

Allometry and population structure of *Nicolea uspiana* (Polychaeta: Terebellidae)

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The relative growth and population structure of the terebellid Nicolea uspiana were investigated in the intertidal zone of a rocky shore on the south-east coast of Brazil, from May 2006 to May 2007. Eight hundred and forty-seven individuals of N. uspiana were analysed: 391 males, 163 females, and 293 immatures. Although significant differences in some morphometric parameters were found, there was no sexual dimorphism between males and females. There were differences in total length, width of segment 5, and length of the notopodial region between matures and immatures. The negative allometry of the total length in relation to five other parameters showed that this feature is a good measure for estimating the individual size, which was then used in the analysis of population structure. This population of N. uspiana showed a bimodal size–frequency distribution, with immature and mature individuals found during the entire year. This pattern indicates continuous reproduction, with each cohort growing for at least three to four months and being responsible for two consecutive settlement peaks.

Keywords: relative growth, age-class structure, population dynamics

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INTRODUCTION

The study of the diversity and biology of the Polychaeta, one of the most important groups of invertebrates in the benthic community, is difficult because of factors such as the breakage and elasticity of their bodies (Warwick & Price, 1975; Yokoyama, 1988; Seitz & Schaffner, 1995; MacCord & Amaral, 2005). These problems usually occur during sampling, when polychaetes tend to lose body parts; or fixation, because their bodies can contract depending on the degree of relaxation of the worms (MacCord & Amaral, 2005). However, analyses of population structure, growth patterns, and secondary production using the entire length of the individual are essential to establish size–frequency and age–frequency histograms. Thus it is necessary to obtain parameters that represent the entire length of the individual with confidence (Desrosiers *et al.*, 1988; MacCord & Amaral, 2005).

Recently, allometric growth, or changes in body proportions during ontogeny (Katsanevakis *et al.*, 2007), has been used to obtain reliable morphometric parameters. The allometric equation is the most extensively used method of analysis for this kind of growth. However, the classic allometric equation frequently fails to adequately represent the data, because of the existence of either non-linearity or break-points (Protopapas *et al.*, 2007). Thus investigations that simply estimate the relative growth by means of log-transformed data using only linear models have yielded poor and misleading results (Katsanevakis *et al.*, 2007).

In this case, it is necessary to investigate allometric models that account for the influence of heteroscedasticity and the absence of linearity in the data. An alternative solution to this problem is the theory of model selection. The information-theory approach to model selection is based on alternative inferences to quantify the plausibility of each model, by extending the concept of maximum-likelihood of the parameters given both the data and model (Burnham & Anderson, 2002; Katsanevakis *et al.*, 2007).

Relative growth varies widely among different polychaete families (MacCord & Amaral, 2005), and information on population dynamics is unavailable for many species that are found in hard- and soft-sediment communities (Seitz & Schaffner, 1995). This is especially true for species of the Brazilian coast, where only a few studies have been done (Spionidae: *Scolelepis gaucha* by Santos, 1991, 1994; *S. squamata* by Shimizu, 1997; Souza & Borzone, 2000; *S. goodbodyi* and *S. chilensis* by MacCord, 2005; Nereididae: *Laeonereis acuta* by Florêncio, 2000; Omena & Amaral, 2000, 2001; MacCord, 2005; and *Nereis oligohalina* by Pagliosa & Lana, 2000; and Ophelidae: *Euzonus furciferus* by Souza & Borzone, 2007).

Nicolea uspiana (Nogueira, 2003) is a gregarious sedentary terebellid that constructs mucus tubes covered by sand grains and shell fragments in the midst of aggregates of algae, ascidians, hydroids, and bryozoans. This species is commonly found in the intertidal zone of rocky shores, always as dense populations with large numbers of individuals in different stages of maturity (Nogueira, 2003; Garraffoni & Amaral, 2009). No information regarding the relative growth, population ecology, and reproductive mode are available for this species.

The present study assessed the relative growth during ontogeny of *N. uspiana*. First, the models provided by Katsanevakis

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et al. (2007) were used to identify the parameters that best represented the growth of various body parts. Then, based on analyses of size–frequency distributions, the population structure of *N. uspiana* was characterized, as well as its recruitment.

MATERIALS AND METHODS

From May 2006 to May 2007, specimens of *Nicolea uspiana* were collected monthly in the intertidal zone along the rocky shore of Porchat Island, on Itararé Beach (23°57'35''S 46°23'15''W, São Vicente, Brazil). The specimens were collected by removing the sand-covered mucus tubes from the rocks by means of a scalpel. Samples were kept on ice in an insulated container, in order to relax the animals. The polychaetes were transported to the laboratory and kept in an aquarium with seawater in order to sort them alive. Under a stereomicroscope, the individuals were removed from their tubes, and only complete specimens were selected. Individuals were classified as males, females, or immatures; and anaesthetized in a solution of seawater and magnesium chloride for ~30 minutes. All individuals were measured before any fixation, to avoid shrinkage. After this process, they were fixed in 6% formalin for at least 48 hours, and then transferred to 70% ethanol for storage.

Both mature (females and males) and immature individuals were classified and used in the morphometric and population-structure analyses. The parameters measured included: total length (L), segment number (N_s), total length of the notopodial region (Ln), width of segment 5 (W_5), width of segment 18 (W_{18}), and length of segment 18 (L_{18}). Total length was considered the distance between prostomium (anterior end) and pigidium (posterior end). Student's t -test with log-transformed data were used to compare the means of the parameters between males and females. Logarithmic transformation is generally appropriate because morphological data tend to have a log-normal structure, as they are non-negative, with positively skewed distributions and variances that increase with the mean (Jolicoeur, 1990; Ebert & Russel, 1994; Katsanevakis *et al.*, 2007). The data for both sexes were also subjected to a principal components analysis (PCA), to assess possible intra-population patterns due to size arrangements. This methodology is often used for identifying a series of hypothetical variables (principal components), orthogonal to each other and which account for most of the variance in a data set (Manly, 1986; Preston & Roberts, 2007).

The allometric growth of each parameter versus the total length and the number of segments was investigated by four different candidate models (linear, quadratic, cubic and broken-stick). Either the total length or the number of segments was considered as the independent variable in the regression analyses. Following Katsanevakis *et al.* (2007), the linear model was fitted with simple linear regression ($\log Y = a_1 + b_1 \log X$), while polynomial regression was used for the quadratic ($\log Y = a_1 + b_1 \log X + b_2 (\log X)^2$) and cubic ($\log Y = a_1 + b_1 \log X + b_2 (\log X)^2 + b_3 (\log X)^3$), where a_1 is the intercept and b changes continuously with increasing body size. The broken-stick model ($\log Y = a_1 + b_1 \log X$; $X \leq B$; $\log Y = a_1 + (b_1 - b_2) \log B + b_2 \log X$; $X > B$) assumed that the breakpoint $X = B$ varied between the minimum and maximum value of the independent variable (morphological changes). According to Katsanevakis *et al.*

(2007), to select the most adequate model, the correct form of Akaike's information criterion was calculated: $AIC_c = (n(\log(2\pi RSS/n) + 1) + 2k) + 2k(k+1)/(n-k-1)$ where n is the number of observations, RSS the residual sum of squares, and k the number of regression parameters plus 1 (Hurvich & Tsai, 1989). The model with the smallest AIC_c value ($AIC_{c,\min}$) was selected as the 'best' among those tested. The AIC_c differences, $\Delta_i = AIC_{c,i} - AIC_{c,\min}$ were computed over all models. According to Burnham & Anderson (2002), models with $\Delta_i > 10$ have essentially no support and can be omitted, models with $\Delta_i < 2$ have substantial support, and there is considerably less support for models with $4 < \Delta_i < 7$. To quantify the plausibility of each model, the Akaike weight (w_i) was calculated:

$$w_i = \exp(-0.5\Delta_i) / \sum_{k=1}^3 \exp(-0.5\Delta_k)$$

The Akaike weight is considered as the weight of evidence in favour of model i being the actual best model of the available set of models (Burnham & Anderson, 2002). For the parameters that adequately fitted in the allometric linear model, Student's t -test was used to compare b values with critical values of allometry (MacCord & Amaral, 2005). In this case, when $b < 1$ the type of growth is described as negative allometric, when $b > 1$ as positive allometric, and when $b = 1$ as isometric (Katsanevakis *et al.*, 2007). The parameter that best represented the total length of *N. uspiana* was used to delineate the cohorts and to analyse the population structure.

Cohorts of *N. uspiana* were identified by the modal-progression routine (Bhattacharya) of the FISAT program, which works by decomposing modal distributions and identifying a probable normal distribution of the population. All other analyses were done using the software Microsoft Excel 2000 and Systat 8.0 for Windows.

RESULTS

Eight hundred and forty-seven individuals of *Nicolea uspiana* were analysed: 391 males, 162 females, and 293 immatures. The principal components analysis did not show any pattern of dimorphism in the species (Figure 1). However, females were significantly larger than males in four (L , N_s , W_5 , and L_{18}) of six measured parameters, although they showed no differences in parameters Ln and W_{18} (Table 1). Immatures differed from adults in total length, width of segment 5, and length of the region with notopodia, confirmed by principal component 1, with 81% of data variance, influenced by L , W_5 , and Ln (Figure 1).

The relative growth among parameters L/N_s , L/Ln , L/L_{18} , L/W_{18} , and N_s/Ln was considered to be best assessed by the linear model (Table 2). The total length has a larger growth than the number of segments, length of the notopodial region, and width of segment 18 (Table 3). On the other hand, the number of segments increases in a smaller proportion than the length of the notopodial region (Table 3). An isometric relationship between the ratio L/L_{18} showed that the width of segment 18 was the best measure for assessing size-classes of specimens. The cubic model had the highest plausibility relationships in the ratios L/W_5 , N_s/W_5 , N_s/L_{18} , and N_s/W_{18} (Table 2). In this case, the variation in

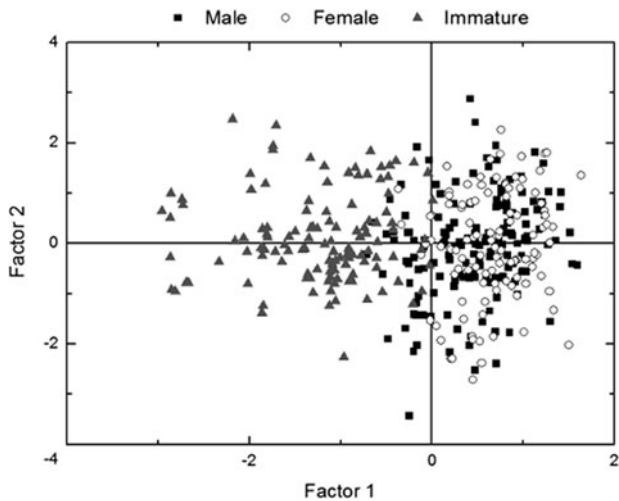


Fig. 1. *Nicolea uspiana*. Principal components analysis of the Itararé Beach population.

the relative growth among the parameters, mainly the number of segments, was observed over time.

The population of *N. uspiana* is composed of immature and adult individuals with lengths of 1 to 37 mm (Figure 2). The size–frequency distribution varied between a unimodal and polymodal distribution, with 11 cohorts (C1 to C11) delineated during the study period (Figure 3). The first cohort was observed in May 2006, and grew until August 2006. The second cohort was detected between July and September 2006, and the third cohort between August and September 2006. In September 2006, the fourth cohort was collected, and was recorded until November 2006. In October 2006, new recruits were detected, from cohort 5, and grew to a size that blended with cohort 6, by December 2006. The sixth cohort was recorded between November and December 2006, and cohort 7 between December 2006 and January 2007. In this last month, recruits from the eighth cohort were observed, and developed until February 2007. The ninth cohort was recorded between March and April 2007, and recruits from C10 between April and May 2007. The last cohort, C11, received new recruits from May 2007.

DISCUSSION

As in most polychaete species (Schroeder & Hermans, 1975; Giangrande, 1997), *Nicolea uspiana* has gonochoric reproduction, with immature individuals being common among lower size–frequencies and matures among the upper ones. Although similar differences in the morphological parameters

were observed, none of them could be used to distinguish between sexes. The only externally visible sexually dimorphic feature is the genital papillae, which are located close to the notopodia (Garraffoni & Lana, 2008). Benham (1927) pointed out that although the number and position of the genital papillae in the two sexes are identical for a given species, the form and relative size vary in the different species. The male papillae are comparatively small, slender tubes or cones, whereas the female papillae are less distinct, resembling a glandular wall in the epidermis, close to the notopodia (the morphology of both types of papillae was clearly observed in *N. uspiana*). In this case, in spite of the significant sexual differentiation observed in the morphometric parameters L , Ns , $L18$, and $W5$ in *N. uspiana*, they cannot be used alone to classify the individuals as males and females.

During the ontogenetic development of *N. uspiana*, most of the morphological features showed an allometric growth pattern (either positive or negative), and few showed isometric growth. The use of non-fixed individuals assures the accuracy of these relations, once we avoided problems with shrinkage. The dependent variables changed in different proportions to the independent variable (total length and total number of segments). In four of nine analysed morphometric relationships, the linear model was not the most plausible, corroborating the hypothesis that it could not detect points of discontinuity in the curves of relative growth (Katsanevakis *et al.*, 2007; Protopapas *et al.*, 2007). However, the linear model was the most plausible for five other relationships (L/Ns , L/Ln , $L/L18$, $L/W18$ and Ns/Ln).

The total number of segments would be expected to be the best measurement for assessing age and size-classes in *N. uspiana*. Some authors have noted that counting the number of chaetigers is the quickest and most efficient measurement to make in polychaetes (Lewis, 1998; Zajac, 1991a; MacCord & Amaral, 2005). This assumption is based on the constant number of segments during fixation, which will not result in misleading size–frequency histograms. However, in the present study, the relationships of the different measurements with the number of segments, as the independent variable, showed a lower r^2 , and were not considered a good parameter. On the other hand, the total length, a measurement that is not commonly used to assess size–frequency because of possible changes during fixation, was considered adequate for *N. uspiana*. The total length showed negative allometry for most of the relationships, and indicates that this parameter is a good indicator of the real size of the specimen.

The size–frequency distribution of *N. uspiana* suggests that individuals breed continuously during the year. The presence of new recruits, represented by individuals shorter than 2.9 mm, was observed during the sampling period.

Table 1. Mean values and standard deviation (SD) for each measured parameter for males and females of *Nicolea uspiana*. The values of Student's t -test (t) and probability (P) are indicated.

	L	Ns	Ln	$W5$	$L18$	$W18$
Male mean (SD)	13.82 (4.65)	48.48 (6.26)	5.96 (3.53)	1.23 (0.36)	0.47 (0.19)	0.82 (0.34)
Female mean (SD)	15.13 (4.96)	49.85 (6.01)	6.33 (1.64)	1.36 (0.33)	0.52 (0.19)	0.89 (0.34)
t	2.61	2.14	0.57	3.38	2.20	1.76
P	<0.05	<0.05	n.s.	<0.05	<0.05	n.s.

L , total length; Ln , length of the notopodial region; Ns , number of segments; n.s., non-significant; $L18$, segment 18 length; $W5$, segment 5 width; $W18$, segment 18 width.

Table 2. Values of AIC_c, AIC_c difference (Δ_i), and Akaike weight (w_i) for the four models applied to each relation of *Nicolea uspiana*. The most plausible models are indicated by bold characters.

		<i>L/Ns</i>	<i>L/Ln</i>	<i>L/W5</i>	<i>L/L18</i>	<i>L/W18</i>	<i>Ns/Ln</i>	<i>Ns/W5</i>	<i>Ns/L18</i>	<i>Ns/W18</i>
AIC _c	<i>Lr</i>	-1651.5	-1042.8	-748.6	-336.0	-206.4	-267.2	-422.6	-32.0	-150.6
	<i>Q</i>	-1618.0	-828.1	-773.8	78.1	-204.6	-201.8	-422.2	78.1	-148.8
	<i>C</i>	-1617.6	-834.5	-790.5	-334.7	-205.5	-216.3	-449.0	-56.5	-153.5
	<i>BS</i>	-1620.9	-833.1	-786.4	-333.8	-203.8	-211.9	-439.6	-43.4	-147.1
Δ_i	<i>Lr</i>	0	0	41.88	0	0	0	26.42	24.52	2.87
	<i>Q</i>	33.50	214.67	16.68	414.21	1.77	65.34	26.86	134.77	4.67
	<i>C</i>	33.88	208.28	0.00	1.33	0.91	50.83	0	0	0
	<i>BS</i>	30.63	209.69	4.02	2.18	2.59	55.22	9.41	13.10	6.41
w_i (%)	<i>Lr</i>	100.00	100.00	0.00	54.06	43.07	100.00	0.00	0.00	17.31
	<i>Q</i>	0.00	0.00	0.02	0.00	17.82	0.00	0.00	0.00	7.05
	<i>C</i>	0.00	0.00	88.18	27.78	27.30	0.00	99.10	99.86	72.69
	<i>BS</i>	0.00	0.00	11.80	18.16	11.81	0.00	0.90	0.14	2.95

AIC_c, Akaike's information criterion; *BS*, 'broken-stick' model; *C*, cubic model; *L*, total length; *Ln*, length of the notopodial region; *Lr*, linear model; *L18*, segment 18 length; *Ns*, number of segments; *Q*, quadratic model; *W5*, segment 5 width; *W18*, segment 18 width.

Table 3. Linear regressions of most plausible regression models of *Nicolea uspiana* and Student's *t*-test results to evaluate allometry critical values.

Regression	N	<i>a</i>	<i>b</i> ± SD	<i>r</i> ²	<i>P</i>	Regression type
<i>L/Tn</i>	551	28.773	0.2 ± 0.008	0.518	<0.001	Negative allometry
<i>L/Ln</i>	390	0.598	0.844 ± 0.011	0.934	<0.001	Negative allometry
<i>L/W18</i>	392	0.121	0.683 ± 0.033	0.525	<0.001	Negative allometry
<i>L/L18</i>	199	0.038	0.932 ± 0.025	0.874	n.s.	Isometry
<i>Tn/Ln</i>	389	0.001	2.201 ± 0.111	0.503	<0.001	Positive allometry

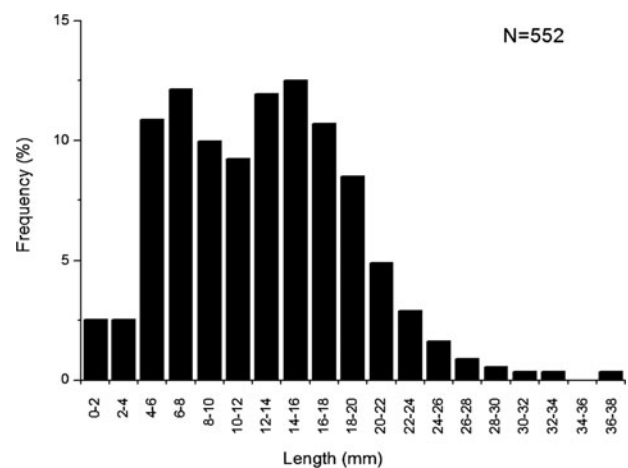
a, Y-intercept; *b*, regression coefficient; *L*, total length; *Ln*, length of the notopodial region; *L18*, segment 18 length; *N*, number of individuals; *Ns*, number of segments; n.s., non-significant; *P*, probability; *r*², coefficient of determination; SD, standard deviation; *W5*, segment 5 width; *W18*, segment 18 width.

The relationship between the life span and the length ratio is one of the main influences on the population structure (Giangrande, 1997). Thus, analysing the post-larval development (Garraffoni & Amaral, 2009) and the egg size–frequency distribution, we concluded that this is an iteroparous species, as the mature individuals can breed several times during their lifetime. The species showed extremely variable recruitment periods, with settlement of new juveniles occurring in several different months. Furthermore, this population has a high abundance, and a short maturation time, as the juveniles take two months to mature and begin a new reproductive cycle. A prolonged recruitment period, with numerous cohorts throughout the year, seems to be a common characteristic of terebellid polychaetes (McHugh, 1993; Giangrande, 1997).

This kind of lifespan may be related to the availability of food, which may allow constant and high recruitment of juveniles in small and medium size-classes, which have high growth rates and productivity (Gillet & Gorman, 2002; Martin & Bastida, 2006). Itararé Beach has fine sediments, and receives domestic wastewater from permanent drainage channels (the volume of wastewater increases on weekends and holidays, because São Vicente is a tourist centre). Thus the populations of *N. uspiana* may face temporary variations in the quantity and quality of food, where benthic habitat conditions may not be predictable and homogeneous, reducing the survivorship of individuals which recruit and mature during this period (Zajac, 1991b). This variation constrained an allocation of energy for a constant reproductive mechanism during the year, with continuous oocyte production (and consequently larval production) over the period. The frequency of

ovigerous females in *N. uspiana* was low, and the sex-ratio was biased in favour of males. As pointed out by Méndez *et al.* (1997), who studied the population dynamics of *Capitella capitata*, the low frequency of females in the samples was an effect of high amounts of organic matter, with the relatively few females able to produce large numbers of gametes.

In conclusion, our results indicated the desirability of careful selection of the most appropriate model to study morphometric growth in polychaetes. Furthermore, the use of anaesthetized individuals is more appropriate once it avoids the existence of bias because of the influence of fixation and storage. Alternative models need to be taken into account,

**Fig. 2.** *Nicolea uspiana*. Size-class distribution of the Itararé Beach population.

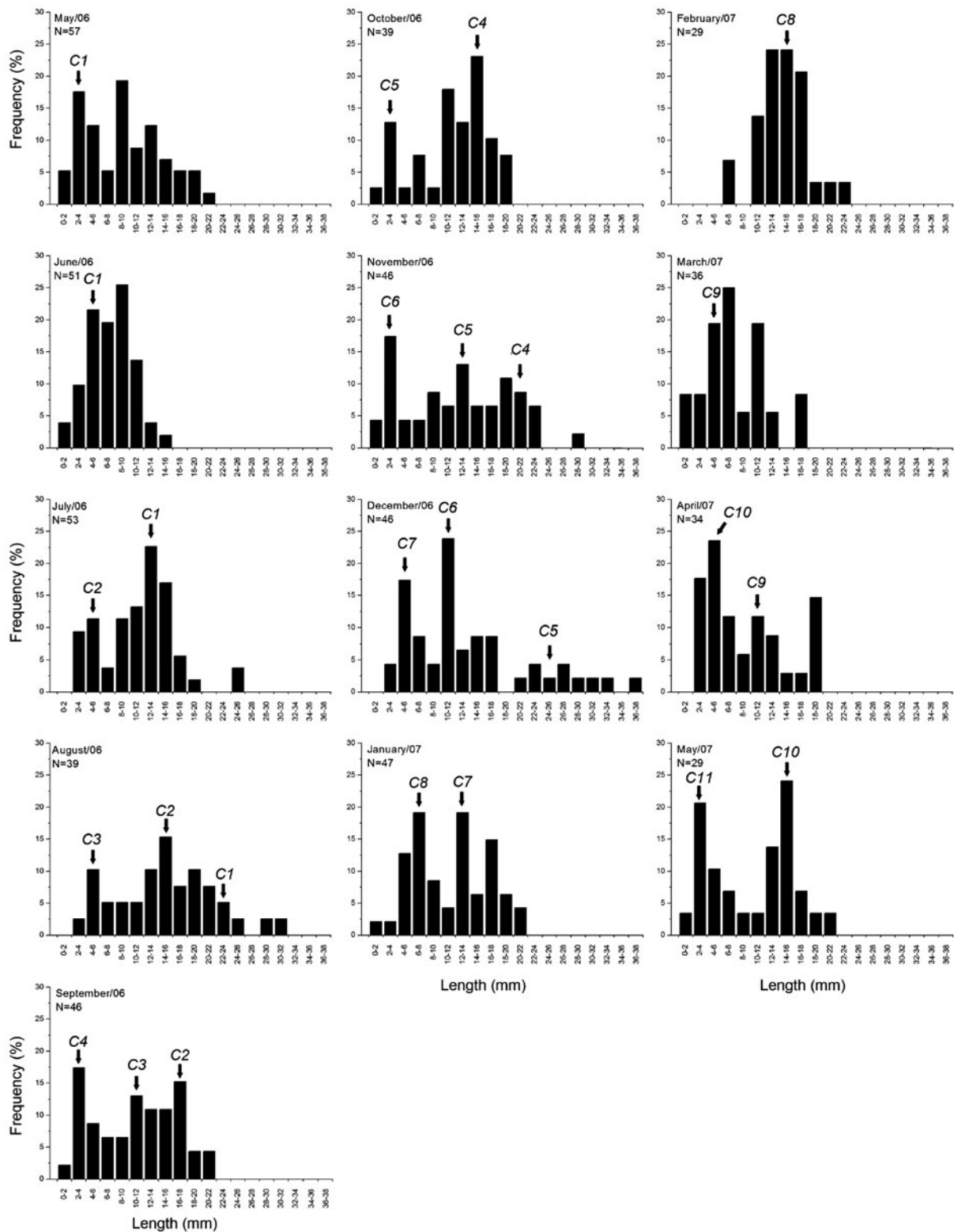


Fig. 3. *Nicolea uspiana*. Monthly size-class distribution of the Itararé Beach population. Arrows indicate the mean mode total length of the cohort.

to avoid the generation of misleading information or results. Furthermore, observation of the seasonal variation of body length in *N. uspiana*, together with inspection of the size–frequency, allowed us to detect long periods of settlement, suggesting a continuous reproductive pattern, with multiple

spawning occurring over the study period. Thus, because *N. uspiana* has a small adult size, high birth and death rates, a short maturation time and life span, it can be assumed that this species is opportunistic (Yokoyama, 1990; Lewis, 1998) and could be used as a pollution indicator.

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