Crisp's method was similar to the one obtained by assuming $Z = P/B$, thus supporting the adequacy of the employed mortality and growth models. The values of P/B are among the highest values obtained for polychaetes (see Robertson 1979, Chesney 1985, Lambeck & Valentijn 1987), showing once again the importance of small polychaete species.

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