Document format: TIFF-5.0

Document Destination: ???.???.???.???

Document ID: Bulletin of Marine Science

Supplier Name: Ariel/Windows

Date Sent: 10-25-05

Note: Bulletin of Marine Science (67) 1, 221-233, 2000

Number of Pages: 13

BULLETIN OF MARINE SCIENCE, 67(1): 221–233, 2000

POPULATION DYNAMICS AND SECONDARY PRODUCTION OF *SCOLELEPIS SQUAMATA* (POLYCHAETA: SPIONIDAE) IN AN EXPOSED SANDY BEACH OF SOUTHERN BRAZIL

José R. B. Souza and Carlos A. Borzone

ABSTRACT

Scolelepis squamata is a common component of sandy beach environments. It is the most abundant species on some Brazilian intertidal beaches, but little is known about its population dynamics and secondary production. The distribution, population dynamics and secondary production of this species on Atami Beach (Southern Brazil) was studied from February 1992 to February 1993. The organisms were concentrated in a narrow band along the middle intertidal beach, reaching mean maximum densities of 20,277 m^{-2}. Ovigerous females were present throughout the year with the highest percentages in February and August. Two peaks of recruitment were identified, one in April and the other in October. This population produced two identified cohorts during the year. The life span was of 0.66 and 0.49 yrs, and the mortality was 2.52 and 5.52 y^{-1}, for each cohort respectively. Mean annual biomass was 0.21 g m^{-2} (AFDW), and mean annual production was 0.57 g m^{-2} y^{-1} (AFDW). The P/B ratio was low, 2.70 y^{-1}, in particular when compared with species of similar life span. Data suggested that this species presented r-strategist characteristics (sensu McArthur), with a short life span, great reproductive effort, and an opportunistic behavior.

Scolelepis squamata is a common component of sandy beach environments with a wide geographical distribution. It was been recorded from England, Mediterranean Sea, North Pacific, North and South Atlantic, South Africa, India and Senegal (Day, 1967; Bolívar and Lana, 1987). It is, however, possible that this large distribution actually represents a series of morphologically similar species and the identify of the Brazilian species is currently under review (A. Mackie, pers. comm.). The species reaches greatest abundance on some exposed beaches of North and Southwestern Atlantic coasts (McDermott, 1983; Knott et al., 1983; Borzone et al., 1996).

This species lives in vertical tubes formed by sand and mucus. Dauer (1983) suggested that this species was restricted to sediments with a high permeability, necessary for the maintenance of its respiratory requirements. It collects food particles almost exclusively above the sediment-water interface with a pair of palps lacking a food groove (Dauer, 1983).

On some Brazilian intertidal beaches *S. squamata* is the most abundant species, showing a high tolerance to different environmental conditions (Amaral, 1979). Despite this dominance there have been no previous studies of its population dynamics or production. Borzone et al. (1996) and Barros (1997) described this organism as characteristic of the middle intertidal of sandy beaches with great variation in abundance among beaches. The factors responsible for this variation are poorly understood.

The aim of this study was to investigate the population dynamics and secondary production of this species on a southern Brazilian sandy beach, and to examine the factors controlling its beach-to-beach variations in abundance.

MATERIALS AND METHODS

The littoral region of Paraná State (Fig. 1) includes several open Atlantic Ocean beaches. To the north, Mel Island divides the Paranaguá Bay estuarine system's access to the open sea. South of this, the Leste Coastal Plain comprises one beach along which both the shore profile and sand structure exhibit considerable change. Atami Beach (25°20'S, 48°05'W), about 10 km south of Mel Island, is the first major named beach on the Plain. From February 1992 to February 1993, samples were taken monthly at 16 stations at 15 and 30 m intervals along a transect, from a reference point at the beginning of the vegetation to a depth of about 3 m (Fig. 2). Triplicate samples were collected at low tide at each station with an iron core with 25 cm diameter (≈ 0.05 m^2) to a depth of 20 cm. Sand was sieved through a 0.5 mm mesh and organisms fixed in 10% formalin. All organisms in the samples were identified and counted. Separate samples with a plastic core with 5 cm diameter were collected nearby for grain size analysis. Statistical parameters of mean, standard deviation (sorting), skewnees and kurtosis were computed according to the Moments Method (Tanner, 1995) and results expressed as ϕ values. Beach slope, water salinity and temperature in the surf zone, and wave height and period were measured each month. Beach morphodynamic states were computed employing the parameters dimensionless fall velocity (Ω) of Dean (1973) and surf-scaling (Σ) of Guza and Inman (1975) (Wright et al., 1979).

S. squamata abundance were expressed as the mean square-meter density (ind m^{-2}) or as linear abundance (density per meter transect) (ind m^{-1}) that is the integral values of square-meter densities at each station along the extension of the sampled transect (Ansell et al., 1972).

The fifth setiger width of all individuals was measured with a microscope using a calibrated eyepiece, and used as the length (size) measure. A subsample of 200 individuals was used to obtain length vs weight relationships. The organisms were pooled into 0.02 mm size classes and dried at 70°C until constant weight to the nearest 0.01 mg. Ash-free dry weight (AFDW) was assessed after combustion of samples for 6 h at 500°C.

The ELEFAN program (Brey et al., 1988; Gayanilo et al., 1996) was used to estimate growth and mortality functions from the monthly length measurements in the population (13 length-frequency samples).

The von Bertalanffy growth function (VBGF) and the seasonal oscillating model of Pauly and Gaschütz (1979), as modified by Hoenig and Hanumara (1982, 1990) was used:

$$Lt = L_{\infty}\left[1 - e^{\left[-k(t-to)+(KC/2\pi)\mathrm{sen}(2\pi(t-ts))-(KC/2\pi)\mathrm{sen}(2\pi(to-ts))\right]}\right],$$

where: L_t = length at age t; L_{∞} = maximum asymptotic length; k = growth curve parameter; t_0 = computed age at length zero; C = parameter reflecting the intensity of seasonal oscillation; t_s = start of a sinusoid growth oscillation with respect to t = 0, and WP (Winter Point, which corresponds to the moment of lowest growth rate during the year cycle) = $t_s + 0.5$ yr. The growth parameters were estimated in two steps: (1) preliminary estimates of L_{∞} were obtained by the method of Wetherall (1986) as modified by Pauly (1986), and (2) this estimated L_{∞} was the used as a 'seeded' value for fitting a growth curve to the length-frequency data—Rn, the 'goodness of fit' index of the ELEFAN I routine. Total mortality Z was calculated by the single negative exponential model, using the method of length-converted catch curve of the ELEFAN II routine (Gayanilo et al., 1996).

Annual somatic production was calculated by two methods. The first was the mass specific growth rate method (MSGR) according to Crisp (1984), wich considers the size-frequency distribution, the size growth function and the size-body mass relation. Production was computed by $Ps = \Sigma N_i M_i G_i$, where N_i is the number of individuals in size class i, M_i is the mean individual body mass in size class i and G_i is the corresponding mass-specific growth rate obtained from VBGF

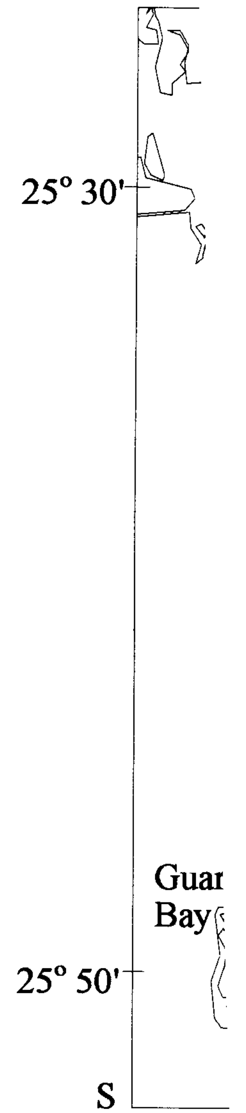

Figure 1. Study area. A'
Beach, MC: Monte Carl

parameters. The seconc
Hamilton, 1969; Benke,
where n_j is the number of
successive length classes
the size class and CPI is

Published data (Borzc
design were used, along v

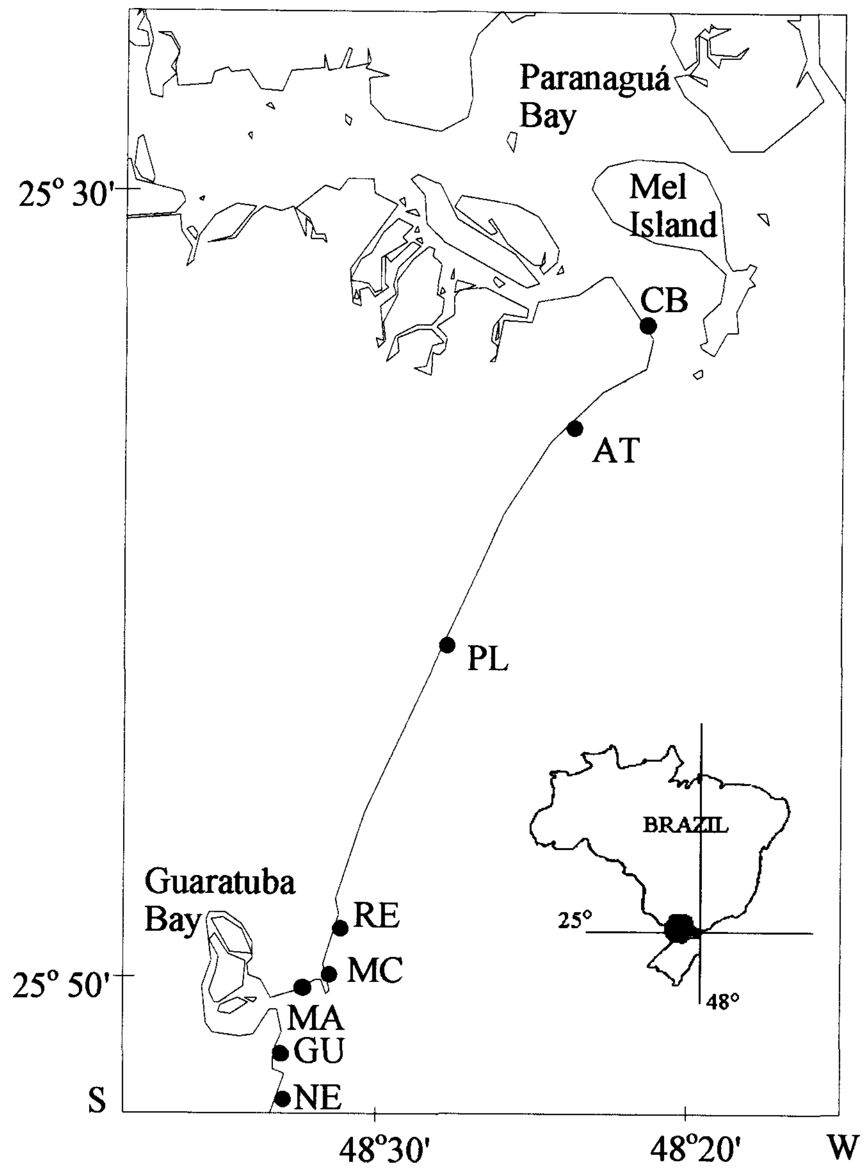

Figure 1. Study area. AT: Atami Beach, CB: Centro Beach, GU: Guaratuba Beach, MA: Mansa Beach, MC: Monte Carlo Beach, NE: Nereidas Beach, PL: Leste Beach, RE: Real Beach.

parameters. The second method was the size-frequency method (Hynes and Coleman, 1968; Hamilton, 1969; Benke, 1979; Menzie, 1980) estimated by: $P = [\,\Sigma\,(n_j + n_{j+1})\,(W_t\,W_{t+1})^{0.5}]\; i/\mathrm{CPI}$ where n_j is the number of individuals in size class j; $(W_t\,W_{t+1})^{0.5}$ is the mean geometric weight of two successive length classes, *i* is the number of length classes, n is the mean number of individuals in the size class and CPI is the time from hatching to death of the largest size class.

Published data (Borzone et al., 1996; 1998) from seven other beaches with the same sample design were used, along with the results from Atami Beach, to correlate winter and summer values

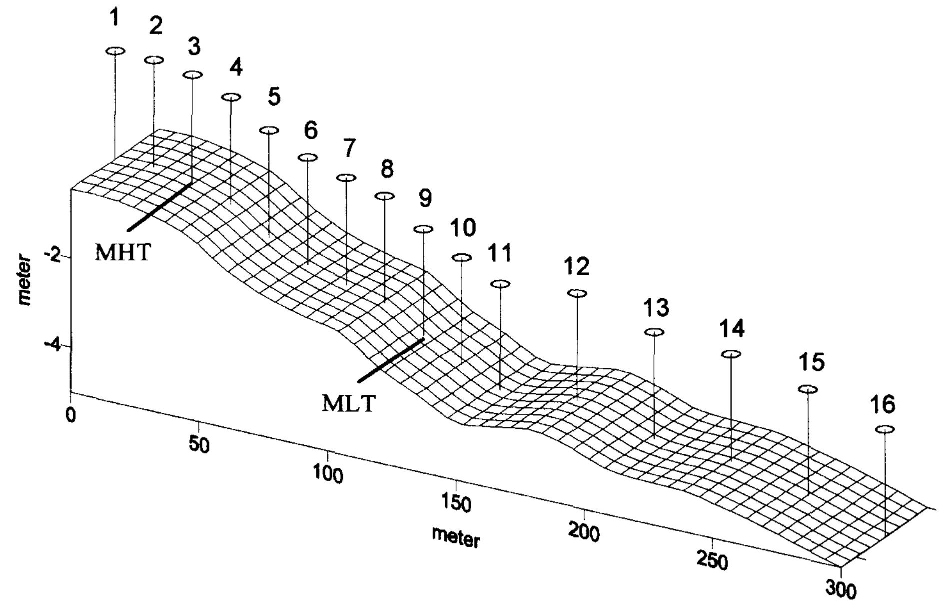

Figure 2. Beach profile scheme with sample stations at Atami Beach. MHT and MLT: mean high and low tide levels, respectively.

of *S. squamata* abundance and dominance (numbers of *S. squamata* individuals over the total macrobenthic individuals sampled multiplied by 100) with their associated station granulometric characteristics and the two morphodynamic indices (Ω, Σ). For this, a Principal Component Analysis was performed using a correlation matrix from standardized data of the following variables: maximum and mean square-meter density, lineal abundance, dominance, sediment parameters of mean grain size, sorting, asymmetry and kurtosis, and 'omega' and 'surf scaling parameters' morphodynamic indices. The season when data samples were collected, expressed as winter (0) or summer (1), was also included as a variable into the analysis.

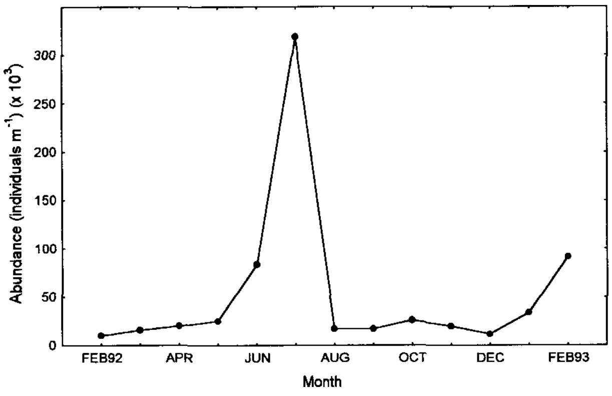

Figure 3. Monthly variation of *Scolelepis squamata* abundance (linear abundances on 300 m transect) at Atami Beach from February 1992 to February 1993.

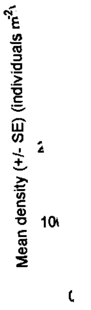

Figure 4. Distribution
throughout the profile

Atami beach preser
(Ω) value of 7.34 (n =
(Σ), 228 (n = 12, SD =
(Borzone and Souza,
was composed of fin
water temperatures o
29°C in January 199
Peak abundances
1993, with 318,735
trated in a narrow bar
20,277 m^{-2} (Fig. 4).

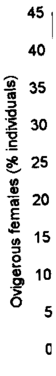

Figure 5. Proportion
from February 1992

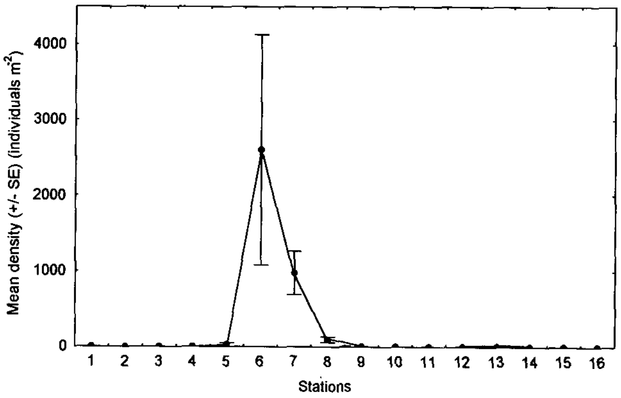

Figure 4. Distribution of *Scolelepis squamata* (annual mean square-meter density, n = 13 months) throughout the profile at Atami Beach.

RESULTS

Atami beach presented a modal dissipative morphodynamic state with a mean omega (Ω) value of 7.34 (n = 12, SD = 3.38). The high mean value of the surf scaling parameter (Σ), 228 (n = 12, SD = 142) indicate highly dissipative conditions for all the observations (Borzone and Souza, 1997). The beach showed a gentle slope (about 1°), and sediment was composed of fine to very fine sands, with an average of 2.9 ϕ at the beach face. The water temperatures of the surf zone ranged from a low of 15°C in July 1992 to a high of 29°C in January 1993.

Peak abundances of *S. squamata* at this beach occurred in July 1992 and February 1993, with 318,735 and 91,680 m^{-1}, respectively (Fig. 3). The organisms were concentrated in a narrow band in the middle intertidal beach reaching mean maximal densities of 20,277 m^{-2} (Fig. 4).

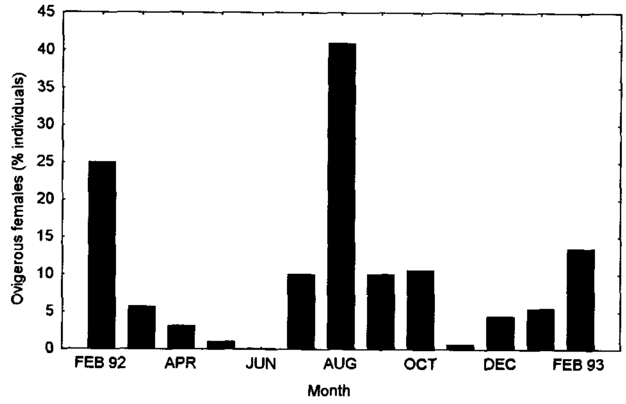

Figure 5. Proportion of females with oocytes in the *Scolelepis squamata* population at Atami Beach from February 1992 to February 1993.

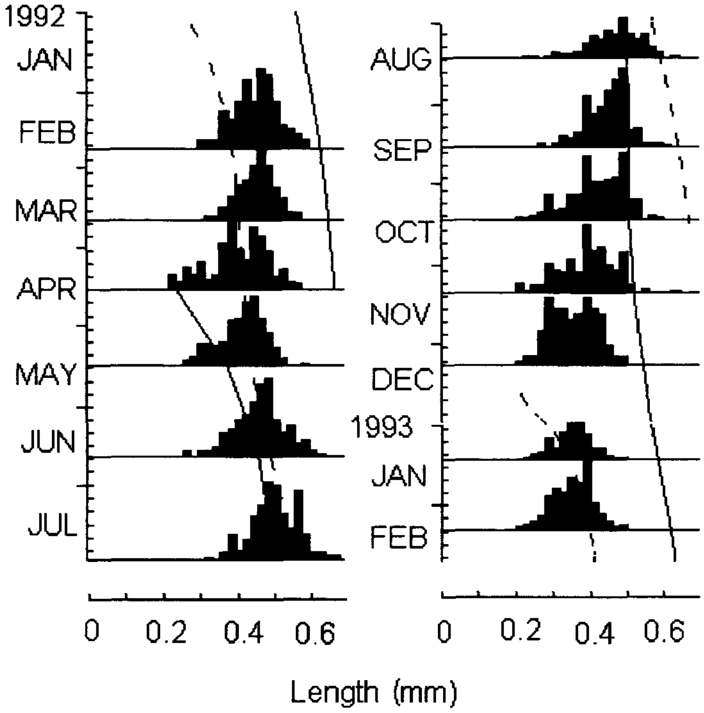

Figure 6. Growth curves of *Scolelepis squamata* at Atami Beach, plotted over size-frequency data (Length = fifth setiger width in mm; frequency data as percent samples). The growth parameters for each cohort are L_∞ = 0.70 mm, K = 2.6, C = 1.00, WP = 0.70 (solid line) and L_∞ = 0.705 mm, K = 3.5, C = 0.85, WP = 0.25 (dotted line).

Full ovigerous females, defined as those in which the coelomic cavities in all or most of the segments in the reproductive region of their bodies were full of oocytes (Joyner, 1962), were present throughout the year with peaks in February and August (Fig. 5). In these females, oocytes diameter (longed axis) ranged from 90 to 150 μm.

Length-frequency distribution indicated two main recruitment periods, one from April to May and the other from October to December (Fig. 6). Growth parameters were obtained for these two cohorts, the first resulted in L_∞ = 0.70 mm, K = 2.6, C = 1.00, WP = 0.70 (Rn = 0.28); and the second in L_∞ = 0.705 mm, K = 3.5, C = 0.85, WP = 0.25 (Rn = 0.29). The life span was of 0.66 and 0.49 yrs, and the mortality was 2.52 and 5.52 y^{-1}, respectively.

The values of production estimated by MSGR method were lower than the size-frequency method for the two principal cohorts (Table 1). Mean annual biomass was 0.21 g m^{-2}. An annual production of 0.57 g m^{-2} y^{-1} was obtained from the mean of the four described values of production with a final P/B ratio of 2.70 y^{-1}.

S. squamata showed a dominance greater than 60% at six of the eight beaches analyzed. The exceptions were Mansa Beach (13 and 18%) and Real Beach where this species did not occur (Table 2). This last beach, excluded from the numerical analysis, was characterized by coarse sand, showing a sedimentological limitation to *S. squamata* distribution. PCA results indicated that first two components explain 69% of total variation.

Table 1: Secondary production estimation for the two principal cohorts (1: $L_\infty = 0.70$ mm, $K = 2.6$; 2: $L_\infty = 0.705$ mm, $K = 3.5$) of *Scolelepis squamata* at Atami Beach using the size frequency method (Pa) and MSGR (Pb). L =width of 5° setiger in mm; N_j = average number of individuals in class j (individuals m^{-2}); M_j = AFDW of individuals belonging to class j; M_L = production of each class. G_i = mass-specific growth rate.

L	Nj	M_j	$N_j + N_j$+1	$(M_j * M_{j+1})^{0.5}$	M_L	Biomass	G_i1	Pb1	G_i2	Pb2
0.21	1.90	0.05				0.09	10.44	0.91	14.20	1.24
0.23	3.22	0.05	−1.32	0.05	−0.06	0.17	9.14	1.58	12.44	2.15
0.25	5.80	0.06	−2.58	0.06	−0.15	0.36	8.05	2.90	10.96	3.95
0.27	12.60	0.07	−6.80	0.07	−0.45	0.89	7.13	6.36	9.70	8.66
0.29	27.48	0.08	−14.88	0.07	−1.12	2.20	6.33	13.93	8.62	18.98
0.31	25.96	0.09	1.52	0.08	0.13	2.33	5.63	13.13	7.68	17.91
0.33	34.80	0.10	−8.84	0.09	−0.84	3.48	5.02	17.47	6.84	23.84
0.35	42.54	0.11	−7.74	0.10	−0.81	4.71	4.47	21.08	6.11	28.78
0.37	55.74	0.12	−13.21	0.12	−1.53	6.79	3.99	27.11	5.45	37.05
0.39	102.41	0.13	−46.66	0.13	−5.95	13.66	3.56	48.60	4.87	66.48
0.41	61.11	0.14	41.30	0.14	5.75	8.89	3.16	28.12	4.33	38.51
0.43	72.25	0.16	−11.14	0.15	−1.69	11.40	2.81	32.04	3.85	43.93
0.45	100.30	0.17	−28.04	0.16	−4.60	17.12	2.49	42.56	3.41	58.43
0.47	115.44	0.18	−15.14	0.18	−2.68	21.23	2.19	46.50	3.01	63.95
0.49	149.83	0.20	−34.39	0.19	−6.56	29.61	1.92	56.78	2.64	78.26
0.51	103.06	0.21	46.77	0.20	9.57	21.82	1.67	36.37	2.30	50.25
0.53	68.20	0.23	34.86	0.22	7.63	15.43	1.43	22.14	1.99	30.68
0.55	46.30	0.24	21.90	0.23	5.11	11.16	1.22	13.62	1.70	18.95
0.57	80.74	0.26	−34.44	0.25	−8.56	20.70	1.02	21.12	1.43	29.53
0.59	33.90	0.27	46.84	0.26	12.37	9.22	0.83	7.69	1.17	10.83
0.61	9.83	0.29	24.07	0.28	6.74	2.83	0.66	1.87	0.94	2.66
0.63	9.12	0.30	0.71	0.30	0.21	2.78	0.50	1.38	0.72	1.99
0.65	5.44	0.32	3.68	0.31	1.15	1.75	0.34	0.60	0.51	0.89
0.67	5.44	0.35	0.00	0.33	0.00	1.84	0.20	0.37	0.31	0.58
					13.64	210.48		464.25		638.48

CPI1 = 0.656; i = 24 Pa1 = (i/CPI) Σ ML Pa1 = 672.28 mg m^{-2} y^{-1}
CPI2 = 0.487; i = 24 Pa2 = (i/CPI) Σ ML Pa2 = 499.09 mg m^{-2} y^{-1}

R-mode graph showed that dominance was highly correlated with mean grain size diameter, and abundance measures was highly correlated with morphodynamics indices and mean grain size diameter. The season showed a poor correlation with other physical and biological variables except for kurtosis sediment values (Fig. 7). The three abundance measures (maximal and mean square-meter density and lineal abundance) included into the analysis exhibit a strong correlation occupying practically the same place in the bidimensional space. This result indicate that no differences existed between these measures when used for comparative purpose. The square meter was a more adequate measure because its widespread usage.

Table 2. *Scolelepis squamata* values of dominance (D), maximal and mean square meter density (δM and δm), lineal abundance (La) and sediment parameters of mean grain size (Md), sorting (σ), skewnees (Sk), kurtosis (Kg), and 'omega' (Ω) and 'surf scaling parameters' (Σ) morphodynamic indices at eight beaches for winter (w) and summertime (s) samples. (See beach abreviations in the legend of Figure 1).

	D (%)	δM (m^{-2})	δm (m^{-2})	La (m^{-1})	Md (ϕ)	σ (ϕ)	Sk (ϕ)	Kg (ϕ)	Ω	Σ
GUw	92	2,058	769	21,507	2.50	0.41	0.21	2.93	5.8	17
GUs	63	489	228	4,809	2.18	0.69	−0.43	2.20	5.2	19
MAw	13	41	22	709	1.95	1.19	−0.62	2.04	1.4	4
MAs	18	41	19	611	1.81	0.89	−0.33	2.07	1.1	2
MCw	92	4,991	1,808	40,674	2.73	0.40	−0.67	3.64	7.2	48
MCs	96	5,365	1,752	68,849	2.83	0.22	0.68	3.98	8.9	13
NEw	87	1,229	432	9,030	1.79	0.83	−0.24	2.55	4.0	36
NEs	88	3,619	1,426	50,277	2.68	0.39	−0.41	3.30	5.3	21
REw	0	0	0	0	0.81	0.96	0.38	2.38	0.9	75
REs	0	0	0	0	0.70	0.67	0.91	4.80	2.7	33
CBw	84	2,173	1,093	32,805	2.77	0.48	−1.13	4.47	4.5	44
CBs	93	7,008	3,163	126,510	2.79	0.26	−1.42	15.70	1.2	7
PLw	75	2,024	1,146	51,555	2.06	0.72	−0.04	2.06	1.7	3
PLs	93	4,258	1,262	94,635	2.44	0.50	−0.67	3.38	1.3	12
ATw	83	20,277	7,078	318,510	2.89	0.25	0.63	2.95	10.3	233
ATs	66	2,723	864	77,495	2.92	0.25	0.81	2.30	4.3	137

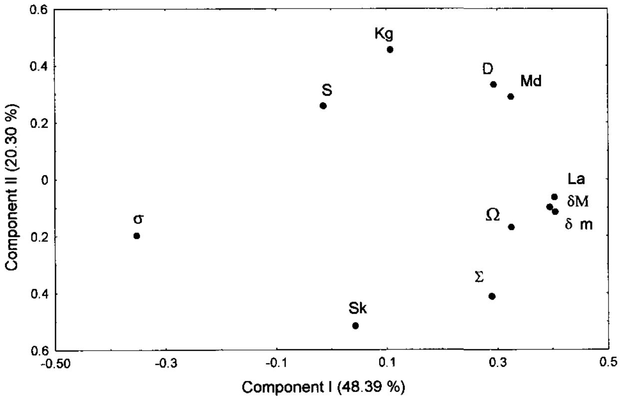

Figure 7. Principal component analyses on R-mode, relating *Scolelepis squamata* abundance and dominance at seven beaches to sediment characteristics, morphodynamic indexes and seasonallity. D = dominance, Kg = kurtosis, S = season, s = sorting, Md= median grain size, Sk = skewnees, W = omega index, S = surf scaling parameter, La = linear abundance, δM = maximal square meter density, δm = mean square meter density.

Distribution of *S. squam*
region, although its occurr
This distribution pattern w
1995; Borzone et al., 199
intertidal region, except fc
Jersey (McDermott, 1983
We identified two cohor
cohort started in the begir
the final of the other recru
rences of ovigerous femal
duration of larval develop
recruited in April present
gust, and the cohort recrui
rate beginning in March..
each cohort coincided w
effort of the last cohort, tl
life span. Santos (1994) a
Scolelepis gaucha at Cas
difference to seasonal
morphodynamics.
Secondary production
8.06 gAFDW m^{-2} and fro
and within species (Tabl
Scolelepis gaucha from
south of the outlet of Pa
stability of sediment de
Prionospio caspersi sho
consecutive years that w
et al. 1993). On the oth
between 2 yrs were due l
the cold weather could c
species that settles after
have exploited newly av
Inter-annual variations
and February 1993. Sou
inter-annual differences
variations where related
tions in abundance may
annual cohort.
Data of *S. squamata* a
beaches showed that ab
at Atami beach. *S. squa*
morphodynamic charac
termined by dissipative
curred in winter on som

Discussion

Distribution of *S. squamata* at Atami Beach showed a dense band in the mid-intertidal region, although its occurrence extended over the intertidal and subtidal stations sampled. This distribution pattern was found at others Paraná's open beaches (Souza and Gianuca, 1995; Borzone et al., 1996; Barros, 1997). This species was generally dominant in the intertidal region, except for its seaward movement in winter in a temperate beach of New Jersey (McDermott, 1983). The factors that regulate this distribution are unknown.

We identified two cohorts during the probably continuous season of reproduction. One cohort started in the beginning of the recruitment period in April and the other cohort in the final of the other recruitment period in December. The lag between maximum occurrences of ovigerous females and recruitment of principal cohorts could be related to the duration of larval development and to selectivity of the used mesh (0.5 mm). The cohort recruited in April presented a longer life span and a slow growth rate beginning in August, and the cohort recruited in December presented a shorter life span and a slow growth rate beginning in March.. The winter point of the seasonal oscillating growth model for each cohort coincided with peaks of reproduction. Moreover, the greater reproductive effort of the last cohort, that reproduced in February and August, may explain its shorter life span. Santos (1994) also found difference in growth parameters between cohorts for *Scolelepis gaucha* at Cassino Beach, Southern Brazil. However, this author related this difference to seasonal morphological variation of the beach profile or beach morphodynamics.

Secondary production values for species of the Family Spionidae ranged from 0.08 to 8.06 gAFDW m^{-2} and from 3.0 to 60.5 gDW m^{-2} showing a great variation among species and within species (Table 3). Santos (1994) found a spatial variation of production for *Scolelepis gaucha* from four sandy beaches located at 2, 8, 26 and 76 km, respectively, south of the outlet of Patos Lagoon, Southern Brazil. This variation was related to the stability of sediment deposits in the intertidal zone during the recruitment periods. *Prionospio caspersi* showed a temporal variation in secondary production between two consecutive years that was attributed to environmental stress (Ambrogi, 1990; Ambrogi et al. 1993). On the other hand, the differences in production of *Marenzelleria viridis* between 2 yrs were due largely to differences in successful recruitment. In the first year, the cold weather could cause a high mortality in sediment, where *M. viridis* is the first species that settles after sandy organic sediments thaw in late winter and could readily have exploited newly available sediments (Sardá et al., 1995).

Inter-annual variations of abundance were observed in Atami between February 1992 and February 1993. Souza and Gianuca (1995) and Shimizu (1991, 1997) also found inter-annual differences in abundance of *S. squamata* in other Brazilian beaches. These variations where related to a successful recruitment. Consequently, intra-annual variations in abundance may be explained by the successful recruitment of more than one annual cohort.

Data of *S. squamata* abundance collected during winter and summertime at other eight beaches showed that abundance was not always maximum during winter as was the case at Atami beach. *S. squamata* peaks of abundance appeared to be related to sediment and morphodynamic characteristics. High values of omega and surf scaling parameters, determined by dissipative conditions, together with high values of ϕ mean grain size occurred in winter on some beaches and in summertime on others. The intra-annual varia-

Table 3. Secondary production of different spionid species (fixed organisms). P: production of ash free dry weight or *dry weight, B: mean biomass of ash free dry weight or *dry weight, L: life span, Lat: geographic latitude, DTH: depth, RTMP: seasonal temperature range.

SPECIES	Lat (°)	DTHH (m)	RTMP (° C)	P g m^{-2} yr^{-1}	B g m^{-2}	PB	L	Author
Spiophanes kroyeri	55N	80		0.20	0.14	1.4	2	Buchanan and Warwick, 1974
Spiophanes bombix	51N	13	7–16	3.34	0.69	4.9		Warwick et al., 1978
Paraprionospio pinnata	37S	65		4.53	1.89	2.4	2	Carrasco and Arcos, 1980
Spiophanes bombix	51N			0.08	0.06	1.3		Warwick and George, 1980
Polidora quadrilobata	52N	3	0.20–2.60	1.50	8.2	1–1.5		Lambeck and Valentjin, 1987
Prionospio caspersi	45N	5	5–25	8.06	1.97	4.1	0.58	Ambrogi, 1990
Prionospio caspersi	45N	5	5–25	2.53	0.42	6.0	0.58	Ambrogi et al., 1993
Prionospio caspersi	45N	5	5–25	3.28	0.42	7.8	0.58	Ambrogi et al., 1993
Streblospio benedicti	42N	0		3.00*	0.50*	5.4	<1	Sardá and Martin, 1993
Streblospio shrubsolii	40N	0		15.65*	3.55*	4.4	<1	Sardá and Martin, 1993
Scolelepis gaucha	33S	0	14–26	0.50	0.07	6.9		Santos, 1994
Scolelepis gaucha	33S	0	14–26	1.85	0.14	12.9		Santos, 1994
Scolelepis gaucha	33S	0	14–26	0.15	0.04	3.4		Santos, 1994
Scolelepis gaucha	33S	0	14–26	2.82	0.78	3.6		Santos, 1994
Marenzelleria viridis	42N	0	0–25	60.50*	9.90	6.1	1–2	Sardá et al., 1995
Marenzelleria viridis	42N	0	0–25	26.30*	5.90*	4.5	1–2	Sardá et al., 1995
Scolelepis squamata	25S	0	17–27	0.57	0.21	2.7	0.57	This study

tions of abundance related to sediment affinities point to an opportunistic behavior in *S. squamata*.

In addition, the P/B ratio estimated for *S. squamata* at Atami Beach was the highest when compared with other macrofaunal species of this beach (Souza,1998), although is in the lower range of published values for spionids (Table 3). In general, Spionid polychaetes showed high P/B ratios and short life span (about 1 yr) which could suggest an opportunistic behavior for all the group.

ACKNOWLEDGMENTS

We wish to thank two anonymous referees for critically reading an early version of the manuscript. This study was supported by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) through grants to C.A.B. and J.R.B.S.

LITERATURE CITED

Amaral, A. C. Z. 1979. Ecologia e contribuição dos anelídeos poliquetos para a biomassa bêntica da zona das marés, no litoral norte do Estado de São Paulo. Bolm. Inst. Oceanogr. São Paulo 28: 1–52.

Ambrogi, R. 1990. Secondary production of *Prionospio caspersi* (Annelida:Polychaeta: Spionidae). Mar. Biol. 104: 437–442.

__________, P. Fontana and P. Ricobene. 1993. Population dynamics and secondary production of the spionid polychaete *Prionospio caspersi* in front of the Po River Delta. Vie Milieu 43: 165–172.

Ansell, A. D., P. Sivadas, B. Narayanan, V. N. Sankaranarayanan and A. Trevallion. 1972. The ecology of two sandy beaches in southwest India. I. Seasonal changes in physical and chemical factors and in the macrofauna. Mar. Biol. 17: 38–62.

Barros, F. C. R. Jr. 1997. A macrofauna bentônica nas praias arenosas dos arredores da Baía de Guaratuba – PR, Brasil. São Paulo. MSc. Thesis, Instituto de Biociências, Univ. São Paulo, Brazil, 100 p.

Benke, A. C. 1979. A modification of the Hynes method for estimating secondary production with particular significance for multivoltine population. Limnol. Oceanogr. 24: 171–176.

Bolivar, G. A. and P. C. Lana. 1987. Spionidae (Annelida:Polychaeta) do litoral do Estado do Parana. Neritica 2: 107–148.

Borzone, C. A. and J. R. B. Souza. 1997. Estrutura da macrofauna bentônica no supra, meso e infralitoral de uma praia arenosa do sul do Brasil. Oecologia Brasiliensis 3: 197–212.

____________, ___________ and A. G. Soares. 1996. Morphodynamic influence on the structure of inter and subtidal macrofaunal communities of subtropical sandy beaches. Rev. Chile Hist. Nat. 69: 565–577.

____________, Y. A. G. Tavares and F. C. R. Jr. Barros. 1998. Beach morphodynamics and distribution of *Mellita quinquiesperforata* (Leske, 1778) on sandy beaches of southern Brazil. Pages 581–586 *in* R. Mooi and M. Telford, eds. Echinoderms: San Francisco, Proc. 9th Int'l. Echinoderm Conf. Balkema, Rotterdam.

Brey, T., M. Soriano and D. Pauly. 1988. Electronic length frequency analysis. a revised and expanded user's guide to ELEFAN 0, 1 and 2 (2nd ed.). Ber. Inst. Meereskd. Christian -Albrechts-Univ. Kiel 177: 1–31.

Buchanan, J. B. and R. M. Warwick. 1974. An estimate of benthic macrofaunal production in the offshore mud of the Northumberland coast. J. Mar. Biol. Ass. U.K. 54: 197–222.

Carrasco Vazquez, F. and D. Arcos Rojas. 1980. Estimación de la producción secundaria de *Paraprionospio pinnata* (Spionidae, Polychaeta) frente a Bahia de Concepción, Chile. Bolm. Inst. oceanogr., São Paulo 29: 79–82.

Crisp, D. J. 1984. Energy flow measurements. Pages 197–279 *in* N. A. Holme and A. D. McIntyre, eds. Methods for the study of marine benthos. Blackwell, Oxford.

Dauer, D. M. 1983. Functional morphology and feeding behavior of *Scolelepis squamata* (Polychaeta: Spionidae). Mar. Biol. 77: 279–285.

Day, J. H. 1967. A monograph on the Polychaeta of Southern Africa. Trust. Brit. Mus. (Nat. Hist.), London. 878 p.

Dean, R. G. 1973. Heuristic models of sand transpor in the surf zone. Pages 208–214 *In* Proc. Conf. Eng. Dynamics in the surf zone, Sydney, Australia.

Gayanilo, F. C. Jr., P. Sparre and P. Pauly. 1996. FISAT, FAO-ICLARM stock assessment tools - User's manual. FAO Computerized information Series (Fisheries). vol. 8. 126 p.

Guza, R. T. and D. L. Inman. 1975. Edge waves and beach cusps. J. Geophys. Res. 80: 2997–3012.

Hamilton, A. L. 1969. On estimating annual production. Limnol. Oceanogr. 14: 771–782.

Hoenig, J. M. and R. C. Hanumara. 1982. A statistical study of a seasonal growth model for fishes. Tech. Rpt., Dept. Computer Science and Statistics, Univ. Rhode Island, Kingston.

__________ and ______________. 1990. An empirical comparison of seasonal growth models. ICLARM Fishbyte 8: 32–34.

Hynes, H. B. N. and M. J. Coleman, 1968. A simple method of assessing the annual production of stream benthos. Limnol. Oceanogr. 13: 569–573.

Joyner, A. 1962. Reproduction and larval life of *Nerine cirratulus* (Delle Chiaje) family Spionidae, including the description of a new species of *Scolelepis*. Proc. Zool. Soc. Lond. 138: 655–666.

Knott, D. M., D. R. Calder and R. F. Van Dolah. 1983. Macrobenthos of sandy beach and nearshore environments at Murrells Inlet, South Carolina, U.S.A. Estuar. Coast. Shelf Sci. 16: 573–590.

Lambeck, R. H. D. and P. Valentjin. 1987. Distribution, dynamics and productivity of a colonizing (*Polydora quadrilobata*) and an established (*P. ligni*) polydorid polychaete in Lake Grevelingen: an enclosed estuary in the SW Netherlands. Neth. J. Sea Res. 21: 143–158.

McDermott, J. J. 1983. Food web in the surf zone of an exposed sandy beach along the Mid-Atlantic coast of the United States. Pages 529–538 *in* A. McLachlan and T. Erasmus, eds. Sandy beaches as ecosystems. W. Junk, The Hague, Netherlands.

Menzie, C. A. 1980. A note on the Hynes method of estimating secondary production. Limnol. Oceanogr. 25: 770–773.

Pauly, D. 1986. On improving operation and use of the ELEFAN programs. Part II. Improving the estimation of L_∞. ICLARM Fishbyte 4: 18–20.

_______ and E. Gaschütz. 1979. A simple method for fitting oscillating length growth data, with a program for pocket calculators. Int'l. Council Exploration of the Sea, CM 1979/G.24. 266 p.

Santos, J. P. 1994. Population dynamics and production of *Scolelepis gaucha* Polychaeta: Spionidae) on the sandy beaches of Southern Brazil. Mar. Ecol. Prog. Ser. 110: 159–165.

Sarda, R. and D. Martin. 1993 . Populations of *Streblospio* (Polychaeta: Spionidae) in temperature zones: demography and production. J. Mar. Biol. Ass. U.K. 73: 769–784.

_______, I. Valiela and K. Foreman. 1995. Life cycle, demography and production of *Marenzelleria viridis* in a salt marsh of southern New England. J. Mar. Biol. Ass. U.K. 75: 725–738.

Shimizu, R. M. 1991. A comunidade de macro-invertebrados da região entre marés da Praia de Barequeçaba, São Sebastião, SP. MSc. Thesis, Univ. de São Paulo, Brazil. 72 p.

___________ .1997. Ecologia populacional de *Scolelepis squamata* (Müller, 1806) (Polychaeta : Spionidae) e *Callichirus major* (Say, 1818) (Crustacea :Decapoda: Thalassinidea) da praia de Barequeçaba (São Sebastião, SP). DSc. Thesis, Univ. São Paulo, Brazil. 49 p.

Souza, J. R. B. 1998. Produção secundária da macrofauna bentônica da praia de Atami – Paraná – Brasil. D.Sc. Thesis, Dept. Zoologia, Univ. Federal do Paraná, Brazil. 129 p.

___________ and N. M. Gianuca. 1995. Zonation and seasonal variation of the intertidal macrofauna on a sandy beach of Parana state, Brazil. Sci. Mar. 59: 103–111.

Tanner, W. F. 1995. Environment

Warwick, R. M and C. L. Geor
Pages 517–538 *in* M. B. Coll
Swansea Bay. Pergamon Pre

___________, ___________ a
community. Estuar. Coast. N

Wetherall, J. A. 1986. A new me
frequency data. ICLARM Fi

Wright, L. D., J. Chappell, B. G
reflective and dissipative be
105–140.

ADDRESS: *Centro de Estudos do*
Pontal do Paraná, PR, Brazil. C
CEP: 80060-050, Brazil. E-mai

Tanner, W. F. 1995. Environmental clastic granulometry. Fla. Geol. Surv., Spec. Publ. no. 40. 146 p.

Warwick, R. M and C. L. George. 1980. Annual macrofauna production in an *Abra* community. Pages 517–538 *in* M. B. Collins, ed. Problems of an industrialized embayment: a case study of Swansea Bay. Pergamon Press, Oxford.

__________, __________ and J. R. Davies. 1978. Annual macrofauna production in a *Venus* community. Estuar. Coast. Mar. Sci. 7: 215–241.

Wetherall, J. A. 1986. A new method for estimating growth and mortality parameters from length-frequency data. ICLARM Fishbyte 4: 12–14.

Wright, L. D., J. Chappell, B. G. Thom, H. P. Bradshaw and P. Cowell. 1979. Morphodynamics of reflective and dissipative beach and inshore systems: Southeastern Australia. Mar. Geol. 32: 105–140.

ADDRESS: *Centro de Estudos do Mar, Universidade Federal do Paraná, 83255-000 Pontal do Sul, Pontal do Paraná, PR, Brazil.* CORRESPONDING AUTHOR: C.A.B.) *R. Nilo Cairo 36, Centro, Curitiba. CEP: 80060-050, Brazil. E-mail: <capborza@aica.cem.ufpr.br>.*