

The gametogenic cycle and life history of *Nicolea uspiana* (Polychaeta: Terebellidae) on the south-east coast of Brazil

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The gametogenic cycle and life history of Nicolea uspiana (Nogueira, 2003) (Polychaeta: Terebellidae) was studied by taking monthly samples over a 13 month period. Each month, 10 females were sorted; 50 oocytes were removed from the coelom of each specimen, and the maximum diameter was determined. Additionally, 10 males were sorted and 100 gametes were randomly selected from each specimen to evaluate their shape and maturation stage. This species is gonochoric and exhibits slight external sexual dimorphism (in the shape of the nephridial papillae). The sex-ratio of N. uspiana was 2.4 male for each female. The initial gametic stages of both sexes are produced in special structures called nephromixia. Oogenesis is extra-ovarian, and the germ cells are clumped and surrounded by follicle cells. These cells are ovulated into the coelomic fluid, and yolk synthesis occurs in this cavity. The maximum diameter of oocytes measured, 225 µm, showed that these eggs fall into the size-range for lecithotrophy. Furthermore, N. uspiana is an iteroparous species, as the mature individuals can breed several times during their lifetime. Male gonads release germ cells early in development, and sperm maturation also occurs in the coelomic fluid. The male gametes consist of flattened plaques of germ cells attached on their anterior part by a cytophore assuming a rosette-like appearance. Following maturation of the male cells, the spermatids produce arrays of stiffly vibratile tails, assuming a morula shape. The reproductive patterns and life history of the terebellids are also discussed.

Keywords: Terebellomorpha, gamete development, oogenesis, spermiogenesis

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INTRODUCTION

The great diversity of reproductive and developmental modes exhibited by marine invertebrates is a challenge to researchers seeking to understand the patterns and trends of their life histories (McHugh, 1993; McHugh & Rouse, 1998; Ramirez-Llodra, 2002). The adaptive significance of reproductive and developmental modes in those groups has received some attention in the literature regarding the evolutionary constraints (e.g. Thorson, 1946; Schroeder & Hermans, 1975; Strathmann, 1985; McHugh & Rouse, 1998). This challenge is especially true in polychaete annelids, which have been recognized for their high reproductive diversity (Rouse & Fitzhugh, 1994; McHugh & Fong, 2002; Qian & Dahms, 2006). Wilson (1991) and Giangrande (1997) have identified 17 modes of sexual reproduction in more than 500 species of polychaetes. Among these different reproductive and developmental modes, typical characteristics include the type of oogenesis, type of spermatozoon, maximum oocyte size,

number of eggs per single spawning event, total female body size, development time, fecundity and individual growth rates (McHugh, 1993; Giangrande, 1997; Nylin & Gotthard, 1998; Marshall & Keough, 2007; Moran & McAlister, 2009).

Among the polychaetes, the family Terebellidae contains approximately 70 genera and more than 500 species and is distributed worldwide (Hutchings, 2000; Rouse, 2001; Garraffoni *et al.*, 2006; Garraffoni & Lana, 2008). This high diversity contrasts with the small amount of data regarding their life history and reproduction, as reproductive and developmental traits have been investigated for only 29 terebellid species (Wilson, 1991; McHugh, 1993; Giangrande, 1997).

Nicolea uspiana is a terebellid species which constructs mucous tubes covered by sand grains and shell fragments in the midst of aggregates of algae, ascidians, hydroids and bryozoans (Nogueira, 2003; Garraffoni & Amaral, 2009). It forms dense aggregations with individuals at different stages of development (Garraffoni & Amaral, 2009). Although it is a common Brazilian rocky-shore terebellid from the States of São Paulo and Paraná (latitudinal range: 23°21'S 44°51'W – 25°35'S 48°20'W) (Blankensteyn & Moreno, 1999; Nogueira, 2003; Garraffoni & Amaral, 2009; Santos *et al.*, 2010), no reproductive studies have been performed;

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however, the relative growth and population structure of *N. uspiana* have been studied by Garraffoni *et al.* (2010). Thus, the present study investigated the reproductive biology and gamete development of *N. uspiana*, to elucidate the diversity of reproductive and developmental patterns of the Terebellidae. Data on the mode of reproduction, body size, maximum oocyte size, maximum fecundity, mode of development and breeding strategy were analysed to examine the life history of this species. Furthermore, information about the reproductive patterns and life histories in other known terebellid species were compared in order to summarize the reproductive knowledge about this family.

MATERIALS AND METHODS

Specimens of *Nicolea uspiana* were collected monthly (May 2006–May 2007) 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). Specimens were collected qualitatively by removing the sand-covered mucous tubes from the rocks using a scalpel.

Samples were kept on ice in an insulated container to relax the animals. The polychaetes were transported to the laboratory and kept in an aquarium with seawater to sort them alive. In the laboratory, the specimens were removed from their tubes using a stereomicroscope, and the sex was determined by visual examination of the coelomic gametes or, in the smallest individuals, with a microscope. Females were identified by their whitish-yellow body coloration and the presence of yolk in the oocytes. Males were off-white in colour and possessed sperm-morule structures. Juvenile specimens lacked visible sexual characteristics (Eckelbarger, 1974). After these procedures, the specimens were anaesthetized in a solution of seawater and magnesium chloride for approximately 1 h, fixed in 6% formalin for at least 48 h, and then stored in 70% ethanol.

The histological analysis of gametogenesis in 10 mature individuals (5 males and 5 females) was performed by obtaining longitudinal sections from individuals of different sizes (10–18 mm in length). The specimens were dehydrated in an ethanol gradient (80, 95 and 100%), infiltrated and embedded in glycol-methacrylate resin, and serially sectioned at a thickness of 3–5 µm with glass knives in a microtome. Sections were stained with toluidine blue and later analysed by light microscopy and photographed.

To determine the size and volume of the oocytes in the vitellogenic stage, the coelomic content was examined monthly from 10 females randomly selected from the total number of females collected each month. These females were placed on a slide and gently compressed with a cover slip to let the oocytes shed from the coelomic fluid. Thus, fifty oocytes from each female were squashed under a cover slip, and their diameters were measured. The oocyte volume was determined under the assumption that it was spherical (total oocyte volume = $3/4\pi r^3$, where $2r$ is the diameter of the oocyte). A series of histograms of oocyte sizes were constructed to evaluate the pattern of oocyte maturation over the study period. The criteria used for identifying the stage of oogenesis followed those of Eckelbarger (1974), allowing the growth cycles of oocytes to be divided into the gonadal, follicular and vitellogenic phases.

The frequency of the occurrence of sperm stages was determined from a random selection of 100 gametes from the coelomic content of 10 randomly selected males collected between October 2006 and May 2007. The criteria used for staging sperm followed those of Blake *et al.* (2005), and allowed the growth cycles of sperm to be classified as rosettes of spermatocytes, early spermatids and morulae composed of tailed spermatids.

RESULTS

General characteristics

Nicolea uspiana is a gonochoric species with slight sexual dimorphism verified by the shape of the genital papillae,

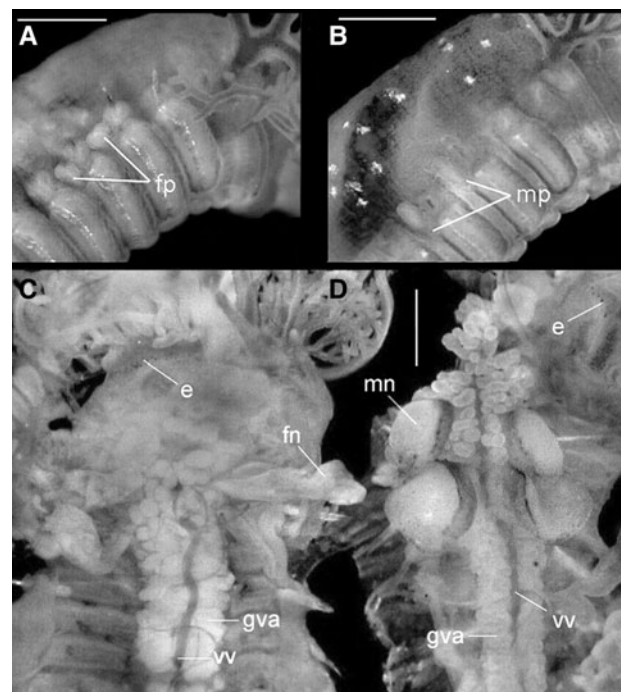


Fig. 1. *Nicolea uspiana*: size and shape of the nephridial papillae in female (A) and male (B) and internal morphology showing the female nephromixia (C) and male nephromixia (D). fp, female nephridial papillae; mp, male nephridial papillae; fn, female nephromixia; mn, male nephromixia; gva, glandular ventral area; e, eyespot; vv, ventral vessel. Scale bars: A,B, 300 µm; C, 250 µm; D, 150 µm.

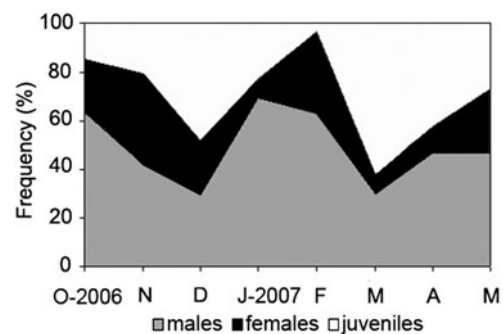


Fig. 2. *Nicolea uspiana*: relative monthly frequency (%) of juveniles, females, and males from October 2006 to May 2007.

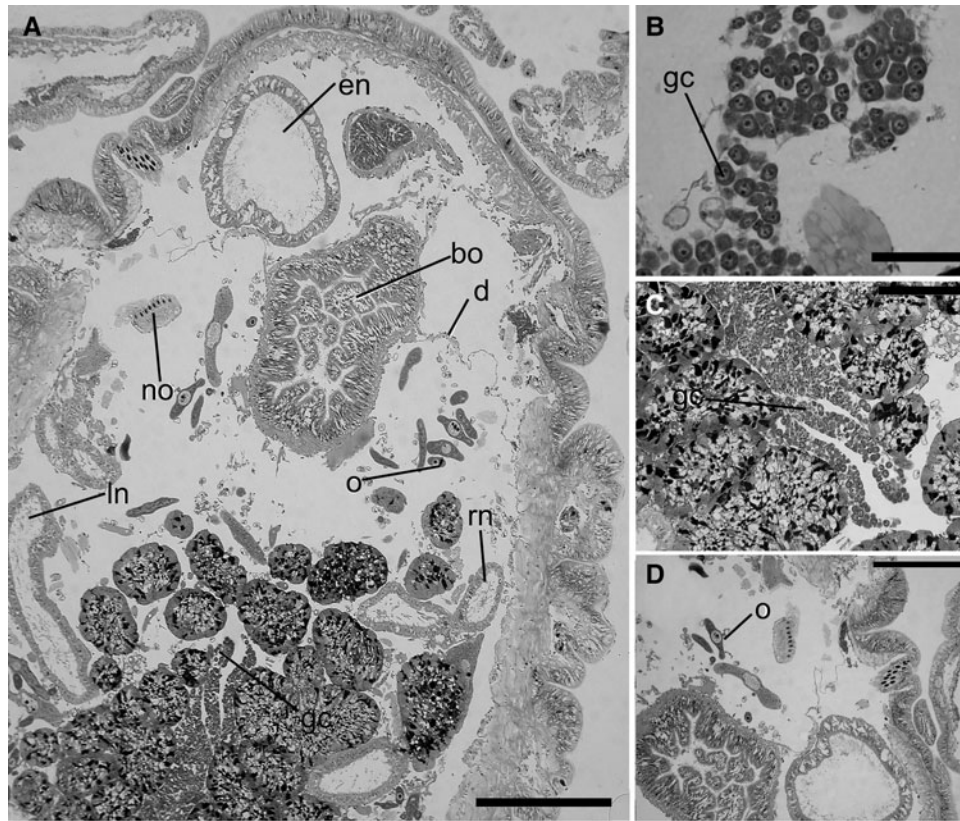


Fig. 3. *Nicolea uspiana*: longitudinal histological section of the anterior region and first segments of the mature female showing the two pairs of nephridia and the mature oocytes (A). Details of the mature oocyte and large clumps of oocytes bulged into the coelom (B–D). bo, buccal organ; d, diaphragm; gc germinative cell; ln; left nephridia, en, nephromixia; no, notochaeta; o, mature oocyte; rn, right nephridia. Scale bars: A, D, 400 μ m; C, 200 μ m; B, 100 μ m.

which are located dorsally and posterior to the notopodia (Figure 1A, B). The number and position of the genital papillae in the two sexes are identical; however, in the female, they are restricted to glandular walls and real papillae are not visible (Figure 1A), whereas papillae in the male are slender tubes or cones and are much more evident (Figure 1B). Both sexes have nephromixia composed of two inflated loops, one distal

and the other proximal, and they are usually projected upward in the coelomic spaces around the gut. The excretory nephromixia of *Nicolea uspiana* occur on segment 3, and the reproductive nephromixia occur on segments 6 and 7. Internally, the distinction between the reproductive nephridial structure of males and females is evident (Figure 1C, D). However, both mature male and female specimens lack distinct ovaries or testes.

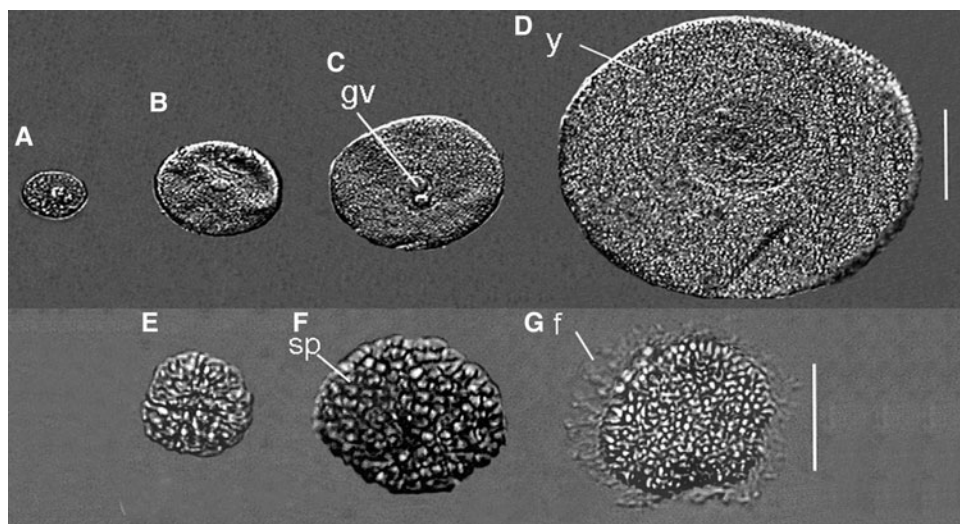


Fig. 4. *Nicolea uspiana*: distinct maturation stages of the oocytes (A–D) and spermatozoon (E–G). (A–C) immature oocyte; (D) mature oocyte; (E) spermatogonia; (F) spermatocyte; (G) spermatid. f, flagellum; gv, germinal vesicle; sp, spermatozoon; y, yolk. Scale bars: A–D, 50 μ m; E–G, 30 μ m.

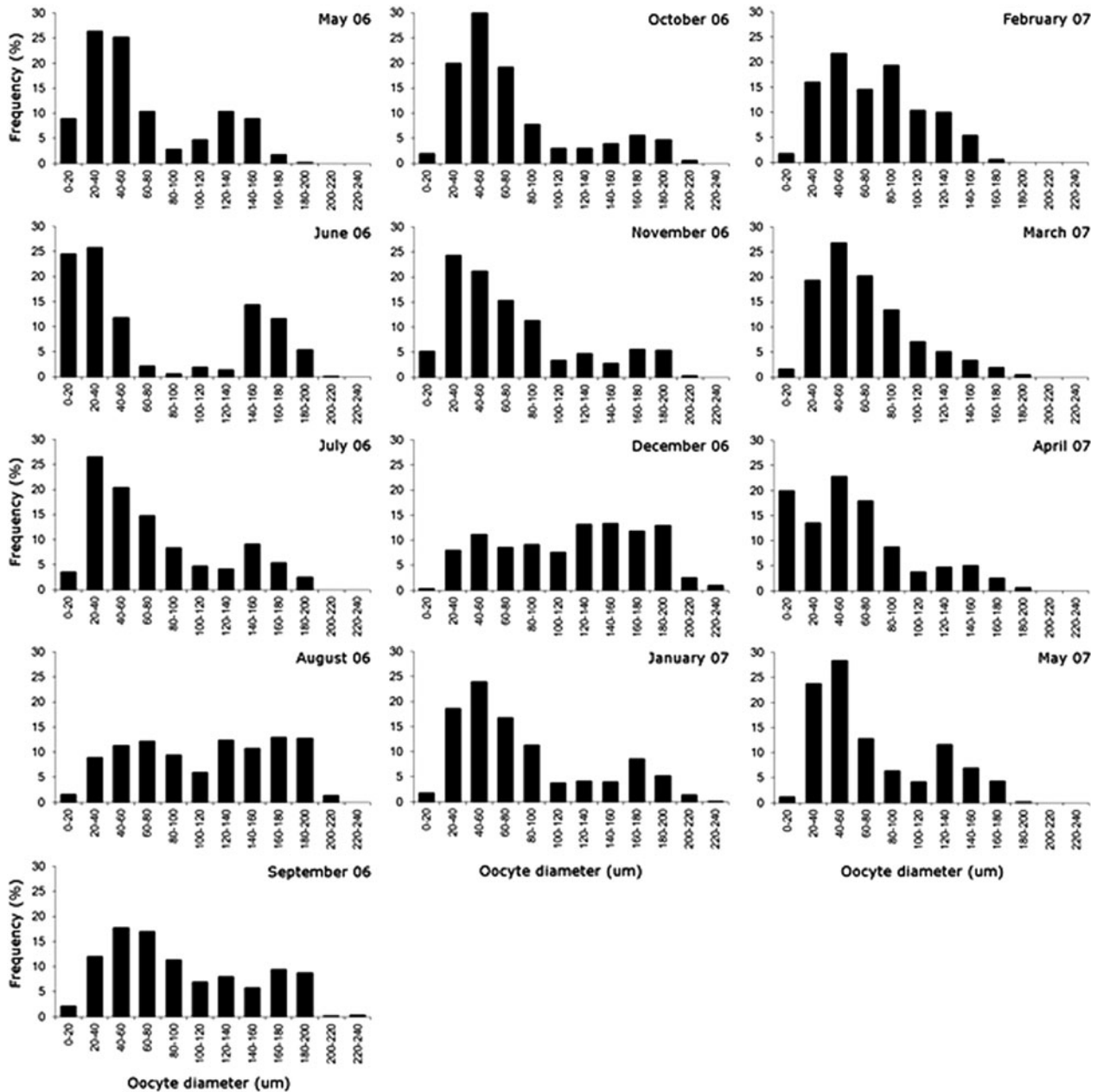


Fig. 5. *Nicolea uspiana*: monthly size—frequency histograms of maximum oocyte diameter from May 2006 to May 2007. In each month, 50 oocytes were measured from each of the 10 females.

Of the 847 total specimens of *Nicolea uspiana* examined, 163 were females (19.3%), 391 were males (46.2%), and 293 were juveniles (34.6%). The sex-ratio of *N. uspiana* was 2.4:1 (male:female), which is significantly different from a 1:1 ratio ($\chi^2 = 93.834$; $df = 1$; $P < 0.05$). Males dominated the population in all samples (Figure 2).

Oogenesis

The oocytes of *Nicolea uspiana* change shape from flattened to spherical during oogenesis. Histological characterization of the follicular and vitellogenic phases is shown in Figures 3A–D and 4A–D. In the follicular stage of gametogenesis, large clumps of oocytes (approximately 25 μm in diameter)

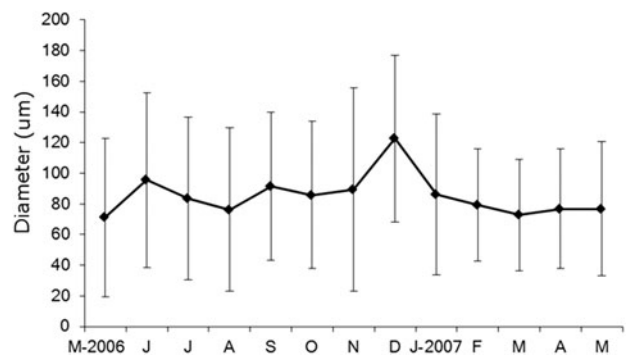


Fig. 6. *Nicolea uspiana*: mean and standard deviation of egg sizes from May 2006 to May 2007.

are surrounded by follicular cells bulging into the coelom. At this stage, it is possible to observe the germinal vesicle in a central position in the oocyte with an oval nucleus (7–8 μm in diameter) surrounded by a cytoplasmic component. In the next stage, the vitellogenic phase, the degeneration of the peritoneal membrane occurs, releasing oocytes that float freely in the coelomic fluid. During this phase, oocytes of various sizes, resulting from the different amount of cytoplasmic components in the oocytes that substantially increase during maturation, are observed in the coelom (Figures 3B–D, 4D).

Oocyte development was not synchronized in the Itararé population, with individuals in different gonadal and vitellogenic phases and also some with no gametes. The analysis of the distribution of oocyte sizes of *N. uspiana* showed a wide range of oocyte sizes throughout the year (Figure 5), from less than 10 μm to greater than 240 μm (mean \pm standard deviation: $85.2 \pm 49.2 \mu\text{m}$). The mean diameter was greatest in June 2006, September 2006 and December 2006, corresponding to the periods with fewer small oocytes (this pattern is clearest in December 2006). After each of these months, the mean diameter decreased and the number of small oocytes in the coelomic cavity increased.

Generally, monthly samples had a bimodal pattern with many small oocytes and a small proportion of large (>200 μm in diameter) oocytes (Figure 6). These bimodal distributions occurred mainly within May, June, July, September and November of 2006 and January, February, March, April and May of 2007.

Spermatogenesis

The histological characterization of the three reproductive stages of male specimens is shown in Figure 4. In the males examined in Itararé, the most common sperm stages were rosettes of spermatocytes (48.9%—Figures 4F, 7) and spheres of spermatogonia (48.1%—Figures 4E, 7). Morulae were much less common (3%—Figures 4G, 7).

The spermatogonia are the initial stage of spermatozoon development and occur in the nephromixia structures (Figure 8A). After this stage, sperm platelets are found throughout the coelomic cavity as ovoid, flattened plaques of germinal cells. The anterior portion of each ascosome is positioned toward, and held together by, a cytoplasmic

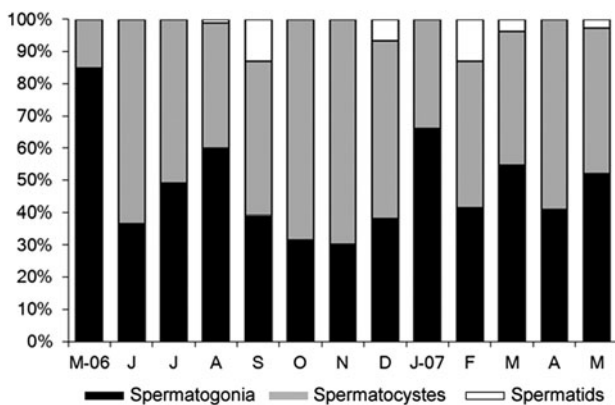


Fig. 7. *Nicolea uspiana*: relative monthly frequency (%) of spermatogenic stages males into rosettes of spermatocytes, early spermatis, and morulae. In each month 100 spermatozooids were measured from 10 males.

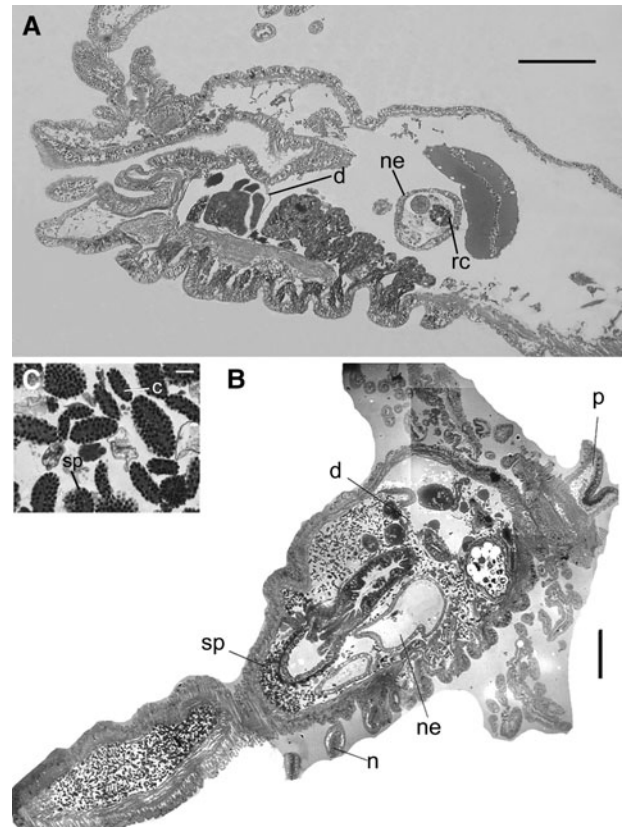


Fig. 8. *Nicolea uspiana*: transversal histological section of the anterior region of the mature male with cores in nephridial loop (A), anterior region showing the first pair of nephromixia (B), detail of the spermatogonia (C). c, cytophore; d, diaphragm; n, notopodia; ne, nephridia; p, prostomium; sp, spermatogonia; rc, residual core. Scale bars: A, 200 μm ; B, 100 μm ; C, 15 μm .

mass, the cytophore (Figure 4E, F). In these clusters, it is possible to observe distinct spermatozoon development stages as spheres of spermatogonia, rosettes of spermatocytes and morulae spermatis (Figure 4E, F). During this last stage, meiosis occurs and spermiogenesis results in elongate, tailed spermatis held together as morulae.

Without exception, males with non-motile sperm plates in the coelomic fluid had empty nephromixial ducts (Figure 8B, C). On the other hand, males in which the number of plates in the coelomic fluid was reduced or absent had nephromixial ducts filled with what appeared to be the 'cores' or cytophores of sperm plates.

Reproductive and developmental traits in Terebellidae

Table 1 summarizes the reproductive characteristics of 29 known terebellid species. Some species such as *Artacama proboscidea*, *Eupolymnia crescentis*, *Amaena occidentalis* and *Amphitrite ornate* are free spawning with lecithotrophic development. *Lanice conchilega* and *Loimia medusa* are free spawning with planktotrophic development. *Nicolea zostericola* deposits its gametes in gelatinous masses with direct development. On the contrary, *Eupolymnia nebulosa* deposits its gametes in gelatinous masses with lecithotrophic development, and *Eupolymnia heterobranchia*, *Ramex californiensis*, *Thelepus crispus*, *Thelepus setosus*, and *Neoleprea*

Table 1. Summary of reproductive characteristics available for the family Terebellidae. (-) missing information; (*) inapplicable information; A, maximum eggs diameter (mm); B, egg volume (calculated from maximum diameter (mm³); C, maximum fecundity; D, adult volume (mm³); E, breeding strategy; F, development type; G, larva type; H, sperm release; I, egg release; authors; BS, broadcast spawner; EB, extratubular brooder; IB, intratubular brooder; IT, iteroparous; LE, lecithotrophic; PL, planktotrophic; SE, semelparous.

Species	A	B	C	D	E	F	G	H	I	J
<i>Amaena occidentalis</i>	210	0.00485	21.000	2827.43	SE	Indirect	LE	BS	*	Fauchald, 1983; McHugh, 1993
<i>Amphitrite ornata</i>	100	0.00052	–	–	IT	Indirect	LE	BS	*	Scott, 1909, 1910; McHugh, 1993
<i>Artcama proboscidea</i>	170–180	0.00305	–	1246.83	–	Indirect	LE	BS	*	Thorson, 1946; Wilson, 1991
<i>Eupolymnia crescentis</i>	210	0.00485	128.500	10006.9	–	Indirect	LE	BS	*	McHugh, 1993
<i>Eupolymnia heterobranchia</i>	350	0.02245	–	6037.89	–	Direct	*	*	IB	Wilson, 1991
<i>Eupolymnia nebulosa</i>	190–287	0.01225	60.000	1496.77	IT	Indirect	LE	*	IB	Bhaud, 1988a, 1991; Bhaud & Grémare, 1988; Smith, 1989a; Wilson, 1991
<i>Lanassa nuda</i>	170	0.00257	–	–	–	–	–	–	–	Giangrande, 1997
<i>Lanice conchilega</i>	150	0.00177	160.000	60.31	IT	Indirect	PL	BS	*	Heimler, 1981; Bhaud, 1988b; Smith, 1989a, b; McHugh, 1993; Giangrande, 1997; A.R.S. Garraffoni, personal observation
<i>Loimia medusa</i>	150	–	–	–	IT	Indirect	PL	BS	*	Wilson, 1928; Seitz & Schaffner, 1995; Giangrande, 1997
<i>Loimia</i> sp. (Brazil)	–	0.00359	1,000.000	5428.67	–	Indirect	PL	BS	*	A.R.S. Garraffoni, personal observation
<i>Neoamphitrite robusta</i>	180	0.00305	829.833	32674.5	–	Indirect	LE	BS	*	McHugh, 1993
<i>Neoleprea macrocercus</i>	120–180	0.00305	–	163.45	–	–	–	–	–	Hutchings & Glasby, 1988
<i>Neoleprea streptochaeta</i>	600	0.11311	300	2239.32	IT	Direct	*	*	IB	Duchêne, 1980; McHugh, 1993
<i>Nicolea venustula</i>	250–350	0.02245	–	482.54	–	Indirect	LE	BS	*	McHugh 1993
<i>Nicolea zostericola</i>	220–300	0.01414	665	4.84	SE	Direct	*	*	IB	Eckelbarger, 1974, 1975, 1976; Wilson, 1991; McHugh, 1993; A.R.S. Garraffoni, personal observation
<i>Nicolea uspiana</i>	150	0.00177	–	87.16	SE	Indirect	LE	BS	*	Garraffoni et al., 2010; present study
<i>Polycirrus hematoides</i>	100	0.00052	–	–	–	Indirect	LE	–	–	Giangrande, 1997
<i>Ramex californiensis</i>	410	0.03609	44	84.94	IT	Direct	*	*	IB	Wilson, 1991; McHugh, 1993; Blake, 1991
<i>Streblosoma oligobranchiatum</i>	–	–	–	–	SE	Indirect	LE	BS	*	A.R.S. Garraffoni, personal observation
<i>Terebellides anguicomus</i>	105	0.00059	–	1266.69	–	–	–	–	–	A.R.S. Garraffoni, personal observation
<i>Terebellides stroemii</i>	135–150	0.00177	–	599.00	IT	Indirect	LE	*	EB	Willemoës–Suhm, 1871; Thorson, 1946; Wilson, 1991; Giangrande, 1997
<i>Thelepus cincinnatus</i>	762	0.23167	–	528.10	–	Direct	*	–	–	Thorson, 1946
<i>Thelepus crispus</i>	400	0.26808	51.555	49480	IT	Direct	*	*	IB	McHugh, 1993
<i>Thelepus setosus</i>	200	0.00419	150.000	1963.49	IT	Direct	*	*	EB	Duchêne, 1979, 1991; McHugh, 1993
<i>Trichobranchus glacialis</i>	150–200	0.00419	–	76.34	IT	Indirect	LE	BS	*	Christie, 1986
<i>Trichobranchus roseus</i>	95–110	0.00419	–	109.95	–	–	–	–	–	Thorson, 1946

streptochaeta brood inside the tube and show direct development. Regarding gametogenesis, only a few species have been as well studied as *Nicolea zoostericola*, *Lanice conchilega* and *Eupolymnia nebulosa*.

DISCUSSION

Nicolea uspiana is one of the most abundant and widespread terebellid species on the south-eastern coast of Brazil with well-established populations occurring over a wide geographical range from the States of São Paulo to Paraná (Blankensteyn & Moreno, 1999; Nogueira, 2003; Garraffoni & Amaral, 2009; Santos et al., 2010).

Garraffoni & Amaral (2009) argued that *N. uspiana* has indirect development with a brief planktonic stage, characteristic of lecithotrophic larvae. This conclusion was based on the absence of intra- or extratubular brooding (an indication of direct development) and the presence of larvae with statocysts

on the second segment (an indication of indirect development with planktonic larval stage). Moreover, *N. uspiana* can be considered an iteroparous species, as the mature individuals can breed several times during their lifetime (Garraffoni et al., 2010). This species exhibits extremely variable recruitment periods, with multiple spawning events and the settlement of new juveniles occurring in several different months (Garraffoni et al., 2010). Thus, because this species develops from relatively large eggs and has an abbreviated larval period without a feeding apparatus (Allen & Pernet, 2007), it can be assigned the reproductive and developmental traits of free spawning with lecithotrophic development.

Although individuals of *N. uspiana* have a maximum egg size (240 µm) close to that of other terebellid species (e.g. *Eupolymnia crescentis*—210 µm; *Amaena occidentalis*—210 µm; *Thelepus crispus*—220 µm; *Nicolea zoostericola*—230 µm), maximum fecundity (i.e. maximum number of full-grown oocytes) differs among these species because of their different sizes. *Nicolea uspiana* has a smaller body length

(ranges from 30 to 40 mm) than other species such as *Amaena occidentalis* (100 mm), *Eupolymnia crescentis* (130 mm) and *Neoamphitrite robusta* (250 mm). Thus, the reproductive output (percentage of total body volume given to a single brood or spawn) of individual *N. uspiana* will be lower than for individuals of other terebellid species.

Although *N. uspiana* and *N. zostericola* are in the same genus, oogenesis proceeds differently. *Nicolea uspiana* showed small cycles of oocyte production, with fluctuations on the oocyte diameter distributions over short periods of time. Eckelbarger (1974, 1975) reported that *N. zostericola* is a semelparous species with annual growth cycles and with oogenesis divided into gonadal, follicular and vitellogenic phases. In the preliminary stages of oogenesis in *N. zostericola*, only small and flat oocytes (25–50 µm diameter) are present. During the follicular phase, the oocytes (50–75 µm diameter) are floating into the coelomic fluid. In the vitellogenic phase, the deposition of yolk increases and the diameter of the oocyte may reach a maximum of 300 µm (Eckelbarger, 1974, 1975). The sex-ratio of *N. uspiana* is distinctly different compared to *Nicolea zostericola*. Eckelbarger (1975) observed in the latter species that females comprised 44.8%, males 37.9% and juveniles 12.8%, with no significant difference in sex ratio, while here we determined that *N. uspiana* females comprised 19.3%, males 46.2%, and juveniles 34.6% with a significant difference in the sex-ratio.

In the classification system proposed by Rouse & Jamieson (1987), there are three sperm types: (1) ect-aquasperm: spermatozooids are released into the water and fertilize similarly released eggs; (2) ent-aquasperm: spermatozooids are released freely into the ambient water but are gathered by or, in some other way, reach the female; and (3) introsperm: the spermatozooids have no contact with the water when passed from male to female (Rouse & Jamieson, 1987; Jamieson & Rouse, 1989; Rouse, 2005). The species studied in the present paper appears to fit the ect-aquasperm type (Thorson, 1946; Franzén, 1956; Eckelbarger, 1974, 1975; Jamieson & Rouse, 1989; Rouse & McHugh, 1994; McHugh, 1995), as do most of the Terebellidae (*N. zostericola*, *Ramex californiensis* and *Terebellides stroemii*—only *Streblosoma acymatum* fits the ent-aquasperm type) because, this type of sperm is frequently correlated with species that have life history traits such as small egg size and external fertilization (Giangrande, 1997). However, to confirm this hypothesis a sperm ultrastructure study needs to be conducted.

Comparative data of reproduction and development in terebellids

In terebellid species, male and female specimens are not easily distinguished by their external anatomy (Benham, 1927). The only exception is the shape of the genital papillae or external gonopores, which are slender tubes in males and papillae in females (Benham, 1927; Smith, 1992, 1994; present study). Regarding the position of the genital papillae, this structure can be found from segment 6 onward and can be located in three different positions: (a) dorsal to the notopodia; (b) aligned with the notopodia and posterior to them; and (c) inserted between the parapodial lobes (Nogueira *et al.*, 2010). The number of pairs of the external gonopores in the genera may vary from two in *Terebellides*, *Lanicides*, *Nicolea*, *Pista*, *Thelepus* and *Streblosoma* to three in *Leaena*,

four in *Amphitrite*, eight in *Terebella* and nine in *Neoamphitrite* (Benham, 1927; Smith, 1992; Nogueira *et al.*, 2010; present study).

Regarding the internal anatomy in terebellid species, the body coelom is divided into two distinct parts by a septum or diaphragm: one anterior with excretory functions and nephridial papillae and a posterior one with reproductive functions and genital papillae (Rouse & Fauchald 1997; Zhadan & Tzetlin, 2002). The development and proliferation of the early stages of the gametes occurs only in the interior of the nephromixia, positioned posterior to the diaphragm, and gametes are then shed to the coelomic cavity where they are directly exposed to the coelomic fluid and can develop there for a long period (Eckelbarger, 1975; Smith, 1992; McHugh, 1993). This type of gametogenesis was observed in *N. uspiana*, and is very similar to that reported by Smith (1989a, b, 1992), Eckelbarger (1975) and McHugh (1993), who studied the terebellids *L. conchilega*, *N. zostericola*, *Eupolymnia crescentis*, *Neoamphitrite robusta*, *Ramex californiensis* and *Thelepus crispus*.

Egg size is an important life history trait, as an indicator of the energy invested by the parental generation in its offspring (Giangrande *et al.*, 1994; Giangrande, 1997). This relationship between egg diameter and mode of development is well-established and delimited in marine invertebrates (Wray & Raff, 1991; Jeffery & Emet, 2003). Thorson (1950) and Schroeder & Hermans (1975) have reported that egg size is correlated with fecundity and development mode in several marine invertebrate groups, including polychaetes. Among terebellids, a huge range of egg diameter is observed (Table 1) from less than 100 µm in diameter (e.g. *Polycirrus haematoides*, *Amphitrite ornata* and *Trichobranchus roseus*) to larger than 762 µm in *Thelepus cincinnatus* (Fauchald, 1983; Wilson, 1991; McHugh, 1993; Giangrande, 1997). However, most of those terebellids have small eggs (15 species) with a planktonic larval phase, compared to a few species with large eggs (seven species) that develop directly into juveniles (Thorson, 1950; Schroeder & Hermans, 1975). For this reason, Giangrande (1997) grouped the Terebellidae together with other families (e.g. Cirratulidae or Maldanidae) according to their different larval types as 'coastal and deep benthic forms with a tendency for parental care and lecithotrophy'.

Regarding the terebellids that have small eggs and a planktonic larval phase, there are two types of larval development: lecithotrophic and planktotrophic, also called aulophore (Marcano & Bhaud, 1995; Garraffoni & Lana, 2010). The main difference between the lecithotrophic and planktotrophic larvae is that the former remain in the planktonic phase for a restricted period (a few hours to a week) and complete development without feeding because the larvae utilize the energy reserves of the yolk stored in the egg. On the other hand, aulophoric larvae (the only known larvae with a larval tube and a short planktonic feeding phase), even in the early stages of development when it has few segments, uses its ciliated tentacles to move to capture food particles. Moreover, this type of larvae is present in only two genera of the family Terebellidae, *Lanice* and *Loimia* (Bhaud, 1988b; Smith, 1989a; Marcano & Bhaud, 1995; Garraffoni & Lana, 2008, 2010), unlike what was reported by Strathmann (1993), and it appears as one of the shared putative exclusive synapomorphies between the two genera in the terebellid phylogenetic study of Garraffoni & Lana (2008).

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