POPULATION BIOLOGY AND REPRODUCTION OF *KALLIAPSEUDES SCHUBARTII* MAÑÉ-GARZÓN, 1949 (PERACARIDA, TANAIDACEA) IN A TROPICAL COASTAL LAGOON, ITAIPU, SOUTHEASTERN BRAZIL

BY

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ABSTRACT

A population of the tanaidacean, *Kalliapseudes schubartii* Mañé-Garzón, 1949 was sampled monthly in order to study its life cycle in a southeastern Brazilian tropical lagoon. The species' density changed seasonally, increasing in the beginning of the wet season and presenting peaks following precipitation peaks in other periods. Density changed due to oscillations in numbers of larval stages and juveniles. Females were larger than males, and the size at onset of sexual maturity of females was 5.9 mm. The sex-ratio was female-skewed during all months, in accordance with studies of the same species at other sites along the Brazilian coast and on other species of tanaids. Ovigerous females and other developmental stages were observed in all samples. Peaks in the frequencies of larval stages and juveniles were followed by peaks in ovigerous female frequency. Comparisons of populations of *K. schubartii* at different sites along the Brazilian coast showed an intraspecific difference in their life cycles according to a latitudinal gradient, with longer reproductive activity occurring in the tropics.

RÉSUMÉ

[Les études de biologie des populations des espèces-proies fournissent des informations utiles pour la gestion de la ressource et aident à prévoir les changements à venir concernant les espèces exploitées commercialement.] Une population de tanaidacés *Kalliapseudes schubartii* Mañé-Garzón, 1949 a été échantillonnée mensuellement dans une lagune tropicale du sud-est du Brésil afin d'étudier son cycle de vie. Les résultats montrent une variation saisonnière de la densité, celle-ci augmentant au début de la saison des pluies et présentant des pics à la suite des précipitations pour les autres périodes de l'année. Les densités mesurées varient avec le changement de stade larvaire à juvénile. Les femelles sont plus grandes que les individus mâles, la taille de celles-ci au début de la maturité sexuelle est de 5,9 mm. Le «sex-ratio» apparaît déséquilibré pour chaque mois avec une prédominance des individus femelles, ce qui concorde avec des études réalisées chez la même

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espèce sur d'autres sites le long de la côte brésilienne ainsi que chez d'autres espèces de tanaidacés. Des femelles ovigères ainsi qu'à d'autres stades de développement ont été observées dans tous les échantillons. Les pics de fréquence concernant les stades larvaires et les individus juvéniles sont suivis par des pics de fréquence des femelles ovigères. Enfin, la comparaison avec des populations de *K. schubartii* de différents endroits de la côte brésilienne a montré une différence intraspécifique dans leurs cycles de vie selon un gradient de latitude, avec une activité reproductrice plus longue sous les tropiques.

INTRODUCTION

Tanaids are cosmopolitan, benthic crustaceans that occur from intertidal to abyssal zones including lagoons and estuaries (Holdich & Jones, 1983). They live buried or inside tubes in the sediment, in small holes or chinks in the rocks, or on the surface of marine plants (Gardiner, 1975; Johnson & Attramadal, 1982; Nakaoka, 2002). Most tanaids are deposit-feeders, but the Kalliapseudidae are suspension-feeders (Ogle et al., 1982), such as *Kalliapseudes schubartii* Mañé-Garzón, 1949, which occurs in the southwestern Atlantic (Young, 1998).

Life history studies, both of species lacking commercial value and exploited species, are essential to understand the functioning of marine ecosystems (Pardo et al., 2007). Those studies are useful to predict changes in time and space of species densities, and provide necessary knowledge to the management of harvesting and threatened species (Akçakaya, 1999). Distributions of species may be altered by anthropogenic effects and natural causes, such as food availability and predation pressure. *K. schubartii* is a tiny species that is supposed to be an important link in estuarine food webs, being a constant item in the diet of the swimming crab, *Callinectes sapidus* Rathbun, 1896 (cf. Kapusta & Bemvenuti, 1998) and the preferential prey of the fish, *Micropogonias furnieri* (Desmarest, 1823) (cf. Figueiredo & Vieira, 2005).

K. schubartii is a tubiculous species that occurs in high densities and shows a patchy spatial distribution. Variations in population density have been related to sediment grain size and organic matter load (Nucci et al., 2001; Leite et al., 2003). In areas composed mainly of sand and low percentages of silt and clay, the tubes are restricted to the near surface of the sediment, leading to an increase in mortality by predation and/or unsuccessful recruitment (Rosa-Filho & Bemvenuti, 1998). Females of *K. schubartii* develop eggs, embryos, and manca stages in a brood pouch, where the juveniles emerge from (Leite & Leite, 1997). Males can appear in two different forms, which differ in cheliped morphology, suggesting that this species may be a protogynic hermaphrodite (Leite & Leite, 1997; Leite et al., 2003). Besides local scale variations, the life history traits of the marine fauna, such as abundance, growth and mortality rates, recruitment seasons, and fecundity, may exhibit latitudinal trends (Conover, 1992; Fiori & Defeo, 2006; Linse et al., 2006).

Despite its wide geographic distribution and high densities, few studies have been conducted on the marsupial and post-marsupial developmental stages, or on the reproduction and population structure of tanaids. The aim of the present study was to assess the population biology and reproduction of *K. schubartii* in a tropical coastal lagoon in southeastern Brazil, and comparing the results with tanaid populations occurring worldwide.

MATERIAL AND METHODS

Study area

Itaipu Lagoon (22°58′S 43°02′W) is nearly 1.5 km wide and 2 km long, and is connected to the sea through a canal that allows quick exchange between marine and lagoon waters (Barbieri & Coelho-Neto, 1999; Kjerve & Knoppers, 1999). Salinity does not show significant changes, remaining around 30 PSU throughout an annual cycle. Water temperature oscillates between 17 and 20°C in winter and maintains around 30°C in summer (Kjerve & Knoppers, 1999). The main organic matter input is from gross domestic sewage, which makes the lagoon a mesotrophic system. Despite this high anthropogenic input, nitrogen is a limiting factor in both the lagoon and the rivers of the drainage basin (Knoppers et al., 1999).

The present study was carried out at the margin of the lagoon next to the channel, where a patch of *Kalliapseudes schubartii* can be encountered (fig. 1).

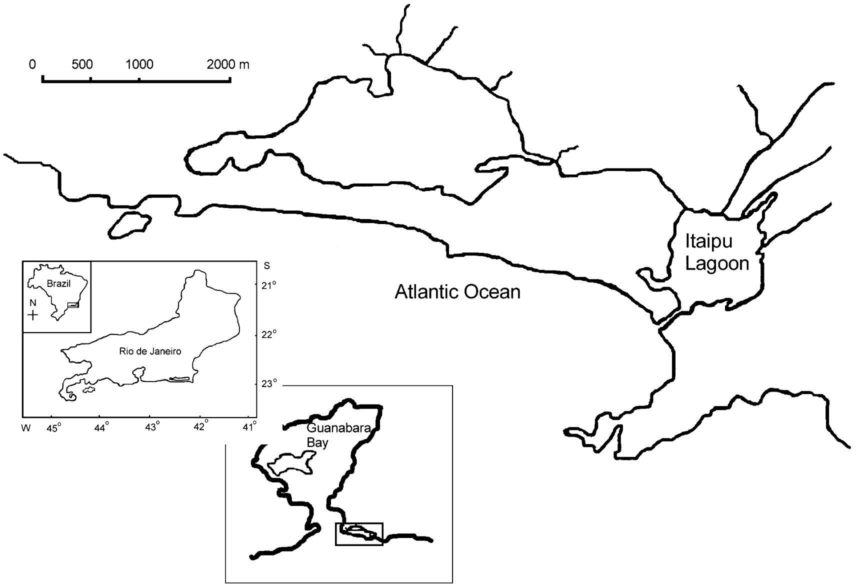

Fig. 1. Location of Itaipu Lagoon (22°58′S 43°02′W) in Niterói, Rio de Janeiro State, southeastern Brazil.

The sediment of the study area was characterized as fine sandy by Brendolan & Soares-Gomes (2006).

Biological sampling and data analysis

Ten sediment samples were collected monthly, from July 2003 to December 2004, with a corer of 10 cm in diameter, at low tide. Samples were washed through a 0.5 mm sieve, fixed in 4% formalin, and conserved in 70% ethanol.

Identification of the post-marsupial developmental stages followed Messing (1983) and Leite & Leite (1997). Individuals were sorted into males and females based on cheliped morphology. Females were sorted into (a) non-ovigerous females (oostegites present) and (b) ovigerous females (marsupium present). Males were classified into type I or II, according to cheliped morphology (the cheliped of type II is longer than that of type I) (Leite & Leite, 1997). Those individuals with pereiopod VII fully developed and lacking secondary sexual characters were called juveniles. Individuals with pereiopod VII not fully developed were classified as larval phases. Tanaids were measured from the tip of the rostrum to the extremity of the pleotelson (total length) and grouped into 0.5-cm size classes. The intramarsupial stages (eggs, embryos, mancas I, and mancas II) were identified according to Leite & Leite (1997). Eggs were measured along their major diameter, and the other intramarsupial stages along their major extension.

Monthly densities of *K. schubartii* were compared by one-way ANOVA, followed by a Tukey test. The chi-square test (χ^2) was performed to verify statistical deviations from the 1 : 1 sex ratio ($p < 0.05$). The total length of post-marsupial stages was compared using the Kruskal-Wallis and Mann-Whitney tests. The length at which 50% of females are sexually mature (L_{50}) was estimated using the logistic model:

$$P_i = 1/(1 + e^{-r(L_i - L_{50})})$$

where P_i is the number of individuals in length class i, r is the angular coefficient, and L_i is the midpoint of length class i. Preparatory and ovigerous females were classified as adult, according to Leite & Leite (1997). Monthly mean fecundity rates were compared using one-way ANOVA and the Tukey test. The mean numbers of eggs, embryos, mancas I, and mancas II in the marsupium were compared using the Kruskall-Wallis test. The same test was used to compare lengths of intramarsupial stages. The total numbers of eggs per marsupium (independent variable) and egg length (mm) (dependent variable) were compared using one-way ANOVA. The relationship between total length and fecundity of ovigerous females was estimated by the Pearson linear correlation. The intramarsupial finite mortality rate was calculated according to Krebs (2001).

Precipitation data were provided by the Universidade Federal Fluminense Meteorological Station, located at 23°53′S 43°07′W.

RESULTS

From from July 2003 to December 2004, a total of 15,903 individuals was collected, including 5871 larval phase individuals, 4649 juveniles, 1615 males, 2031 preparatory females, 1553 ovigerous females, and 184 females with empty marsupium. The highest densities (ind $\cdot$ m^{-2}) were recorded in December 2003 and July 2004, and the lowest in July 2003 and September 2004 (ANOVA, $F_{17} = 101.1$; $p < 0.01$) (fig. 2). Tanaids varied in accordance with the precipitation pattern (Pearson Correlation = 0, 56; $p = 0.02$) (fig. 2).

The frequencies of larval phases and juveniles were always above 48%. Low frequencies of larval stages and juveniles were observed from January to March 2004 and from August to October 2004, whereas high frequencies were observed in December 2003 and April, July, and November 2004. Ovigerous females and other developing stages were observed in all samples. Peaks in the frequencies of larval stages and juveniles were followed by peaks in ovigerous female frequency, except in November 2004, when they coincided (fig. 3).

Male to female sex-ratio of all individuals was 1 : 2 ($p < 0.05$). The mean size was 4.11 ± 0.02 (SE) mm. Developing stages differed in length (Kruskal-Wallis H = 7441.331, df = 5, $p < 0.01$). Females (7.4 ± 0.03 mm) were statistically longer than males (6.3 ± 0.03 mm) (Mann-Whitney, Z = 22.23898, $p < 0.01$), while males I (6.0 ± 0.02 mm) were smaller than males II (7.4 ± 0.05 mm) (Mann-Whitney Z = −17.1221, $p < 0.01$). The smallest larval phase was 1.2 mm long,

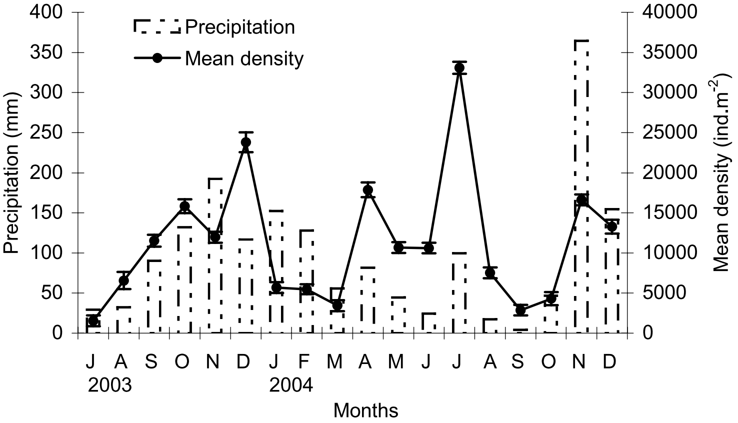

Fig. 2. Mean density (±SE) of *Kalliapseudes schubartii* Mañé-Gazón, 1949 and precipitation rates (mm) from July 2003 to December 2004 at Itaipu Lagoon, southeastern Brazil.

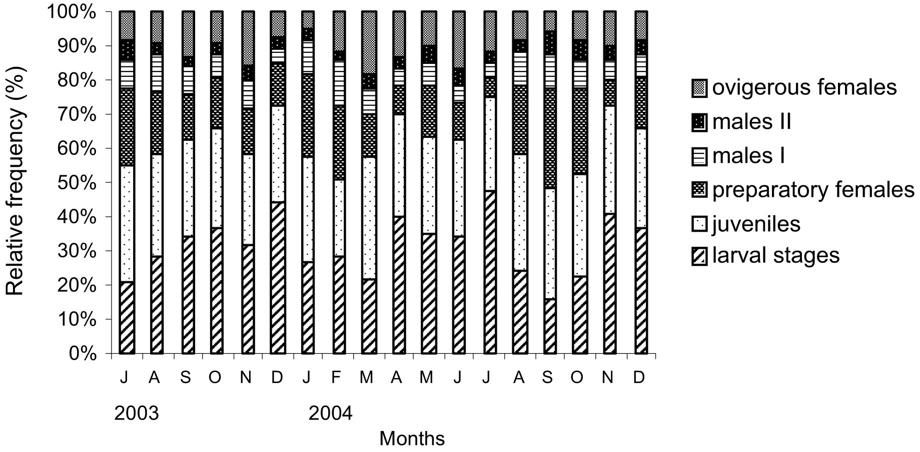

Fig. 3. Relative frequency of developing stages of *Kalliapseudes schubartii* Mañé-Gazón, 1949 in Itaipu Lagoon, southeastern Brazil.

and the smallest ovigerous female 6.1 mm. The length of all developing stages ranged from 1.2 to 12 mm, fig. 4 gives the frequency of the size classes.

The size at onset of sexual maturity of females (L_{50}) was 5.9 mm (fig. 5). The simultaneous presence of successive intramarsupial stages in the same marsupium was observed in less than 1% of the total female fraction. A weak correlation was observed between the total length of ovigerous females and the abundance of intramarsupial stages ($r = 0.4575$; $p < 0.01$) (fig. 6).

Mean fecundity was 17.81 ± 10.91 ($N = 1553$ ovigerous females), ranging from 1 to 63 eggs, embryos, and mancas. The highest values of mean fecundity were observed at the end of the wet season (February to April 2004) (ANOVA, $F_{17} = 35.062$; $p < 0.01$; $N = 1553$). Mean fecundity and mean lengths of eggs, embryos, mancas I, and mancas II are shown in table I.

High-fecundity females carried more small eggs (ranging from 0.25 to 0.37 mm) than low-fecundity females (ANOVA, $F_{14} = 10.316$; $p < 0.01$; $N = 476$ eggs) (fig. 7). Finite mortalities between intramarsupial stages were: 1.86% (eggs); 1.62% (embryos); 11.27% (mancas I). Total finite mortality of intramarsupial stages was 14.4%.

DISCUSSION

Fluctuations in population density are frequent in peracarids, high densities indicating periods of intense reproduction and recruitment (Modlin & Harris, 1989; Kneib, 1992; Cardoso & Veloso, 1996; Maranhão et al., 2001; Schmidt et al., 2002; Gamito & Marques, 2003; Leite et al., 2003). At Itaipu Lagoon, changes in density were due to oscillations in larval stages and juveniles.

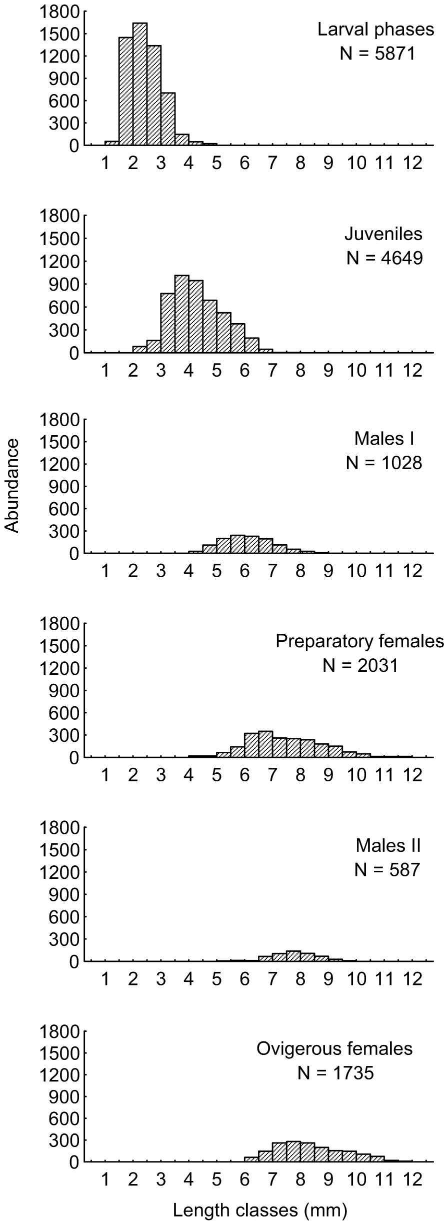

Fig. 4. Size frequency distribution of larval phases, juveniles, males I and II, and preparatory and ovigerous females of *Kalliapseudes schubartii* Mañé-Gazón, 1949 from Itaipu Lagoon, southeastern Brazil.

Peracarids may also show intraspecific differences in their life cycles along latitudinal gradients, with longer reproductive activity occurring in the tropics (Kalejta & Hockey, 1991; Corbera et al., 2001; Johnson et al., 2001; Maranhão

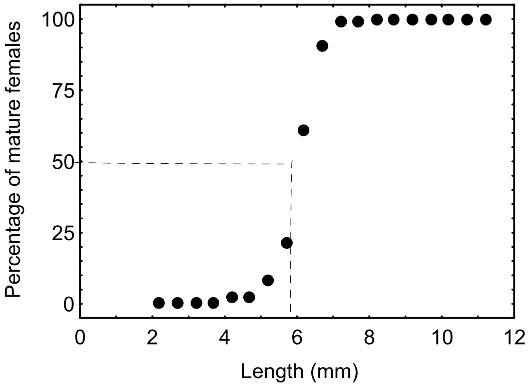

Fig. 5. Percent distribution of mature females according to total length in *Kalliapseudes schubartii* Mañé-Gazón, 1949 from Itaipu Lagoon, southeastern Brazil.

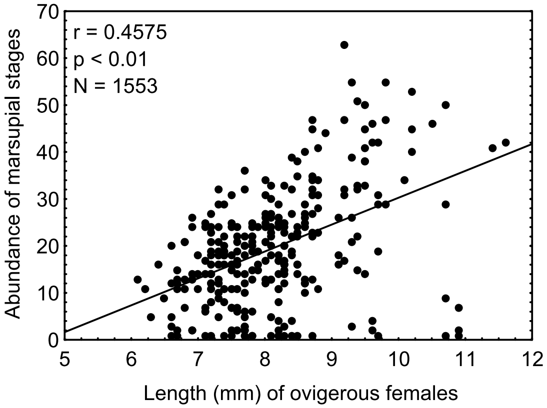

Fig. 6. Correlation between the total length of ovigerous females and the abundance of intramarsupial stages in *Kalliapseudes schubartii* Mañé-Gazón, 1949 from Itaipu Lagoon, southeastern Brazil.

et al., 2001). In Itaipu Lagoon (present study) (22°58′S 43°02′W) and Araçá (23°49′S 45°24′W) (Leite et al., 2003), both located in the tropics, *Kalliapseudes schubartii* showed peaks of density and a high frequency of ovigerous females and juveniles along a two-year period, even in the winter season. On the other hand, in Patos Lagoon (32°01′S 52°07′W) (Fonseca & D'Incao, 2003; Rosa & Bemvenuti, 2006) and around Mel Island (25°33′S 48°19′W) (Almeida, 1994), both located at the subtropical coast of Brazil, higher population densities and higher ovigerous female frequencies occurred in spring and summer. Those differences support evidence for latitudinal gradients governing the life cycle of *K. schubartii*.

In Itaipu Lagoon, tanaid density changed seasonally, increasing in the beginning of the wet season and presenting peaks following those of precipitation in other periods. Rainfall might play an important role in the increase of nutrient con-

TABLE I

Length (mm) and fecundity of intramarsupial stages of *Kalliapseudes schubartii* Mañé-Gazón, 1949 from Itaipu Lagoon, southeastern Brazil

Length (mm)

Stage	Mean	Standard deviation	N
Egg	0.36	0.05	476
Embryo	0.47	0.06	60
Manca I	0.79	0.10	60
Manca II	1.00	0.08	60

Kruskal-Wallis H = 251, 259; df = 3, $p < 0.01$.

Fecundity

Stage	Mean	Standard deviation	N (ovigerous females)
Egg	18.30	11.19	477
Embryo	17.95	12.63	433
Manca I	17.66	8.82	440
Manca II	15.67	10.65	393

Kruskal-Wallis H = 741, 107; df = 3, $p < 0.01$.

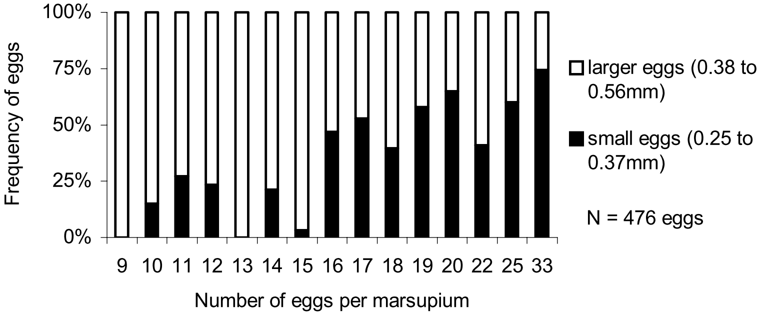

Fig. 7. Frequency of egg length according to number of eggs per marsupium of ovigerous females in *Kalliapseudes schubartii* Mañé-Gazón, 1949 from Itaipu Lagoon, southeastern Brazil.

centrations in coastal zones. In a nearby lagoon, Knoppers et al. (1999) observed that nitrogen deposition from rain water contributed to the increase of primary production. Since Itaipu Lagoon is limited in nitrogen (Knoppers et al., 1999), nitrogen enrichment by rain may enhance the primary production of the waters of Itaipu Lagoon and, consequently, have an effect on the populations of *K. schubartii*. What is more, an increase in river input during the wet season (Barbieri & Coelho-Neto, 1999) may also contribute to an increase in the organic matter load of the lagoon. Knoppers et al. (1999) reported an increase in chlorophyll-*a* in the wet season in Itaipu Lagoon. During periods of low precipitation rates, the density of *K. schubartii* could drop as a response to the diminished load of organic matter in the lagoon.

In summer (January to March), in spite of the high precipitation rates, population density was low. According to Kjerve & Knoppers (1999), in that season Itaipu Lagoon reaches its highest water temperature (about 30°C). Laboratory assays on *K. schubartii* from Itaipu Lagoon demonstrated that survival of adults decreased significantly at temperatures above 25°C, and salinities of 30-35 (Brendolan & Soares-Gomes, 2006). As Itaipu Lagoon presents a salinity of up to 30 all year round (Kjerve & Knoppers, 1999), the synergism between high temperatures and high salinity may explain the decrease of *K. schubartii* densities.

Besides mortality due to harsh conditions, a reduction in population density may occur as a consequence of adult mortality during the reproductive period. Since tanaid copulation occurs inside the female's tube, the displacement of the male in search for a mate exposes it to predators (Fonseca & D'Incao, 2006). Moreover, the intense competition between males may contribute to an increase in mortality (Highsmith, 1983). Almeida (1994) suggested that a great number of *K. schubartii* females dies before spawning, even though they are capable of reproducing more than once.

Tanaid females that reproduce more than once were described as having an intermediary female instar between couplings. Johnson & Attramadal (1982) observed an intermediary female of *Tanais cavolinii* Shiino, 1951, characterized by the absence of oostegites, but with marks of the ovisacs originated during the last spawning. Schmidt et al. (2002), studying the tanaid *Allotanais hirsutus* (Beddard, 1886), pointed out an overlap between the length frequencies of juveniles and females. The authors suggested that those larger juveniles (classified as juveniles due to the absence of oostegites or other signs) could in fact be females in an intermediary instar, as already described by Johnson & Attramadal (1982) for *T. cavolinii*.

As in the case of *A. hirsutus*, Leite et al. (2003) found a wide overlap between the length frequencies of juveniles (non-reproductive individuals), and ovigerous and preparatory females of *K. schubartii* in Araçá, Brazil, which suggests the probable existence of at least two instars (intermediary and preparatory) between successive ovigerous stages in those populations. In the present study, however, a wide overlap was observed only between ovigerous and preparatory females in *K. schubartii*, but not with juveniles. This could indicate that in Itaipu Lagoon (1) the period of the intermediary instar (without oostegites) is very short, or that (2) the females of *K. schubartii* from Itaipu Lagoon only have preparatory stages (with oostegites) between the ovigerous stages. Preparatory females as the only stage interposing ovigerous stages were already described for the tanaids *Apseudes heroae* Sieg, 1986 (cf. Schmidt et al., 2002) and *Pagurapseudes largoensis* M. C. Sweeny, 1982 (cf. Messing, 1983). The females of *P. largoensis* exhibit oostegites between the copulatory (ovigerous) instars, and one or two preparatory instars should separate successive couplings (Messing, 1983). Only laboratory assays or field sampling at smaller intervals can elucidate this question.

The wide range of length of *K. schubartii* juveniles in Itaipu Lagoon could also indicate the occurrence of two or more instars in that stage. The majority of tanaid species present two separate juvenile instars: the first cannot be sexed, whereas the second develops immature gonads but can still be defined as immature. However, this differentiation is only possible by means of histological studies (Schmidt et al., 2002).

Juvenile length frequencies also concur with male I frequencies. In this case, it is possible that males in juvenile stage 1 develop directly into males I, while the others go on to juvenile stage 2 before being males I. This behaviour would be similar to that of *P. largoensis* and *A. heroae*: for *P. largoensis*, two or three juveniles stages were recorded (Messing, 1983), and for *A. heroae* two stages (Schmidt et al., 2002).

The total length of *K. schubartii* preparatory females from Itaipu Lagoon was ⩾4.1 mm, overlapping with the length of juveniles. Probably, females have gone through two or three juvenile moultings before attaining the preparatory phase. The initial ovigerous phase may be preceded by one or two preparatory moultings, similar to the situation in *P. largoensis* and *A. heroae* (cf. Messing, 1983; Schmidt et al., 2002).

The lengths of males II coincided with those of males I, and of preparatory and ovigerous females. This trend was also found by Fonseca & D'Incao (2003) for *K. schubartii* in the south of Brazil. In this way, males II would be a subsequent stage of males I, or originate from female sex reversal (protogyny), as suggested by Leite & Leite (1997) and Leite et al. (2003). A developing sequence is here proposed for the *K. schubartii* population in Itaipu Lagoon (fig. 8).

The sex-ratio of *K. schubartii* in the present study was female-skewed during all months, in agreement with studies of the same species from other sites along the Brazilian coast (Almeida, 1994; Leite et al., 2003), and on other tanaid species (Masunari & Sieg, 1980; Modlin & Harris, 1989; Kneib, 1992). Predation pressure on males during the reproductive period may decrease their proportion in the population (Leite et al., 2003). However, Fonseca & D'Incao (2006) did not observe significant differences in the mortality rates of *K. schubartii* between seasons, including the season with intense reproduction, suggesting a similar predation pressure over a year cycle.

However, sex-ratio deviation could not be produced only as a consequence of male depletion, but may also be related to sexual allocation and to the possibility of *K. schubartii* to be a protogynic species (i.e., with sex shifts, from female

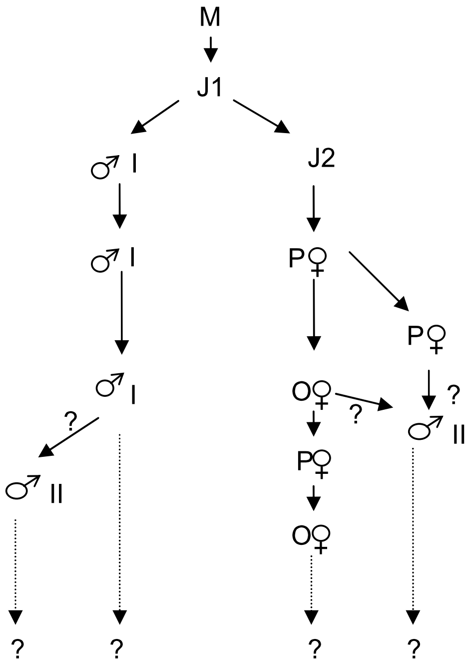

Fig. 8. Schematic diagram of the putative life cycle of the *Kalliapseudes schubartii* Mañé-Gazón, 1949. M, manca stages; J, juvenile; P, preparatory stage; O, ovigerous stage; dashed lines, several moultings.

to male). The sexual allocation theory describes how individuals should allocate their resources between male and female reproduction, and states that when an individual fitness changes with age or length, sex reversal is favoured in the population. In this case, natural selection favours those individuals that first mature in the sex where reproductive value increases more slowly with age (first sex), and which, when they grow older and larger, change their sex (second sex) (Ghiselin, 1969; Charnov & Bull, 1977). Considering a protogynic population, larger and older males will have greater fitness. Thus, given an equal genetic contribution from males and females, the sex ratio will be female-skewed (Allsop & West, 2004). Many peracarids show sex reversal, both protandry (males to females) and protogyny (females to males). Among tanaids, only cases of protogyny have been recorded (Modlin & Harris, 1989; Brook et al., 1994; Allsop & West, 2004). The female-skewed sex ratio, as well as the presence of two types of males in *K. schubartii* populations, may indicate protogynic hermaphroditism.

Compared to other tanaid species *K. schubartii* presents high mean fecundity (table II). Fecundity may be influenced by many factors, such as habitat, seasonality, temperature, salinity, and nutritional state (Johnson et al., 2001; Maranhão et al., 2001; Ramirez-Llodra, 2002; Marshall & Keough, 2007).

TABLE II

Fecundity (number of eggs, embryos, or mancas) in some species of Tanaidacea occurring worldwide (Ø = mean; **maximum; *minimum)

Species	Fecundity	Location	Reference
TANAIDACEA			
Pseudotanaidae			
Cryptocope abbreviata (G. O. Sars, 1866)	7	Raunefjorden, Norway	Greve, 1965
Leptognathiidae			
Leptognathia breviremis (Lilljeborg, 1864)	3-8	Raunefjorden, Norway	Greve, 1965
Leptognathia dentifera G. O. Sars, 1896	6	Raunefjorden, Norway	Greve, 1965
Nototanaidae			
Typhlotanais aequiremis (Lilljeborg, 1864)	15-18	Raunefjorden, Norway	Greve, 1965
T. brevicornis (Lilljeborg, 1864)	2-7	Raunefjorden, Norway	Greve, 1965
Leptocheliidae			
Heterotanais oerstedii (Krøyer, 1842)	6-16	Baltic Sea	Buckle-Ramírez, 1965
Pagurapseudidae			
Pagurapseudes largoensis McSweeny, 1982	4-12	Florida, U.S.A.	Messing, 1983
Pagurapseudes bouryi (Bouvier, 1918)	7	Cuba	Bouvier, 1918
Kalliapseudidae			
Cirratodactylus floridensis Gardiner, 1972	12	Southeast Florida, U.S.A.	Gardiner, 1973b
Kalliapseudes schubartii Mañé-Garzón, 1949	Ø17,8	Itaipu Lagoon, Rio de Janeiro, Brazil	present study
K. schubartii	Ø11,8	Araçá region, São Paulo, Brazil	Leite et al., 2003
K. schubartii	4-25	Mel Island, Paraná, Brazil	Almeida, 1994
K. schubartii	86**	Patos Lagoon, Ri Sul, Brazil	Fonseca and D'Incao, 2003
Tanaidae			
Allotanais hirsutus (Beddard, 1886)	19-31 (Ø27)	Magellan region	Schmidt et al., 2002
Tanais dulongii Audouin, 1826	46*	–	Johnson & Attramadal, 1982
Apseudidae			
Apseudes heroae Sieg, 1986	9-15 (Ø12)	Magellan region	Schmidt et al., 2002
Apseudes latreillei H. Milne Edwards, 1828	60	–	Salvat, 1967

In Itaipu Lagoon, low fecundity and large eggs of *K. schubartii* were observed in periods of low temperature and low chlorophyll-*a*, while high fecundity and small eggs occurred by the end of the wet season (according to Knoppers et al., 1999a, a period of higher temperature and food availability). The same situation was reported for amphipods (Kolding & Fenchel, 1981; Powell, 1992; Pardal et al., 2000; Maranhão et al., 2001; Appadoo & Myers, 2004), and other non-peracarid crustaceans (Marsden, 1991; Guisande & Gliwicz, 1992; Nicolau & Oshiro, 2002). *K. schubartii* is probably able to respond to environmental changes by decreasing its fecundity while increasing egg size in periods of both low temperature and low food availability, thus enabling the offspring to survive under harsh conditions (Guisande & Gliwicz, 1992; Maranhão et al., 2001).

Latitudinal variations and environmental factors, such as temperature, season, and photoperiod, may interfere with growth and metabolism, altering the body length at sexual maturity (Maranhão et al., 2001; Nicolau & Oshiro, 2002). The length at sexual maturity of females of *K. schubartii* in Itaipu Lagoon (southeast Brazil) was lower ($L_{50\%} = 5.9$ mm) than that in Patos Lagoon populations (southern Brazil) ($L_{50\%} = 6.6$ mm) (Fonseca & D'Incao, 2003). Armitage & Landau (1982) stated that maturity may be retarded in regions characterized by low mean temperatures, or that gonads may show early development in regions of high temperature.

Peracarids generally show a positive correlation between the body length of females and fecundity (number of eggs, embryos, and mancas) (Clarke, 1993; Corbera et al., 2000; Johnson et al., 2001; Schmidt et al., 2002). However, this correlation was not found for *K. schubartii* originating from different populations along the Brazilian coast (Almeida, 1994; Fonseca & D'Incao, 2003; Leite et al., 2003). Leite et al. (2003) suggested a possible loss of eggs and other intramarsupial stages during manipulation of samples. Fonseca & D'Incao (2003) pointed out that the weak correlation may be due to the presence of different intramarsupial stages in the same marsupium, a fact frequently observed and indicating non-synchronized development or non-removal of unfertilized eggs by females. However, in the present study, eggs, embryos, and mancas were not found in the same marsupium, indicating, in this case, a synchronized development and/or a fast deterioration of non-fertilized eggs. In Itaipu Lagoon it is likely that the weak correlation between body length and fecundity of *K. schubartii* was due to both variation in the size of the broods along the year, and intramarsupial mortality. Intramarsupial mortality was described for mysids and amphipods (Gorokhova & Hansson, 2000) and also for *K. schubartii* (cf. Leite et al., 2003). Decreases in intramarsupial abundance, as well as concurrent increase in size of the intramarsupial stages, would suggest that intramarsupial mortality might be related to available space in the marsupium (Leite et al., 2003).

Precipitation, temperature, and salinity may influence the recruitment and population density of *K. schubartii*. The presence of two types of males, the wide length frequency of males II, overlapping preparatory and ovigerous females, and the female-skewed sex ratio, are all indications of protogyny in this species. Under harsh conditions, females of *K. schubartii* seem to be able to respond by decreasing brood size while increasing egg size, thereby creating greater chances for survival of the offspring. The high densities, the continuous reproduction, and the predominance of juveniles characterize *K. schubartii* as an opportunistic species in this tropical coastal lagoon. Comparisons of populations denote that a latitudinal factor may be governing the life cycle of *K. schubartii* to an important extent.

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