



SECONDARY PRODUCTION OF *Scolelepis goodbodyi* (POLYCHAETA: SPIONIDAE) IN A TROPICAL SANDY BEACH IN THE SOUTHWESTERN ATLANTIC, BRAZIL

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Abstract: The secondary production is the result of the functional response of populations subject to various environmental factors. Marine habitats vary in terms of quantity and quality of food supply, and the use of secondary production values, as well as renewal rates (P/B), may be used as estimates for understanding the incorporation of organic matter and energy per unit, population or community in each area. This estimative was performed for the population of *Scolelepis goodbodyi* in a tropical beach in the Southwestern Atlantic, located in an upwelling area. A comparison of Spionidae and non-spionid populations from different latitudes was also done. The Mass Specific Growth Rate method (MSGR) and the Production/Biomass ratio (P/B) were used to estimate the somatic annual production and average annual biomass. The mean density and biomass were 16.38 ind. m⁻² and 2.78 g AFDW m⁻², respectively. The secondary production and P/B were 8.3 g AFDW m⁻² y⁻¹ and 2.98 y⁻¹, respectively. The growth rate in weight was greater for the small size than the large size classes. The largest individuals (W3C = 1.0 mm) showed the lowest biomass and secondary production values. The observed high rates of secondary production and P/B suggest that this *S. goodbodyi* population can transfer large amounts of biomass to higher trophic levels of the local food web. Studies of the secondary production of spionidae populations in different latitudes, including the population of *S. goodbodyi* in the beach of Manguinhos, showed variability in their rates probably due to the differences of several factors such as life history and environmental variability.

Key words: invertebrates; macrobenthos; latitudinal gradient; productivity; population dynamics.

INTRODUCTION

The sandy beach ecosystem is a dynamic environment where the physical structure is determined by the interactions between sediment, waves and tides. The interaction of these parameters can form morphodynamically different beaches: beaches with low energy

(protected), where pollutants are not easily dispersed, and beaches exposed to high-energy conditions (Mclachlan & Brown 2006). Natural and anthropogenic ecosystem stressors (e.g. temperature, hydrodynamics, pollutants, sand extraction, trampling by tourists, vehicle traffic and habitat destruction) are capable of shifting the structure and dynamics of sandy beach

populations (Brown & McLachlan 2002, Lecari & Defeo 2003, Schoeman *et al.* 2014).

The integrity of ecosystems can be measured by different ways, using structural or functional approaches (Underwood & Peterson 1988, De Leo & Levin 1997). An ecosystem function's quantification may be done through analysis of the physical, chemical and biological components, as well as the understanding of processes such as nutrient recycling, decomposition, and production (Dolbeth *et al.* 2015).

Secondary production is an integrative functional measure of heterotrophic populations, englobing body mass, reproductive rate, population density, growth rate, development time, life span mortality and survivorship, which highlight the importance of species for the ecosystems. Thus, secondary production is the result of the functional response of populations subject to various environmental factors (Tod & Schmid-Araya 2009, Dolbeth *et al.* 2012, 2015). The importance of studying secondary productivity in dominant species becomes relevant since its results can be expanded for the assessment of environmental health, increasing the importance to describe the environment, especially concerning the maintenance of biological resources and assessment of environmental stress (Dolbeth *et al.* 2012).

In comparison to an instantaneous structural measure, such as density or biomass, secondary production could early reveal threats to natural populations (Benke & Huryn 2010). Among marine invertebrate populations, production shows a large variation (from 0.2 mg to 3.3 kg of dry mass m^{-2}) strongly related to biomass. The turnover rate (Product/Biomass or P/B) also presents a large variation (from 0.004 to 36.7), being related to voltinism (number of generations by year) (Cusson & Bourget 2005). Regarding latitudinal gradient, richness tends to increase toward the tropics (McLachlan & Dorvlo 2005, McLachlan & Brown 2006), while the P/B ratio shows a bimodal pattern for some animal phyla, being higher in temperate regions (Cusson & Bourget 2005, McLachlan & Brown 2006). The increase in species richness can also have a positive correlation with the presence of finer grains, flatter slope and greater tide range in sandy beaches (McLachlan & Dorvlo 2005).

Spionidae (Spionida) polychaetes are currently

represented by c.a. 500 species that occur in different ecosystems and can be found in high-density populations (Rocha *et al.* 2009). Many species of spionids are considered opportunistic and can quickly colonize organically compromised environments (Pearson & Rosenberg 1978). The Genus *Scolelepis* is commonly found on intertidal sandy beaches worldwide. It comprises about 86 species (McLachlan & Brown 2006, Read & Fauchaud 2020, Sikorski & Pavlova 2015). Seven species of *Scolelepis* are recorded in the Brazilian coast (Rocha & Paiva 2012).

Scolelepis goodbodyi (Spionida, Spionidae) is a macrobenthic species occurring in the Caribbean Sea (Jamaica, Port Henderson, Green Bay) and the Atlantic Ocean (Brazil, northern and southern coasts), in dissipative sandy beaches, where they are frequently dominant in abundance and biomass (Souza & Gianuca 1995, Souza & Borzone 2000, Degraer *et al.* 2003). They present continuous reproduction throughout the year (Maccord & Amaral 2007). Population dynamics and secondary production data of *Scolelepis* and other Spionidae are available and differ locally mainly due to variations in the environmental conditions of the studied sites (García-Arberas & Rallo 2004, Kevrekidis 2005, Speybroeck *et al.* 2007, Leão *et al.* 2012), as well as differences in the life history of the species (Cusson & Bourget 2005). However an analysis considering a latitudinal pattern is still a gap in the literature..

In order to shed light on the potential latitudinal pattern, as well as identifying how the latitudinal environmental factors may interfere in the production rates, this study aimed to determine the secondary production of a *S. goodbodyi* population in a tropical beach in the Southwestern Atlantic, and compared it among Spionidae of different localities. We were based on two hypotheses: (1) the physical and biological conditions of the studied beach and the lifestyle habits of *S. goodbodyi* favour the increase of secondary production, contributing to the local benthic biomass, and (2) distinctions between the life histories of the species of species, as well as the differences between biotic and abiotic factors between the different latitudes, can influence the biomass and secondary production rates.

MATERIAL AND METHODS

The study site was located at Armação dos Búzios, a touristic balneary located in the north coast of the state of Rio de Janeiro. It is located in an 8 km long peninsula, with an indented coastline, where 23 beaches are found. These beaches receive currents from Ecuador on one side (from November to February) and on the other sea currents from the south pole due to the southwest wind (from March to June), which lead these beach waters colder.

The Manguinhos beach is located at 22° 46' 12.17"S and 41° 54' 52.44"W (Figure 1). The beach is 1 km long and it has a gentle slope. It is surrounded by mangroves which results in a beach with low wave energy. It presents dissipative features in the northernmost portion.

Specimens were collected monthly in a grid of 100 m² that was limited to the upper level of the intertidal region from June 2009 to May 2010. Ten sampling units from a 25 cm long and 10 cm diameter hand corer were randomly taken every

month for estimation of secondary production. The sediment was washed *in situ* through a 0.5 mm and 0.25 mm mesh sieve and the retained organisms were narcotized with 7 % magnesium chloride.

In the laboratory, samples were fixed in 4 % formalin and preserved in 70 % ethanol after 48-72 h. Extra sediment samples were collected for the analysis of the granulometry, organic matter and microphytobenthic biomass. Grain size analysis was determined according to the techniques described in Suguio (1973) and the sediment was classified according to Shepard (1954). The organic matter content of the sediments was determined by calcination in a muffle furnace at 450 °C for four hours. Microphytobenthic biomass in the sediments was estimated by the determination of pigment concentrations (chlorophyll *a* and phaeopigments) by spectrophotometry. The top 1 cm layer of the sediment column was collected in three replicates with a 2 cm diameter hand corer. The samples were immediately stored in dark plastic containers and frozen. The procedure used

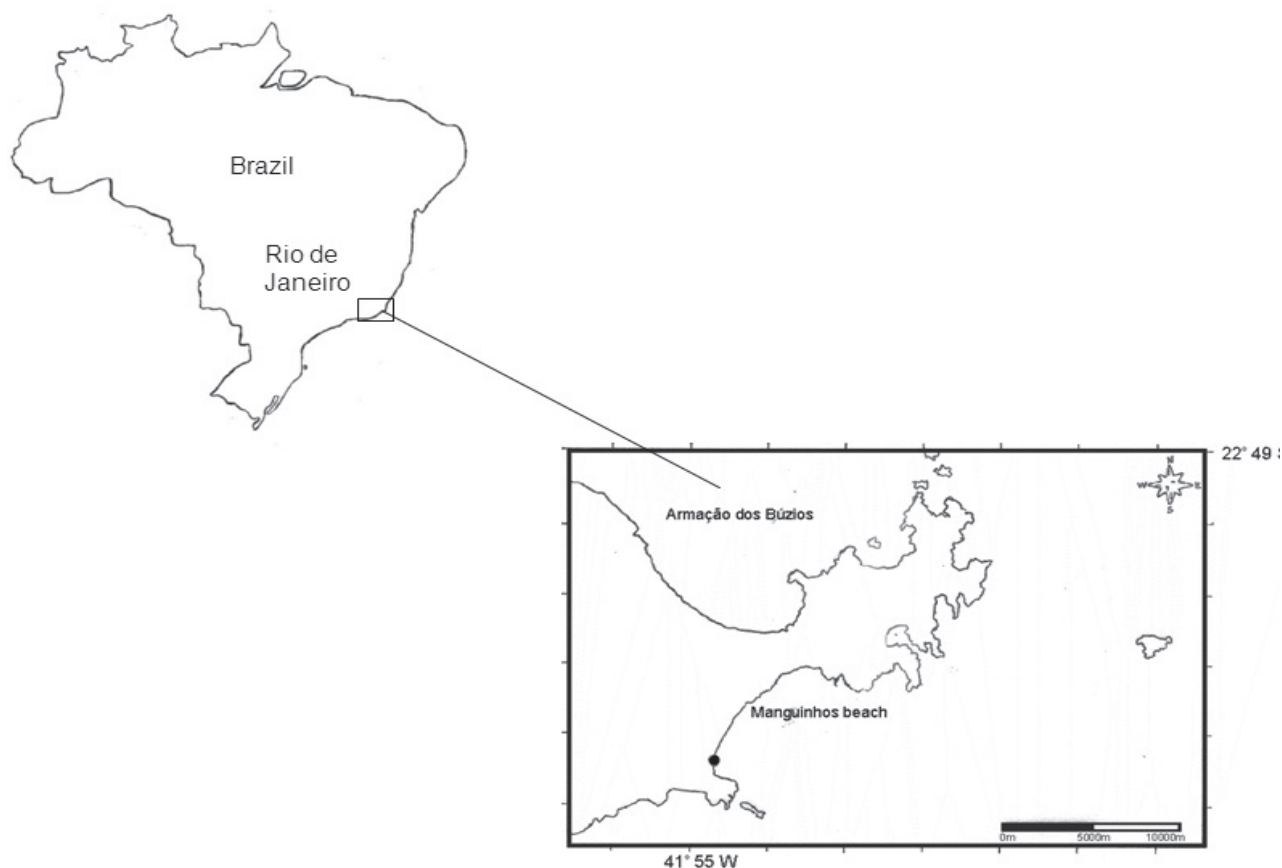


Figure 1: Illustration of the sampling site, Manguinhos beach at Rio de Janeiro, Southeast Brazil. Black dot represents the location of a 100 m² sampling grid.

is described by Strickland & Parsons (1972) and the calculations of the chlorophyll *a* and phaeophytin concentrations were conducted using the equations of Lorenzen (1967).

Animals were counted and measured under a stereomicroscope with a graduated ocular. The third chaetiger width (W3C) was used as the standard measurement for the establishment of size classes and estimates of secondary production. The most appropriate indicator of total body length for the species was previously determined ($N = 30$; $y = 0.012x + 0.185$; $R^2 = 0.71$; $p < 0.05$) (Figure 2) (Leão *et al.* 2012).

Mean population density was estimated from the number of individuals obtained in each month. Kruskal-Wallis non-parametric test was used to test the significance of differences in densities during the studied period ($p \leq 0.05$).

Selected individuals from all size classes were weighted in two steps, DW1 and DW2, to estimate biomass and secondary production. Specimens in the small size classes (0.15 mm to 0.50 mm) were weighted together due to their reduced biomass. All specimens were dried in a Lavoisier oven at 80 °C for 24 hours (DW1), and then burned at 550 °C in

a muffle oven for 2 hours (DW2) before respective weighting. Ash free dry weight (AFDW) was obtained by the difference between DW1 and DW2 (AFDW = DW1 – DW2) (Van Der Meer *et al.* 2005).

The population production was estimated using a size-based method (Mass Specific Growth Rate-MSGR) described by Crisp (1984). This method is commonly used for populations that do not have distinguishable cohorts, such as the population studied here. It uses the size frequency distribution, size growth, and size body mass relation depicted in the equation:

$$P_s = \sum N_i * M_i * G_i,$$

where P_s is the population production, N_i is the number of individuals in size class i , M_i is the mean individual body mass in the same class, and G_i is the corresponding mass-specific growth rate obtained from VBGF parameters (the von Bertalanffy growth function) and the size-mass ratio. The VBGF parameters applied were (L_∞) = 1.23 mm and $K = 1.2$ (Leão *et al.* 2012).

The P/B was estimated based on the somatic annual production and average annual biomass.

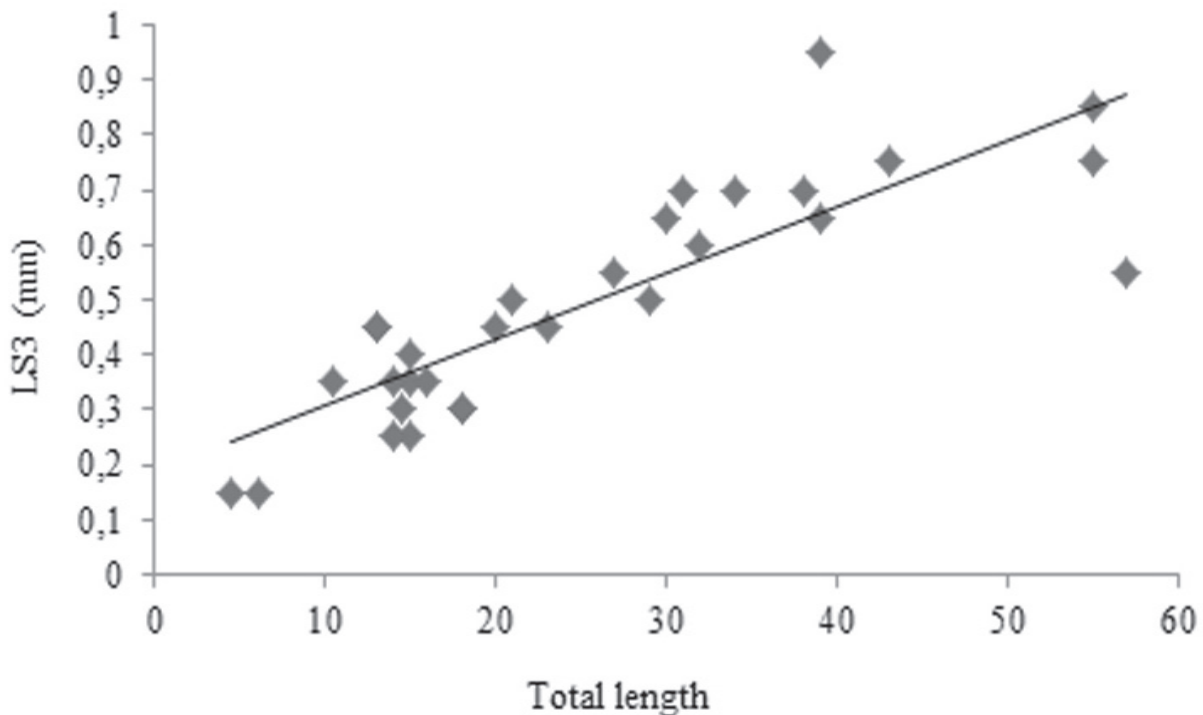


Figure 2. Relationship between total length (mm) and width of 3rd chaetiger (W3C) of *S. goodbodyi* ($R^2 = 0.71$; $p < 0.05$) from Manguinhos beach, Southeast Brazil.

The relationships between patterns of production, biomass and P/B with latitude and between biological variables (mean annual biomass, annual production and P/B ratio) from literature data of spionids and non-spionids polychaetes were evaluated using Spearman correlation. The production and biomass of each size class and body mass were made and the power regression of these data was calculated by the following equation:

$$P/B = 1.61 * \text{body mass}^{-0.26}$$

RESULTS

The secondary production estimated for *S. goodbodyi* from Manguinhos beach was 8.30 g AFDW m⁻² y⁻¹. The annual average biomass was 2.78 g AFDW m⁻². The P/B ratio was 2.98. The growth rate in weight was greater in the smallest size classes. The class of largest individuals (W3S = 1.0 mm) had the lowest values of biomass and secondary production (Appendix 1). Information was collected of secondary production, biomass and P/B of species of spionids at different latitudes, as shown in table 1. Table 2 shows the values related to secondary production, biomass and P/B rate of populations of polychaete species (non-spionids) at different latitudes estimated

by the Mass Specific Growth Rate (MSGR) (Crisp 1984).

A total of 9,242 individuals were collected. The annual mean density was 16.38 ind.m⁻², ranging from 11.5 ind.m⁻² (August 2009) to 26 ind.m⁻² (June 2009) (Figure 3). Significant differences were observed between months (Kruskall-Wallis $p > 0.05$) and no species was obtained in July 2009 sampling.

Individuals were grouped in 18 size classes of 0.05 mm intervals based in the W3C width. The lowest value was 0.15 mm and the highest 1.0 mm, equivalent to total lengths of near 6 and 40 mm, respectively. The size class 0.55 mm - 0.75 mm was the most frequent in the population (Figure 4). The production and biomass of each size class and body mass were negatively correlated (Figure 5) and the power regression of these data was calculated by the following equation:

$$P/B = 1.61 * \text{body mass}^{-0.26}$$

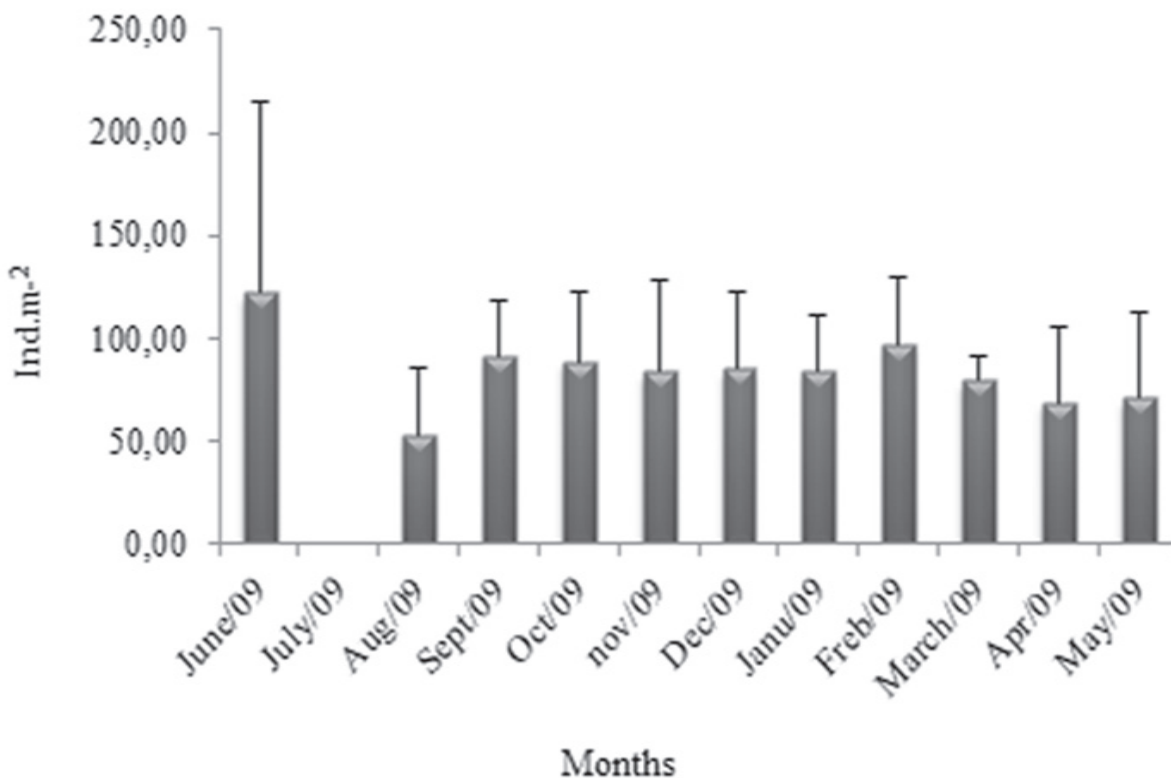
Figure 6 shows that there was no correlation between annual production, P/B ratios and biomass regarding latitudes, both for spionid and non-spionid polychaetes. The mean annual concentration of organic matter was 9.03 % \pm 6.15, chlorophyll *a* was 214.66 μ g/g \pm 3.01, and phaeopigments was 14.41 μ g/g \pm 0.90.

Table 1. Secondary production (P), Biomass (B), and P/B ratio of spionids populations from different latitudes estimated by the Mass Specific Growth Rate method (MSGR) (Crisp 1984). When more than one value was available, the mean was calculated and adopted. Values were calculated as Ash Free Dry Weight (AFDW), except* = dry weight.

Species	P (g m ⁻² y ⁻¹)	B (g m ⁻²)	P/B (y)	Author/Local/Latitude
<i>Scoelelepis goodbodyi</i>	8.3	2.78	2.98	This study/Brazil/22°12S"
<i>Scoelelepis squamata</i>	0.57	0.21	2.7	Souza & Borzone (2000)/Brazil/25°20S"
<i>Scoelelepis gaucha</i>	73.8	5.71	12.9	Santos (1994)/Brazil/34°28S"
<i>Paraprionospio pinnata</i>	4.53	1.8	2.4	Vasquez & Rojas (1980)/Chile/36°35S"
<i>Streblospio benedicti</i>	3.57 *	0.80 *	2.46	García-Arberas & Rallo (2004)/Spain/43°28N"
<i>Streblospio benedicti</i>	0.27 *	2.61 *	5.4	Sardá & Martin (1993)/USA/41°35 N"
<i>Marenzelleria viridis</i>	43.4	7.9	5.3	Sardá, Valiela & Foreman (1995)/USA/41°35 N"
<i>Spiophanes bombix</i>	3.34	0.69	4.9	Warwick <i>et al.</i> (1978)/England/51°19N"
<i>Spiophanes bombix</i>	0.08	0.06	1.3	Warwick & George (1980)/England/51°19N"
<i>Polidora quadrilobata</i>	1.5	8.2	1.5	Lambeck & Valentin (1987)/Netherlands/51°42N"
<i>Spiophanes kryeri</i>	0.20	0.14	1.4	Buchanan & Warwick (1974)/England/55°10N"
<i>Scoelelepis squamata</i>	1.39	0.79	2.08	Speybroeck <i>et al.</i> (2007)/Belgium/50°30N"

Table 2. Secondary production (P), Biomass (B), and P/B ratio of non-spionid populations from different latitudes estimated by Mass Specific Growth Rate method (MSGGR) (Crisp 1984).-

Species/Family	P (g m ⁻² y ⁻¹)	B (g m ⁻²)	P/B	Author/Region/Latitude
<i>Euzonus furcifera</i> (Ophellida, Ophellidae)	0.47	0.22	2.13	Souza & Borzone (2007)/Southern Brazil/25°20S"
<i>Owenia fusiformis</i> (Oweniida, Oweniidae)	10.27	0.330	6.28	Sardá, Pinedo & Dueso (2000)/NW Mediterranean/35°18E"
<i>Leitoscoloplos fragilis</i> (Orbiniida, Orbiniidae)	12.86	0.334	7.85	Sardá, Pinedo & Dueso (2000)/Southern New England, USA/41°10N"
<i>Capitella Capitata</i> (Capitellida, Capitellidae)	47	7.5	23	Méndez, Romero & Flos (1997)/NW Mediterranean/41°23N"
<i>Laeonereis culveri</i> (Phyllodocida, Nereididae)	40.8 – 43.8	5.44	7.2 – 8.7	Martin & Bastida (2006)/Argentine Sea/56°50W"
<i>Laeonereis acuta</i> (Phyllodocida, Nereididae)	3.8	1.95	2.0	Omena & Amaral (2000)/Southern Brazil/23°36S"
<i>Nereis diversicolor</i> (Phyllodocida, Nereididae)	15.9 – 74.2	4.4 – 7.9	3.6 – 10.2	Abrantes, Pinto & Moreira (1999)/NW Portugal/40°4N"

**Figure 3.** Mean (± S.E.) densities of *S. goodbodyi* from Manguinhos beach, Southeast Brazil, from June 2009 to May 2010.

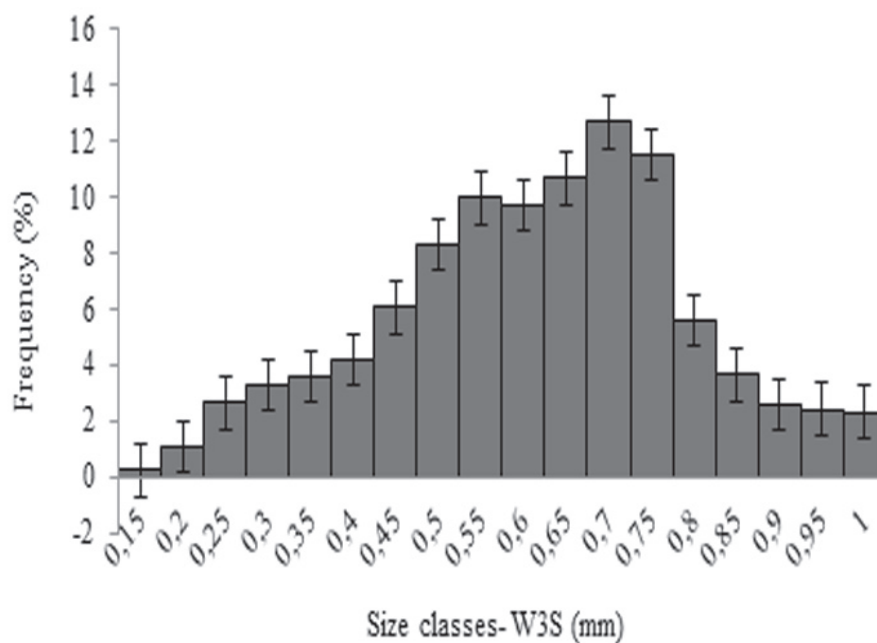


Figure 4. Size frequency distribution (mean ± S.E.) based on the 3rd chaetiger width (W3C) of *S. goodbodyi* from Manguinhos beach, Southeast, Brazil.

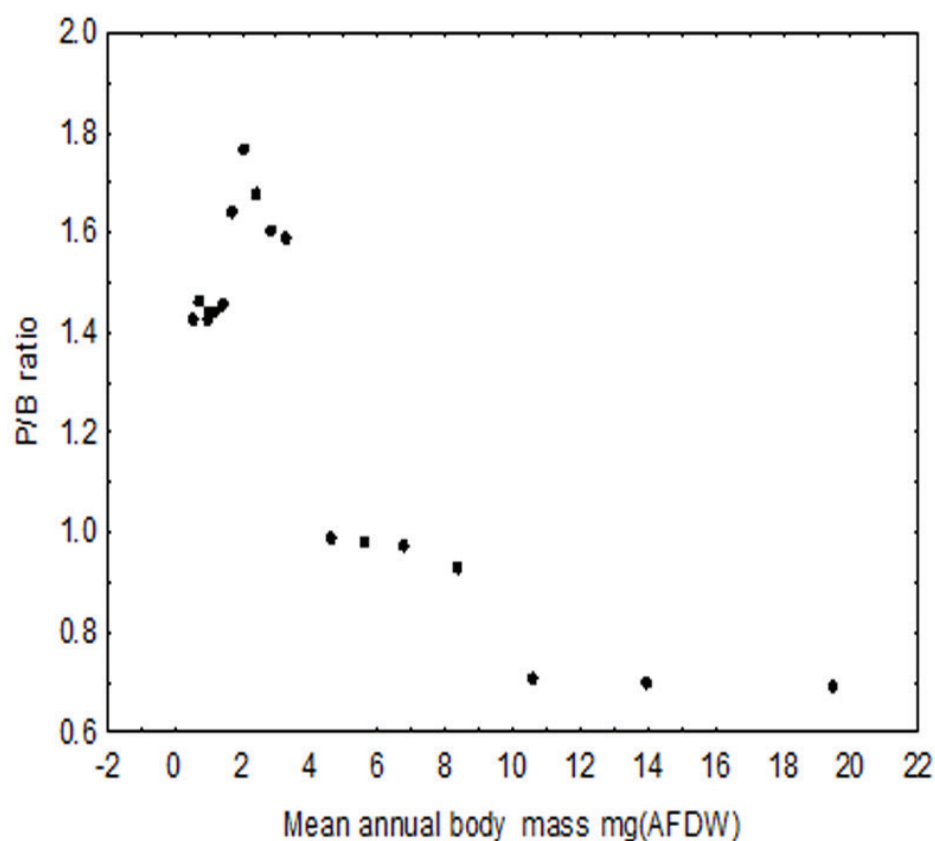


Figure 5. Correlation between production and biomass in each size class and the mean annual individual biomass of *S. goodbodyi* population from Manguinhos beach, Southeast Brazil. The constants of this power regression are: $P/B = 1.61 * \text{Body mass}^{-0.26}$.

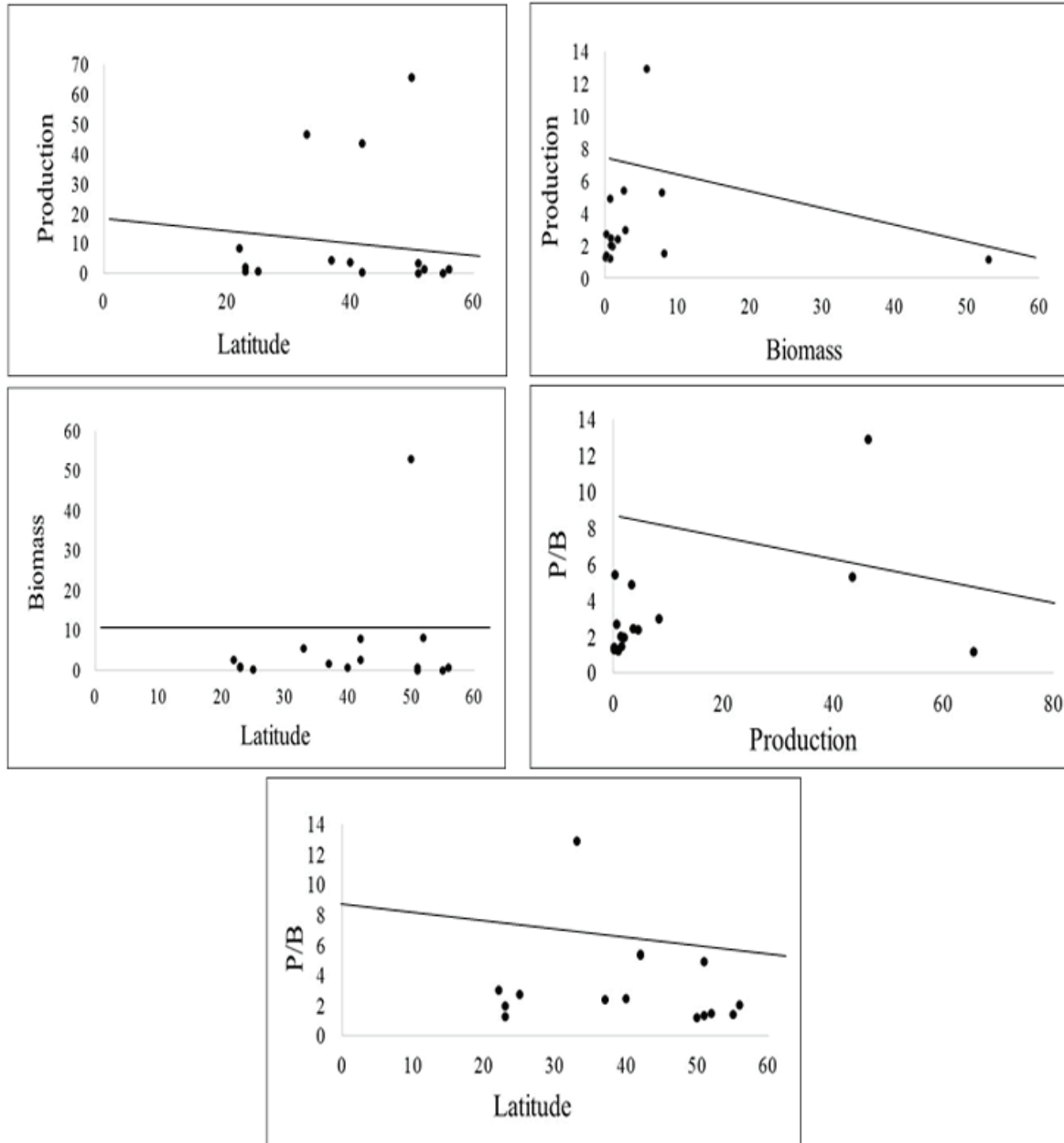


Figure 6. Correlation between productivity (g AFDW $m^{-2} y^{-1}$), biomass (g) and P/B, and between production, biomass and P/B from literature data showed in tables 2 and 3.

Granulometry was classified as medium sand and very poorly sorted according to Suguio (1973) and Sheppard (1994), with no temporal variation.

DISCUSSION

Scolelepis goodbodyi population on the beach of Manguinhos presented a secondary production rate of 8.30 g AFDW $m^{-2} y^{-1}$ time frame, except for the value reported by Santos (1994), Zettler (1997) and Sardá, Pinedo & Dueso (2000), the production of *S. goodbodyi* from Manguinhos beach is among

the highest values reported in the literature for Spionidae. The variation in secondary production among spionids (Table 1) may be caused by local environmental factors, as high productive waters due to the Cabo Frio upwelling (Knoppers *et al.* 2009, Gonzalez-Rodriguez *et al.* 1992). There is a direct relationship between primary and secondary productivity since autotrophs synthesize complex compounds from simple minerals, and these are decomposed by heterotrophic agents. So, these flows of matter and energy are shown as a description of productivity

between these organisms (primary and secondary productivity) in the study period (Van deer Meer *et al.* 2005).

Generally, Spionids are r-strategists and are expected to respond quickly to a productivity increase. Some species are bioindicators of disturbed environments (Pearson & Rosenberg 1978). These functional characteristics, which are related to an opportunistic lifestyle (small species, short generation time, rapid colonization time, high reproductive and mortality rate, with the ability to respond rapidly to resources changes) increases biomass and consequently reflects a high secondary production. R-strategist species contribute more to secondary productivity since they have a short life cycle, enabling a greater and faster nutrient cycling in contrast to k-strategists that are associated with low production, due to their high investment in body mass, reproduction and longevity, at least in the short term (Dolbeth *et al.* 2012). Usually, spionids do not presents a seasonal reproductive activity but rather show constant growth (Leão *et al.* 2012, MacCord & Amaral 2007). In the Manguinhos's population, the recorded high growth rate ($K = 1.20$) and longevity about 2.5 years indicate high rates of secondary production. The results corroborate this claim because the growth rate was greater in smaller individuals whereas the lowest biomass and secondary production rates occurred in the largest individual classes ($W3C = 1.0$ mm).

The annual P/B ratio is indicative of metabolic activity in a population (Warwick 1979). It decreases with increasing body mass in adults because most of the energy assimilated is allocated into reproduction. Energy is highly invested in growth in younger populations, which incorporate biomass rapidly (Tumbiolo & Downing 1994, Cusson & Bourget 2005).

Characteristics of species and peculiarities of life history, such as size range, recruitment, mortality, survivorship and growth rate influence the rate of biomass production (Warwick 1979, Cusson & Bourget 2005, Speybroeck *et al.* 2007). Environmental variables, notably temperature, salinity, and food quality and availability affect metabolism and growth of marine invertebrates, thereafter it could affect the rate of secondary production (Cusson & Burget 2005). The exceptionally high production of *S. gaucha* from

Cassino beach, Southern Brazil, may be explained by the high availability of food provided by the high frequency of surf zone blooms of the diatom *Asterionella glacilis* (Fragiarialis, Fragilariaceae). During such blooms, the chlorophyll *a* concentration could reach $1,647 \text{ mg m}^{-3}$ with a consequent sedimentation of the diatom cells that might fuel the local food web (Rörig & Garcia 2003, Odebrecht *et al.* 2010). The high production of *S. goodbodyi* from Manguinhos beach could also be related to the concentrations of organic matter, chlorophyll *a* and phaeopigments.

The waters of Manguinhos beach, located in the coast of the Southern Brazilian Bight (SBB) are reported to be more oligotrophic than the Southeastern Subtropical Shelf, where the Cassino beach is located (Lopes *et al.* 2006). Both beaches are located in high productive waters. The first is in the Cabo Frio upwelling area, but the oligotrophic conditions prevail off the SBB, with an increasing productivity, result of inner shelf fronts associated with estuarine plumes and coastal upwelling (Gonzalez-Rodriguez *et al.* 1992, Brandini *et al.* 2018). The Cassino Beach is located in a large continental shelf; the biological productivity in shelf waters is directly related to nutrients supplied by the coastal water (i.e. freshwater outflow), and subtropical and subantartic waters (Cioti *et al.* 1995). Studies done by Surugiu (2005) consider that surface-deposit feeder polychaetes, as Spionidae, can reduce the accumulated organic matter in the sediment, transforming and incorporating it into biomass. his way, polychaetes increase the circulation of organic matter into the food web, without being mineralized. Furthermore, macroinvertebrate biomass tends to be higher on dissipative beaches (McLachlan 1990), as Manguinhos beach, because such beaches retain greater amount of organic particles for suspension and deposit feeders.

In relation to biomass and production and P/B and production, the mean annual biomass values are related to low P/B ratios and low production. The results showed that the correlation between biomass and production and P/B and production were significant. The P/B of 2.98 y^{-1} in Manguinhos beach *S. goodbodyi* population was similar to that obtained by other studies in different populations of spionids. However, our results are lower than that obtained by Santos (1994) for *S. gaucha* and slightly

higher than that reported by Speybroeck (2007) for *Scolelepis squamata* (Spionida, Spionidae). The high P/B found in the population of *S. gaucha* by Santos (1994) was probably due to the observed high population density - around 430 % higher than that observed in this study. High degrees of P/B variation in several estuarine species are attributed to differences in age structures and environmental conditions (Sprung 1993).

According to Cusson & Bourget (2005), P/B ratios of benthic invertebrates occurring in different latitudes are usually similar. However, in high latitudes they tend to be lower since low temperatures constrain metabolic processes. For instance, increased temperature can decrease egg development time and increase rates of population growth and feeding, leading to increased production (Tumbiolo & Downing 1994). Our results indicate that there were few variations among production, biomass and P/B with increased latitude (spionids and non-spionids populations). Many studies show that this pattern can change in tropical coastal regions and in high latitude regions where populations are subjected to severe weather disturbances (Ricciardi & Bourget 1999, Brockington & Clarke 2001, Cusson & Bourget 2005). Paradoxically, Arctic shores can support high biomass during ice-free seasons (Warwick 1979, Ricciardi & Bourget 1999, Brockington & Clarke 2001). The high biomass of temperate shore communities can be explained by inputs of organic detritus from kelps beds, for example (Bustamente & Branch 1996). In the present study, we observed high production rates, biomass and P/B, which may be related to the high content of sediment organic matter and the great microphytobenthic biomass recorded in the study area. As previously observed, there are several patterns that demonstrate the strong influence on production, biomass and P/B, such as grain size, wave height, exposure, shore slope, tide and temperature variables and also population characteristics like growth and reproductive strategies (Dolbeth et al. 2012, Mclachlan & Dovlo 2005). For instance, a predation pressure can affect the growth of the surface deposit-feeder polychaete *Ampharete acutifrons* (Terebellida, Ampharetidae). This is an annual species from a high productive intertidal mudflat. The abundance of food favors a rapid growth in this species, but predation by fish reduces its

abundance from several thousand per m² in spring to tens of units for m² observed during the spawning periods, consequently decreasing recruitment and increasing mortality rates (Warwick & Price 1975).

The estimation of secondary production in polychaetes could be difficult to calculate due to the methods employed. Sardá *et al.* (2000) reported that these organisms might exhibit patterns of migration and larval dispersal that add to the obstacle in determining secondary production. These authors suggest that irregular processes, related to the population dynamics of polychaetes, require the adoption of different methods to determine secondary production, which can lead to different results. These differences in biomass and secondary production rates are also reported in polychaetes belonging to different families. Thus, the use of appropriate methods to estimate secondary production in polychaetes is relevant and the need to use different models that are suitable for each population is evident.

Our results demonstrate a high level of productivity in the studied *S. goodbodyi* population, suggesting that it can contribute to the local benthic food web and represent a relevant source into the energy flow of Manguinhos beach ecosystem. In relation to the rates of secondary production of spionids in different latitudes, including the population of *S. goodbodyi* analyzed in this study, we observed no clear pattern in the variation of values along the latitude. This could be an indication that secondary local factors can have a more important influence on them than latitudinal large scale factors, like the rates of breeding and reproduction and the environmental differences among regions.

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Appendix 1: Summary of the data used to calculate the secondary production of *S. cf. goodbodyi* according to the Mass Specific Growth Rate method (Crisp 1984).

Size L3S (mm)	Annual average density (m ²)	Body mass (mg) AFDW	Biomass (mg) AFDW	Mass Specific Growth Rate	Individual production (mg)	Population production (mg)
0.15	4.0	0.687	2.78	19.53	13.42	54.3
0.20	20.8	0.698	14.50	13.97	9.77	204.0
0.25	51.7	0.705	36.400	10.63	7.50	388.0
0.30	63.6	0.929	59.10	8.41	7.82	497.0
0.35	70.0	0.970	67.90	6.62	6.62	463.0
0.40	81.2	0.980	79.60	5.63	5.51	448.0
0.45	118.0	0.986	117.00	4.70	4.64	549.0
0.50	162.0	1.423	231.00	3.96	1.47	238.0
0.55	195.0	1.589	310.00	3.35	5.33	1040.0
0.60	190.0	1.603	305.00	2.85	4.56	870.0
0.65	208.0	1.673	349.00	2.42	4.05	845.0
0.70	248.0	1.765	438.00	2.05	3.62	890.0
0.75	225.0	1.641	371.00	1.73	2.85	643.0
0.80	108.0	1.456	158.00	1.46	2.12	231.0
0.85	71.2	1.440	103.00	1.21	1.75	124.0
0.90	49.5	1.435	71.10	0.99	1.43	70.8
0.95	47.2	1.463	69.10	0.80	1.17	55.3
1.0	0.2	1.420	0.28	0.62	0.89	0.2