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Morphometric analyses of two species of *Scolelepis* (Polychaeta: Spionidae)

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Seven hundred and six specimens of *Scolelepis* cf. *chilensis* and 551 specimens of *Scolelepis goodbodyi* were analysed. Individuals of each species were classified according to sex (male, female, and immature individuals). Width (w) and height (h) of setigers 3 and 5, the position of the first and the last gametogenic setigers, the total number of setigers, and the total length of each worm were measured. The area and volume of the setigers were estimated. Discriminant analysis was used to determine whether there were sexually dimorphic features, apart from the presence of gametes. Linear regression analysis was used to evaluate the relationship between each parameter and the number of setigers. *Scolelepis* cf. *chilensis* was found to be significantly larger than *S. goodbodyi* (t=21.71 and t=36.44, $P<0.05$ for length and number of setigers, respectively). These species also differed in the position of the first gametogenic setiger, which averaged 27 (SD=3) in *S.* cf. *chilensis* and 22 (SD=1) in *S. goodbodyi* (t= 29.18, $P<0.05$). There were no sexually dimorphic features in either sex of *S.* cf. *chilensis* (Wilks' lambda=0.9675, $P>0.05$, eigenvalue=0.034) or *S. goodbodyi* (Wilks' lambda=0.8429, $P>0.05$, eigenvalue=0.186). The total length showed the strongest correlation with the number of setigers in both species (r^2=0.887 and 0.850 for *S.* cf. *chilensis* and *S. goodbodyi*, respectively), followed by the width and the volume of setigers.

INTRODUCTION

The Polychaeta (Annelida) are one of the most important groups of invertebrates in the benthic community because of their predominance and their contribution to the number of species and individuals, productivity, biomass and energy flow (Knox, 1977). Although working with polychaetes should be easy because of their abundance in marine environments, researchers face significant difficulties in assessing the diversity and biology of this group caused by factors such as the breakage and elasticity of these organisms (Warwick & Price, 1975; Yokoyama, 1988; Seitz & Schaffner, 1995). During sampling in the field, polychaetes tend to lose body parts such as segments, antennae, pygidia, gills and the prostomium. In addition, their body length may also vary depending on the degree of relaxation of the worms during fixation. For population studies in which the entire length of the individual is necessary for determining age- and size-classes, incomplete specimens or variations in body length could negatively affect the results. To solve this problem, a measure of some structure that represents the entire length of the individual is often used to define the age- and size-classes of the population (Desrosiers et al., 1988). This structure may be a specific segment (Martin & Grémare, 1997; Shimizu, 1997; Omena & Amaral, 2000), a group of segments (Blake, 1993; Méndez et al., 1997), a hard structure (Glasby, 1986) or the number of setigers in intact individuals (Blake, 1993; Lewis, 1998).

The family Spionidae is an important component of benthic communities in shallow water and intertidal zones (Blake, 1996). This fact, together with their great diversity in reproductive modes and their usefulness as bioindicators (Grassle & Grassle, 1974; Marsh & Tenore, 1990; Wilson, 1991; Zajac, 1991a,b; Bridges, 1993; Souza & Borzone, 2000), makes these polychaetes good models for research. Since spionids have no hard structures (with the exception of setae) that can be measured, the structures commonly used to estimate age- and size-classes include the area of some segments (Ambrogi et al., 1993), the number of setigers (Richards, 1970; Zajac, 1991a; Lardicci et al., 1997) and the width of specific setigers (Santos, 1991; Zajac, 1991a; Lardicci et al., 1997; Shimizu, 1997; Souza & Borzone, 2000).

In the São Sebastião Channel, in south-eastern Brazil, two species of *Scolelepis* were previously identified as *S. squamata* (Müller), but are now considered as *Scolelepis* cf. *chilensis* and *Scolelepis goodbodyi* (Radashevsky*, personal communication). These species co-occur in disturbed areas, alongside two well-known indicator species, the Capitellidae *Capitella capitata* (Fabricius) and *Heteromastus filiformis* (Claparède) (Amaral et al., 1998). The aim of the present study is to define the best structure to be measured in these species of *Scolelepis* before studying their biology and their usefulness as indicators. In addition, the role of these structures during specimen growth and the possible morphometric differences between males and females and between species is assessed.

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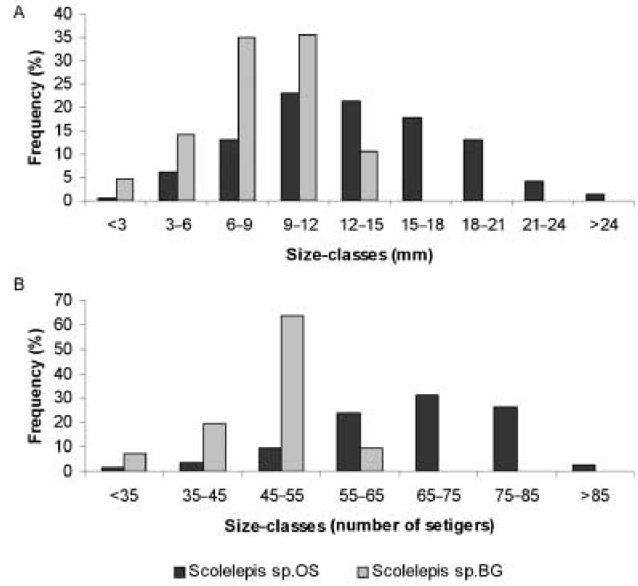

Figure 1. Relative frequencies of size-class distributions for (A) body length (mm) and (B) number of setigers in *Scolelepis* cf. *chilensis* and *Scolelepis goodbodyi*.

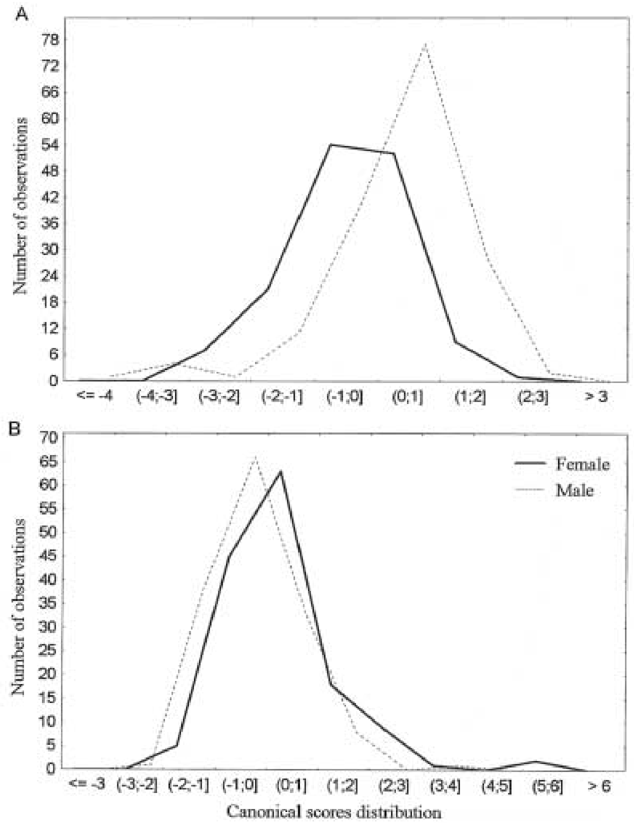

Figure 2. Canonical score distribution for males and females of (A) *Scolelepis* cf. *chilensis* and (B) *Scolelepis goodbodyi*.

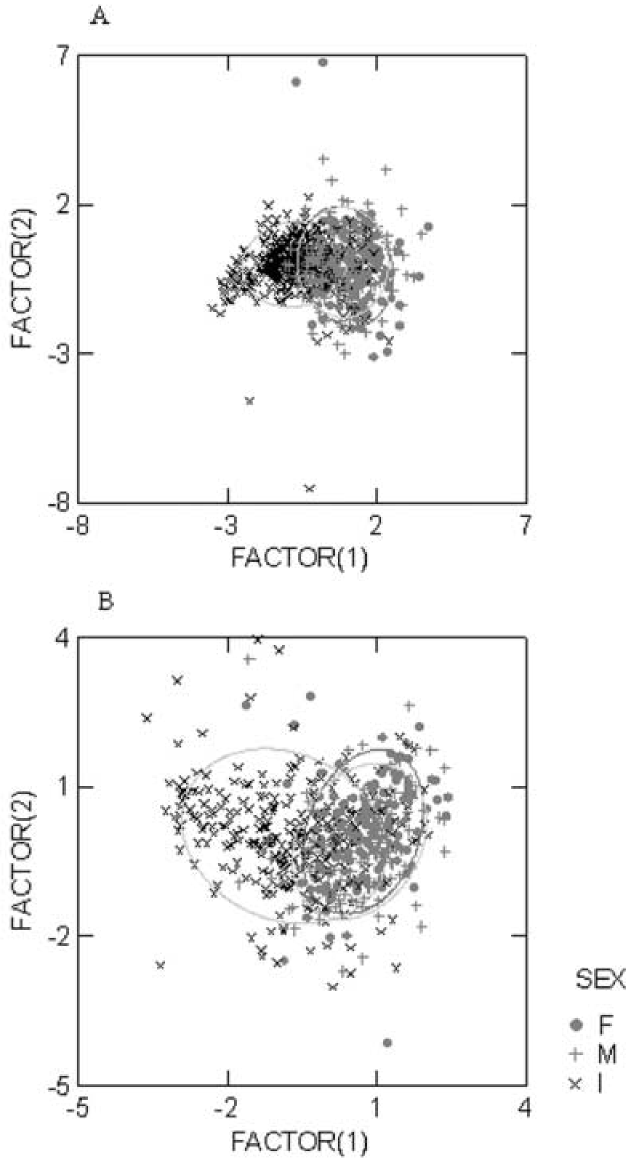

Figure 3. Factors explaining the difference between mature and immature individuals of (A) *Scolelepis* cf. *chilensis* and (B) *Scolelepis goodbodyi*. F, female; M, male; I, immature.

MATERIALS AND METHODS

Specimens of *Scolelepis* cf. *chilensis* (Hartmann-Schröder) were collected at Praia do Cabelo Gordo (23°49′34″S 46°26′25″W) from April 2002 to July 2003. This beach is enclosed by the Centro de Biologia Marinha da USP (Marine Biology Center of the University of São Paulo) (CEBIMar/USP) and is an environmental protection area. The beach is 200 m long, with a low slope, and consists of thin or very thin sediment layers interspersed with medium or coarse sediment layers. Specimens of *Scolelepis goodbodyi* (Jones) were sampled at Praia de Barequeçaba (23°49′42″S 46°26′00″W) from May 2002 to July 2003. This is a dissipative (wide surf zone, large waves, fine sediment and flat profiles) 1.2 km long beach with fine to very fine sand. Permanent and many temporary drainage channels occur along the beach.

Samples were obtained from each beach during spring tides using a 0.01 $m^2 \times 0.2$ m depth core. The first 10 cm of sediment was sieved through 0.5, 0.25 and 0.125 mm mesh sieves. The sediment that remained in the last two sievings was processed by a flotation technique (modified from Anderson, 1959) in order to suspend any juveniles and larvae present in the sediment. Seawater hypersaturated with sugar (1 kg/2.5 l seawater) was poured over the

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Table 1. *Relationship between the number of setigers and each allometric parameter of* Scolelepis *cf.* chilensis.

Par	N	log(a)	b	r^2	*P*	*t*	*P*	$S=a*Par^b$
w3	702	2.017	0.688	0.823	<0.05	−26.00	<0.05	$=103.992*w3^{0.688}$
w5	680	2.013	0.697	0.809	<0.05	−23.31	<0.05	$=103.039*w5^{0.697}$
h3	702	2.430	0.703	0.640	<0.05	−14.85	<0.05	$=269.153*h3^{0.703}$
h5	680	2.452	0.738	0.626	<0.05	−11.91	<0.05	$=283.139*h5^{0.738}$
V3	702	2.203	0.248	0.818	<0.05	−16.47	<0.05	$=159.588*V3^{0.248}$
V5	680	2.206	0.255	0.808	<0.05	−14.00	<0.05	$=160.694*V5^{0.255}$
A3	702	2.068	0.378	0.796	<0.05	−17.43	<0.05	$=116.950*A3^{0.378}$
A5	680	2.069	0.392	0.787	<0.05	−13.50	<0.05	$=117.220*A5^{0.392}$
h3/w3	702	1.485	−0.581	0.166	<0.05	−8.55	<0.05	$=30.549*h3/w3^{-0.581}$
h5/w5	680	1.464	−0.621	0.193	<0.05	−7.74	<0.05	$=29.107*h5/w5^{-0.621}$
Length	706	1.330	0.451	0.887	<0.05	−91.50	<0.05	$=21.380*Length^{0.451}$

Par, parameters; N, number of individuals; a, Y-intercept; b, regression coefficient; r^2, coefficient of determination; *t*, Student's *t*-test comparing b with critical values of allometry; *P*, significance of t; S, number of setigers; W, width (mm); h, height (mm); V, volume (mm^3); A, area (mm^2); 3, setiger 3; 5, setiger 5; length, total length (mm).

sediment and, after sedimentation, the seawater was passed through a 0.125-mm mesh sieve. The remaining sediment was sieved through 1 and 0.5 mm mesh sieves. All specimens of *Scolelepis* were relaxed in 5% MgCl, fixed in 6% formalin and preserved in 70% ethanol.

Individuals of each species were classified as males, females or immature individuals. The width (w) and height (h) of setigers 3 and 5, the position of the first gametogenic setiger, the total number of setigers and the total length of the worm were measured using a stereomicroscope fitted with a graduated eye piece.

The area and volume of each setiger were calculated using the formulas: external area$=2\pi(w/2)h$ and volume$=(\pi(w/2)^2)h$ and assuming a cylindrical shape. Discriminant analysis (Manly, 1998) based on the measurements was used to determine whether there were other sexually dimorphic features apart from the presence of gametes. Regression analysis was used to assess the relationship between each parameter (except the position of the first gametogenic setiger) and the number of setigers. The data were log transformed to change the allometric equation $y=ax^b$ into a straight line ($logy=loga+b*logx$), where b is the slope of the ordinates with values that will show positive allometry, negative allometry or isometry (Teissier, 1960; Gould, 1966). Student's *t*-test was used to compare b with critical values of allometry: 1 (x and y have the same type of measure), 0.5 (x is a measure of area and y is a linear measure), 0.33 (x is a measure of volume and y is a linear measure). Student's *t*-test was also used to compare the means among species. All analyses were done using the software Microsoft Excel 2000 and Systat 8.0 for Windows.

RESULTS

Seven hundred and six specimens of *Scolelepis* cf. *chilensis* were analysed. Their size ranged from 28 setigers to 92 setigers (mean ±SD: 68 ±12 setigers) or from 2.375 mm to 25.875 mm in length (mean ±SD: 13.289 ±4.708 mm) (Figure 1). The 551 specimens of *S. goodbodyi* ranged in size from 28 setigers to 64 setigers (mean ±SD: 49 ±7 setigers) or from 1.880 mm to 14.750 mm in length (mean ±SD: 8.642 ±2.817 mm) (Figure 1). *Scolelepis* cf. *chilensis* was significantly larger than *S. goodbodyi* (t=21.71 and t=36.44, $P<0.05$ for body length and number of setigers, respectively). The two species also differed in the position of the first gametogenic setiger, which occurred

Table 2. *Relationship between the number of setigers and each allometric parameter of* Scolelepis goodbodyi.

Par	N	log(a)	b	r^2	*P*	*t*	*P*	$S=a*Par^b$
w3	550	1.931	0.648	0.747	<0.05	−22.00	<0.05	$=85.310*w3^{0.648}$
w5	523	1.927	0.648	0.760	<0.05	−22.00	<0.05	$=84.528*w5^{0.648}$
h3	550	2.218	0.545	0.604	<0.05	−23.95	<0.05	$=165.196*h3^{0.545}$
h5	523	2.202	0.539	0.607	<0.05	−24.26	<0.05	$=159.221*h5^{0.539}$
V3	550	2.099	0.225	0.768	<0.05	−22.07	<0.05	$=125.603*V3^{0.225}$
V5	523	2.090	0.223	0.776	<0.05	−21.80	<0.05	$=123.027*V5^{0.223}$
A3	550	1.970	0.331	0.748	<0.05	−21.13	<0.05	$=93.325*A3^{0.331}$
A5	523	1.960	0.328	0.755	<0.05	−21.50	<0.05	$=91.201*A5^{0.328}$
h3/w3	550	1.646	−0.058	0.003	>0.05			
h5/w5	523	1.648	−0.057	0.003	>0.05			
Length	551	1.368	0.345	0.850	<0.05	−109.20	<0.05	$=23.335*Length^{0.345}$

Par, parameters; N, number of individuals; a, Y-intercept; b, regression coefficient; r^2, coefficient of determination; *t*, Student's *t*-test comparing b with critical values of allometry; *P*, significance of t; S, number of setigers; W, width (mm); h, height (mm); V, volume (mm^3); A, area (mm^2); 3, setiger 3; 5, setiger 5; length, total length (mm).

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Table 3. *Parameters used in biological studies of species of the family Spionidae.*

Parameter	Species	Reference
Total number of setigers	*Paraprionospio* sp. form A	Yokoyama, 1988
	Dipolydora armata (Langerhans)	Lewis, 1998
	Polydora ligni Webster	Zajac, 1991a,b
	Pseudopolydora diopatra Hsieh	Hsieh, 1994
	Scolelepis squamata (Müller)	Richards, 1970
	Streblospio benedicti Webster	Levin & Huggett, 1990 Bridges et al., 1994
	Streblospio shrubsolii (Buchanan)	Lardicci et al., 1997
Total number of setigers and body length	*Streblospio benedicti* Webster	Levin, 1986
	Spio martinensis Mesnil	Gudmundsson, 1985
	Polydora ciliata (Johnston)	Gudmundsson, 1985
	Pygospio elegans Claparède	Gudmundsson, 1985
	Malacocerus fuliginosus (Claparède)	Gudmundsson, 1985
	Polydora robi Williams	Williams, 2001
Volume 5th setiger	*Streblospio benedicti* Webster	Marsh & Tenore, 1990
Width 3rd setiger	*Scolelepis squamata* (Müller)	Shimizu, 1997
Width 4th setiger	*Streblospio benedicti* Webster	Sardá & Martin, 1993
	Streblospio shrubsolii (Buchanan)	Sardá & Martin, 1993
Width 5th setiger	*Scolelepis squamata* (Müller)	Souza & Borzone, 2000
	Scolelepis gaucha (Orensanz & Gianuca)	Santos, 1991, 1994
	Streblospio shrubsolii (Buchanan)	Lardicci et al., 1997
	Spiophanes bombyx (Claparède)	Steimle et al., 1990
Width 6th setiger	*Spiophanes bombyx* (Claparède)	Warwick et al., 1978
Maximum anterior width	*Marenzelleris* cf. *viridis* (Verril)	Zettler, 1997
	Paraprionospio pinata (Ehlers)	Vázquez & Rojas, 1980
Area from prostomium to 10th setiger	*Prionospio caspersi* Laubier	Ambrogi, 1990 Ambrogi et al., 1993

at setiger 27 ±3 in *S.* cf. *chilensis* and 22 ±1 in *S. goodbodyi* ($t=-29.18$, $P<0.05$).

Of the *Scolelepis* cf. *chilensis* individuals examined, 149 were females, 170 were males and 387 were immature; in *S. goodbodyi*, 156 were females, 156 were males and 239 were immature. There was no sexual dimorphism between males and females of *S.* cf. *chilensis* (Wilks' lambda=0.9675, $P>0.05$, eigenvalue=0.034) or *S. goodbodyi* (Wilks' lambda=0.8429, $P<0.05$, eigenvalue=0.186) (Figure 2). Nevertheless, there was a slight difference in size between mature (larger) and immature (smaller) individuals in of both species (Wilks' lambda=0.5833 and 0.6200, $P<0.05$, for *S.* cf. *chilensis* and *S. goodbodyi*, respectively) (Figure 3).

There was a strong, significant relationship between almost all variables and the number of setigers in *Scolelepis* cf. *chilensis* and *S. goodbodyi* (Tables 1 & 2). The strongest correlation in both species was with total length ($r^2=0.887$ and $r^2=0.850$ for *S.* cf. *chilensis* and *S. goodbodyi*, respectively), followed by the width and the volume of setigers (Tables 1 & 2). There was a negative relationship between the ratio of the height and width (h/w) and the number of setigers in *S.* cf. *chilensis* (Table 1), whereas no such relationship was seen in *S. goodbodyi* (Table 2). All of the variables showed significant negative allometric growth (Tables 1 & 2).

DISCUSSION

In addition to morphological differences, the two species of *Scolelepis* studied here also differed in size, occurrence of the first gametogenic setiger, and the h/w ratio. *Scolelepis* cf. *chilensis* was approximately 54% longer and had 39% more setigers than *S. goodbodyi*. In addition, the gametogenic setigers in the fomer species usually occurred after setigers 26 or 27 (compared with setigers 21 or 22 in *S. goodbodyi*), and never below setiger 25. In *Scolelepis* cf. *chilensis*, the h/w ratio ranged from 0.41 in animals with the fewest setigers to 0.17 in animals with the most setigers, which meant that setiger width increased at a rate greater than length. In contrast, this ratio did not change during the addition of new setigers in *S. goodbodyi*.

There were no morphological differences between males and females in either species: both sexes were similar in size and shape, and there was also no difference in the occurrence of the first gametogenic setiger. Mature and immature individuals differed in size, with immature individuals being more common among smaller size-classes. In *Scolelepis* cf. *chilensis*, this difference also reflected variation in shape since smaller individuals were generally wider than larger ones.

The number of setigers is considered to be the best measure for assessing age- and size-classes in polychaetes since the natural elasticity of polychaetes would have a negative effect on subsequent results if body length were used to estimate age- and size-classes (Yokoyama, 1988). Some workers have also suggested that counting the number of setigers is the quickest and most efficient measurement to make in worms (Zajac, 1991a; Lewis, 1998). In this study, there was a strong relationship between the number of setigers and body length, although the rate of setiger addition diminished as body length increased. Yokoyama (1988) found a similar relationship

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between the number of setigers and body length (b=0.44), primarily because an increase in body length is a response to the addition of new setigers and to an increase in the volume (length and width) of each setiger. In smaller individuals, the addition of new setigers is more important for growth than an increase in setiger volume, but this tendency diminishes with increasing size of the individual. Beyond 60 setigers in *Scolelepis* cf. *chilensis*, or 40 in *S. goodbodyi*, the increase in volume begins to contribute more to body length.

A few studies have used a reference parameter for estimating age- and size-classes. For example, Desrosiers et al. (1988) proposed the use of partial weight (the weight of the first 25 setigers) for population studies of *Nereis virens* (Sars). Fauchauld (1991) studied the relationship among several parameters in eight species of Eunicidae, and Seitz & Schaffner (1995) found the maximum head width to be the most reliable indicator of size for *Loimia medusa* (Savigny) (Terebellidae). Omena & Amaral (2001) tested different measures versus the body length of *Laeonereis acuta* (Treadwell) and chose the length of setiger 7 as an indicator of size.

Biological studies with spionids have used many parameters to estimate age- and size-classes (Table 3), including the number of setigers (Hsieh, 1994) and the measurement of a specific area with an image analyser (Ambrogi, 1990). For some species, such as *Streblospio benedicti*, a variety of parameters have been used, including the number of setigers, body length, volume of the 5th setiger and width of the 4th setiger. The range of parameters is even greater if one considers studies involving different genera (Table 3). Most studies have simply expressed a desired parameter versus body length, number of setigers or body length or weight (Ambrogi, 1990; Zajac, 1991a; Lardicci et al., 1997; Zettler, 1997) or have simply provided the regression equation without further explanation (Santos, 1991; Sardá & Martin, 1993; Souza & Borzone, 2000). An exception is the report by Yokoyama (1988) which analysed the relationship between body length and the width of the 5th setiger versus the number of setigers.

In the present study, we expected to find a strong relationship between volume or area and the number of setigers since a negative variation in one measure would be compensated for by a positive variation in another. However, the simplest measurement (width of each setiger) showed the strongest relationship with the number of setigers, as volume did, for both species. Hence, the choice of a parameter that represents age- and size-class must rely not only on the coefficient of determination, but also on its proximity to the prostomium (since there is a reduced chance of breakage) and on the facility of the measurements to be made. Based on these considerations and that more than one parameter to be measured and/or count (to achieve area or volume) would take greater effort to reach a similar result, it is recommended that the width of setiger 3 to be used in studies of these two species of *Scolelepis*. That is because the width (which is the easiest and most rapid measurement to be made) of this segment shows a high coefficient of determination. It is located very close to the prostomium, and it is possible to measure up to 100% of the individuals.

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REFERENCES

Amaral, A.C.Z., Morgado, E.H. & Salvador, L.B., 1998. Poliquetas bioindicadores de poluição orgânica em praias paulistas. *Revista Brasileira de Biologia,* **58**, 307–316.

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

Ambrogi, R., Fontana, P. & Riccobene, P., 1993. Population dynamics and secondary production of the spionid polychaete *Prionospio caspersi* in front of the Po River Delta. *Vie et Milieu*, **43**, 165–172.

Anderson, R.O., 1959. A modified flotation technique for sorting bottom fauna samples. *Limnology and Oceanography*, **4**, 223–225.

Blake, J.A., 1993. Life history analysis of five dominant infaunal polychaete species from the continental slope off North Carolina. *Journal of the Marine Biological Association of the United Kingdom*, **73**, 123–141.

Blake, J.A., 1996. Family Spionidae Grube, 1850. In *The annelida*. Part 3. Vol. 6. *Polychaeta: Orbiniidae to Cossuridae* (ed. J.A. Blake et al.), pp. 81–224. Santa Barbara: Santa Barbara Museum of Natural History.

Bridges, T.S., 1993. Reproductive investment in four developmental morphs of *Streblospio benedicti* (Polychaeta: Spionidae). *Biological Bulletin. Marine Biological Laboratory, Woods Hole*, **184**, 144–152.

Bridges, T.S., Levin, L.A., Cabrera, D. & Plaia G., 1994. Effects of sediment amended with sewage, algae, or hydrocarbons on growth and reproduction in two opportunistic polychaetes. *Journal of Experimental Marine Biology and Ecology*, **177**, 99–119.

Desrosiers, G., Vincent, B., Retière, C. & Boucher, L., 1988. Comparison de critères utilisables pour l'étude de la structure des populations du polychète *Nereis virens* (Sars). *Canadian Journal of Zoology*, **66**, 1454–1459.

Fauchald, K., 1991. A morphometric study of eunicid polychaetes from Belize, Western Caribbean Sea. *Ophelia*, Supplement, **5**, 47–53.

Glasby, C.J., 1986. Population structure and reproductive biology of *Ceratonereis limnetica* (Polychaeta: Nereididae) at Lower Portland, Hawkesbury River, Australia. *Marine Biology*, **90**, 589–595.

Gould, S.J., 1966. Allometry and size in ontogeny and phylogeny. *Biological Reviews*, **41**, 587–640.

Grassle, J.F. & Grassle, J.G., 1974. Opportunistic life histories and genetic systems in marine benthic polychaetes. *Journal of Marine Research*, **32**, 253–284.

Gudmundsson, H., 1985. Life history patterns of polychaete species of the family Spionidae. *Journal of the Marine Biological Association of the United Kingdom*, **65**, 93–111.

Hsieh, H.L., 1994. Larval development and substrate preference at settlement in *Pseudopolydora diopatra* (Polychaeta: Spionidae). *Invertebrate Reproduction and Development*, **25**, 205–214.

Knox, C.A., 1977. The role of polychaetes in benthic soft-bottom communities. In *Essays on polychaetous annelids in memory of Dr. Olga Hartman* (ed. D.J. Reish and K. Fauchauld), pp. 547–604. Los Angeles: Allan Hancock Foundation.

Lardicci, C., Ceccherelli, G. & Rossi, F., 1997. *Streblospio shrubsolii* (Polychaeta: Spionidae): temporal fluctuations in size and reproductive activity. *Cahiers de Biologie Marine*, **38**, 207–214.

Levin, L.A., 1986. Effects of enrichment on reproduction in the opportunistic polychaete *Streblospio benedicti* (Webster): a mesocosm study. *Biological Bulletin. Marine Biological Laboratory, Woods Hole*, **171**, 143–160.

https://doi.org/10.1017/S002531540501177X Published online by Cambridge University Press

Levin, L.A. & Huggett, D.V., 1990. Implications of alternative reproductive modes for seasonality and demography in an estuarine polychaete. *Ecology*, **71**, 2191–2208.

Lewis, J.B., 1998. Reproduction, larval development and functional relationships of the burrowing, spionid polychaete *Dipolydora armata* with the calcareous hydrozoan *Millepora complanata*. *Marine Biology*, **130**, 651–662.

Manly B.F.J., 1998. *Multivariate statistical methods: a primer*, 2nd edn. London: Chapman & Hall.

Marsh, A.G. & Tenore, K.R., 1990. The role of nutrition in regulating the population dynamics of opportunistic, surface deposit feeders in a mesohaline community. *Limnology and Oceanography*, **35**, 710–724.

Martin, D. & Grémare, A., 1997. Secondary production of *Capitella* sp. (Polychaeta: Capitellidae) inhabiting different organically enriched environments. *Scientia Marina*, **61**, 99–109.

Méndez, N., Romero, J. & Flos, J., 1997. Population dynamics and production of the polychaete *Capitella capitata* in the littoral zone of Barcelona (Spain, NW Mediterranean). *Journal of Experimental Marine Biology and Ecology*, **218**, 263–284.

Omena, E.P. & Amaral, A.C.Z., 2000. Population dynamics and secondary production of *Laeonereis acuta* (Treadwell, 1923) (Nereididae: Polychaeta). *Bulletin of Marine Science*, **67**, 421–431.

Omena, E.P. & Amaral, A.C.Z., 2001. Morphometric study of the nereidid *Laeonereis acuta* (Annelida: Polychaeta). *Journal of the Marine Biological Association of the United Kingdom*, **81**, 423–426.

Richards, S.L., 1970. Spawning and reproductive morphology of *Scolelepis squamata* (Spionidae: Polychaeta). *Canadian Journal of Zoology*, **48**, 1369–1379.

Santos, P.J.P., 1991. Morphodynamical influence of a temporary freshwater stream on the population dynamics of *Scolelepis gaucha* (Polychaeta: Spionidae) on a sandy beach in southern Brazil. *Bulletin of Marine Science*, **48**, 657–664.

Santos, P.J.P., 1994. Population dynamics and production of *Scolelepis gaucha* (Polychaeta: Spionidae) on the sandy beaches of southern Brazil. *Marine Ecology Progress Series*, **110**, 159–165.

Sardá, R. & Martin, D., 1993. Populations of *Streblospio* (Polychaeta: Spionidae) in temperate zones: demography and production. *Journal of the Marine Biological Association of the United Kingdom*, **73**, 769–784.

Seitz, R.D. & Schaffner, L.C., 1995. Population ecology and secondary production of the polychaete *Loimia medusa* (Terebellidae). *Marine Biology*, **121**, 701–711.

Shimizu, R.M., 1997. *Ecologia populacional de* Scolelepis squamata *(Müller, 1806) (Polychaeta: Spionidae) e* Callichirus major *(Say, 1818) (Crustacea: Decapoda: Thalassinidae) da Praia de Barequeçaba (São Sebastião, SP)*. PhD thesis, University of São Paulo, São Paulo, Brazil.

Souza, J.R.B. & Borzone, C.A., 2000. Population dynamics and secondary production of *Scolelepis squamata* (Polychaeta: Spionidae) in an exposed sandy beach, southern Brazil. *Bulletin of Marine Science*, **67**, 221–233.

Steimle, F.W., Kinner, P., Howe, S. & Leathem, W., 1990. Polychaete population dynamics and production in the New York Bight associated with variable levels of sediment contamination. *Ophelia*, **31**, 105–123.

Teissier, G., 1960. Relative growth. In *The physiology of Crustacea*, vol. 1 (ed. T.H. Waterman), pp. 537–560. New York: Academic Press.

Vázquez, F.C. & Rojas, D.A., 1980. Estimación de la producción secundaria de *Paraprionospio pinnata* (Spionidae, Polychaeta) frente a Bahía de Concepción, Chile. *Boletim do Instituto Oceanográfico, São Paulo*, **29**, 79–82.

Warwick, R.M. & Price, R., 1975. Macrofauna production in an estuarine mudflat. *Journal of the Marine Biological Association of the United Kingdom*, **55**, 1–18.

Warwick, R.M., George, C.L. & Davies, J.R., 1978. Annual macrofauna production in a *Venus* community. *Estuarine and Coastal Marine Science*, **7**, 215–241.

Williams, J.D., 2001. Reproduction and larval development of *Polydora robi* (Polychaeta: Spionidae), an obligate commensal of hermit crabs from the Philippines. *Invertebrate Biology*, **120**, 237–247.

Wilson, W.H., 1991. Sexual reproductive modes in polychaetes: classification and diversity. *Bulletin of Marine Science*, **48**, 500–516.

Yokoyama, H., 1988. Effects of temperature on the feeding activity and growth rate of the spionid polychaete *Paraprionospio* sp. (form A). *Journal of Experimental Marine Biology and Ecology*, **123**, 41–60.

Zajac, R.N., 1991a. Population ecology of *Polydora ligni* (Polychaeta: Spionidae). I. Seasonal variation in population characteristics and reproductive activity. *Marine Ecology Progress Series*, **77**, 197–206.

Zajac, R.N., 1991b. Population ecology of *Polydora ligni* (Polychaeta: Spionidae). II. Seasonal demographic variation and its potential impact on life history evolution. *Marine Ecology Progress Series*, **77**, 207–220.

Zettler, M.L., 1997. Population dynamics, growth and production of the neozoon *Marenzelleria* cf. *viridis* (Verril, 1873) (Polychaeta: Spionidae) in a coastal water of the southern Baltic Sea. *Aquatic Ecology*, **31**, 177–186.

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