J. Mar. Biol. Ass. U.K. (2003), **83**, 931–935
Printed in the United Kingdom

Growth and reproductive parameters of *Kalliapseudes schubartii* in the estuarine region of the Lagoa dos Patos (southern Brazil)

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Kalliapseudes schubartii (Crustacea: Tanaidacea) is a tube dwelling invertebrate living in estuarine soft bottoms with distribution along the south-east and southern Brazilian and Uruguayan coasts. Individual growth, and reproduction were examined by taking samples for a year in the estuarine region of the Lagoa dos Patos (southern Brazil). The von Bertalanffy model described growth of *K. schubartii* ($K=4.54\ y^{-1}$, $L_{\infty}=13.22$ mm). Reproductive activity was observed in spring and summer. No relationship was observed between total length of females and brood size. Eggs, embryos, and mancas were often observed in a marsupium. Relative growth analysis showed two levels of allometry in the growth of chelipeds of males.

INTRODUCTION

Tanaids have a worldwide distribution and they are normally very abundant in marine and brackish-water habitats. Despite their ecological importance, the population biology of most of tanaidaceans is poorly understood (Holdich & Jones, 1983).

This study reports findings on individual growth, relative growth, and reproduction parameters of a population of *Kalliapseudes schubartii* Mañé-Garzón, 1949 (Kalliapseudidae) in the estuarine region of the 'Lagoa dos Patos' (Patos Lagoon) (Rio Grande do Sul State, southern Brazil).

Kalliapseudes schubartii is a tube dwelling organism that inhabits estuarine subtidal soft bottoms. A number of studies on benthic communities along the south-east and southern Brazilian, and Uruguayan coasts (e.g. Lana & Guiss, 1991; Leite, 1995; Bemvenuti, 1997; Muniz & Venturini, 2001) have provided qualitative information about *K. schubartii*, but none of these have addressed the population biology of this tanaid. While it is known that the main reproductive season of *K. schubartii* in the estuarine region of the Lagoa dos Patos happens in spring and summer (Bemvenuti, 1997), little is understood about brood size and size at the onset of maturation. Moreover, individual growth rates of populations of *K. schubartii* are qualitatively only known as 'fast', while the relative growth of *K. schubartii* has never been studied.

MATERIALS AND METHODS

Tanaids were collected from subtidal soft bottoms in the estuarine region of the Lagoa dos Patos (32°01′51″S 52°07′96″W). The location sampled has shallow waters (depth <1.5 m) and the sediment is composed mostly by fine sand (~88% sand, 6.5% silt, and 4.8% clay) with 3.8% of organic matter (Rosa-Filho & Bemvenuti, 1998). Monthly samples were taken, from July 1996 to June 1997. Sampling was carried out along a 20 m transect using a stratified design (three stratum, first at the beginning of the transect, the second at 10 m, and the third at 20 m). Twelve replicates (four in each strata) were randomly taken with a 10-cm diameter core (20 cm deep). The collected sediment was washed through a 300-μm sieve and the retained material was taken to the laboratory where the individuals of *Kalliapseudes schubartii* were sorted from the debris, fixed, preserved (4% formalin), sexed, and measured. Total length (TL, from the tip of the rostrum on the carapace to the posterior edge of the pleotelson) and length of the propodus of the cheliped (PL, from the anterior to the posterior border) were measured using an ocular micrometer.

Modal groups were determined on TL frequency distributions using the software PeakFit (SPSS Inc.). Total length frequency distributions were first smoothed (fast Fourier transformation, FFT). Gaussian peaks were then fitted to the smoothed distribution by an automated least squares fitting procedure. Modal values determined in each TL frequency distribution were tentatively linked to visualize the modal progression. Growth curves, based on the von Bertalanffy growth function (VBGF), were estimated for all cohorts determined. Thereafter, a pooled VBGF was estimated. Longevity was calculated by the inverted von Bertalanffy equation using the 99% of the asymptotic length as L_i value (D'Incao & Fonseca, 2000).

Males were sorted into two types (based on the presence of elongated chelipeds) according to description provided by Leite & Leite (1997). Males were sorted from females based on propodus morphology (Mañé-Garzón, 1949). Individuals 2.5 mm TL were defined as juveniles, provided that none of these animals presented secondary characteristics of males. Brooding females were identified by the presence of marsupium.

To analyse the relative growth, plots of total length (TL) vs length of the propodus of the cheliped (PL) were produced. Size at the onset of maturity (L50) was estimated by fitting a logistic function to the cumulative percentage of brooding females by size-class. The number

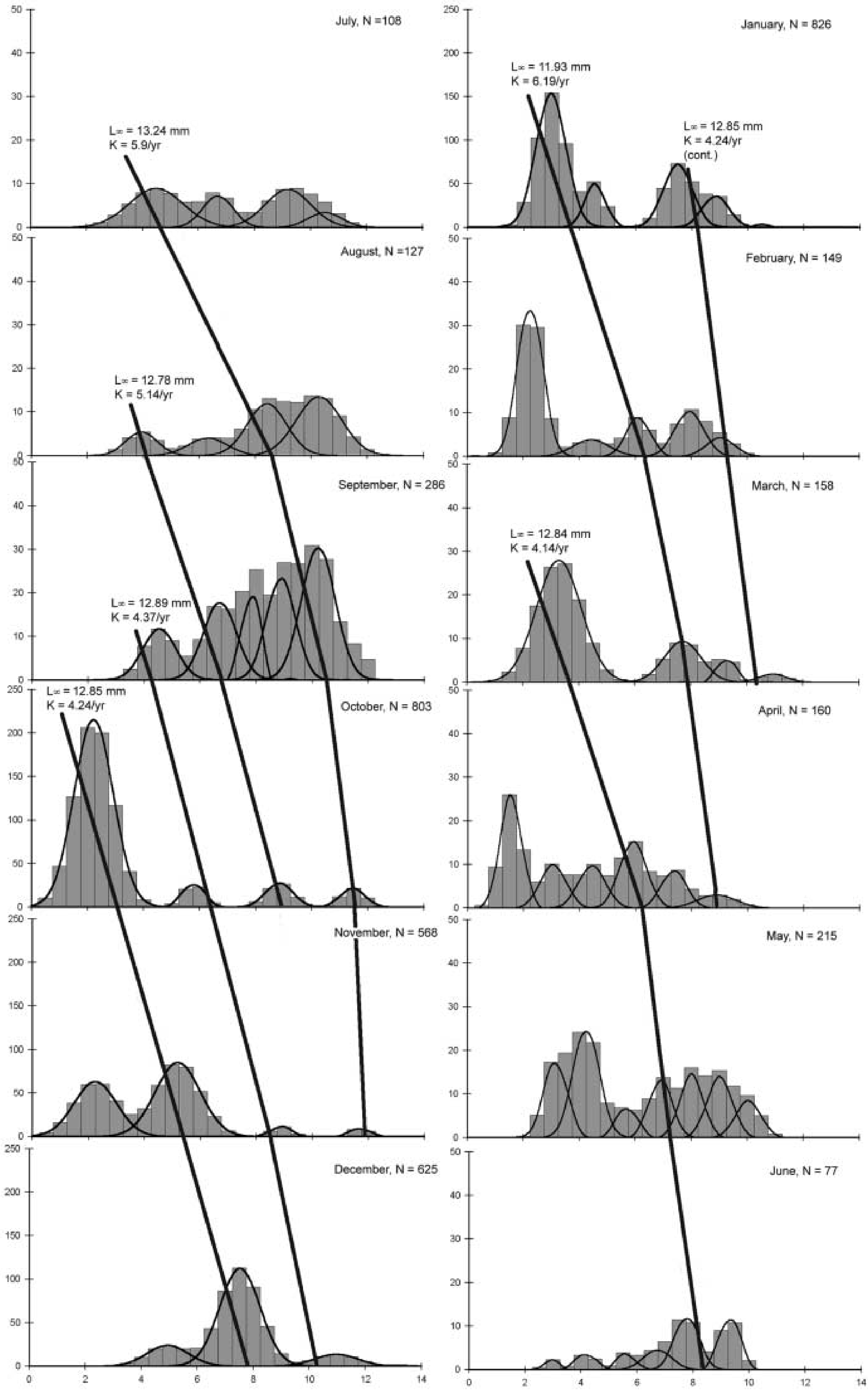

Figure 1. Total length (TL) frequency histograms (after smoothing) and six cohorts, with its respective growth parameters, determined for the period of study.

https://doi.org/10.1017/S0025315403008087h Published online by Cambridge University Press

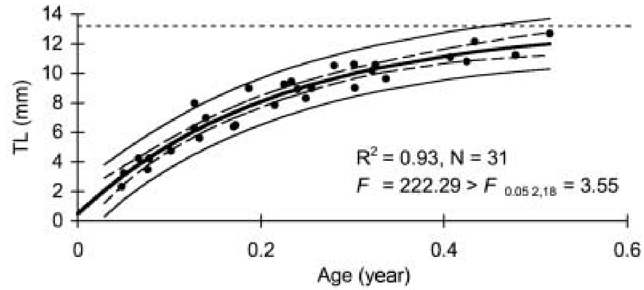

Figure 2. Pooled growth curve estimated using the von Bertalanffy growth model, $L_t=13.22\ [1-e^{-4.54(t-0.008)}]$. 95% confidence limits (– – –) and prediction limits (—) are shown. Horizontal dashed line represents the asymptotic length.

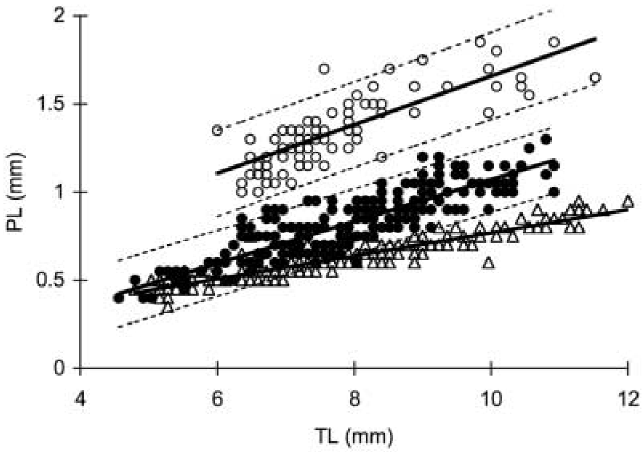

Figure 3. Relative growth of *Kalliapseudes schubartii*. Length of the propodus of the cheliped (PL) is regressed against total length (TL). △, females (PL=−0.99 +0.88 TL; R^2=0.83, P<0.001); ●, Type I males (PL=−1.29+1.34 TL; R^2=0.74, P<0.001); ○, Type II males (PL=−0.79+1.04 TL; R^2=0.64, P<0.001). Full lines represent regressions. 95% prediction limits (only for regressions of males) are shown.

of eggs, embryos, and mancas in the marsupium of females were counted, and a linear regression was estimated between them and TL of females.

RESULTS

A total of 4102 individuals was collected (1799 females, 539 males and 1764 juveniles). The largest male and female caught had 12.32 and 13.3 mm TL respectively.

Six cohorts were determined for the period of study (Figure 1), which resulted in a growth curve shown in Figure 2. Maximum longevity, based on the pooled growth parameters, was estimated as 1 year.

The linear regression observed between length of the propodus of the cheliped (PL) and TL of females was statistically significant (Figure 3). Mean PL of females was 0.63 mm; for Type I and Type II males the values were 0.82 and 1.34 mm respectively. A statistically significant linear regression between PL and TL was estimated for each male type (Figure 3).

Brooding females were observed from September to April. Type II males were observed in August 1996 (three individuals) and from October 1996 to March 1997. In summer the proportion of Type II males was around

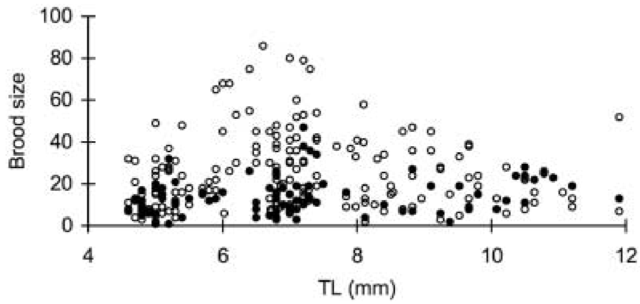

Figure 4. Relationship between brood size and total length (TL) of females; ○, eggs (R^2=0.003, P=0.36), and ●, embryos and mancas (R^2=0.002, P=0.47).

30% of the total catch of males. Juveniles were observed in spring, summer, and early autumn. No juveniles were found in late autumn or winter. Brooding females had a TL from 4.6 to 11.9 mm. Mean TL of the onset of maturity (L50) of females was estimated to be 6.6 mm (R^2 = 0.98, $F=3355>F_{0.05\ 1,53}=4.02$, $P<0.001$. The maximum number of mancas found in a marsupium was 47 (for a female 7.2 mm TL), while the maximum number of eggs was 86 (6.6 mm TL). No significant relationship between both the number of eggs or number of embryos and mancas, and the TL of females (Figure 4) was found. Eggs, embryos, and mancas were often observed in the same brood.

DISCUSSION

Growth

Very clear modal progressions were observed in the first six months of sampling, which included a very strong period of recruitment. Towards the end of the sampling period (winter), modal progression became difficult to determine. Nevertheless, the growth curve estimated, based on the pooled data, is consistent with the size of the first manca stage in the marsupium (TL ≈0.50 mm, D.B. Fonseca, personal observation), and maximum size (Lmax) observed in this population (13.3 mm). The growth curve predicts for t=0 a TL of 0.51 mm, while the asymptotic length (13.22 mm) is very near to the maximum size observed. It has been suggested that the asymptotic length, estimated by length-based methods, should be similar to the maximum observed length (Pauly, 1998). A fast growth trajectory is what would be expected from a peracarid like *Kalliapseudes schubartii*, inhabiting a quite unpredictable environment (Klein, 1997), and subject to high mortality related to predation (Bemvenuti, 1987). However, it is difficult to make comparisons of the present results with other peracarids of subtropical estuarine regions because the population dynamics of species of this group is poorly studied.

While the estimate of maximum longevity (1 y) is obviously a theoretical figure based on the growth curve estimated, it is conceivable that an individual of this short-lived species could reach this age if extrinsic mortality was discounted. Most of the mortality observed in populations in the wild is due to extrinsic reasons rather than due to ageing (Kirkwood & Austad, 2000). Nevertheless, a number of studies on populations of peracarids, inhabiting harsh, somewhat unpredictable environments such as sandy beaches, have reported lifespans longer than one year (Williams, 1978; Alava & Defeo, 1991; Gomez & Defeo, 1999; Fonseca et al., 2000). Altogether, it seems that the growth parameters estimated reflect consistently the individual growth of *K. schubartii* in the wild.

Relative growth and reproduction

A linear regression model described the relative growth of males and females of *K. schubartii*. The pattern observed in the plot of relative growth shows two phases in the life cycle of males and it indicates that there are two distinct levels of allometry in males. This is a novel finding for *K. schubartii*. A wide overlap in size was observed in the plot of relative growth of both types of males, indicating that there is no defined size for the transition between these two phases.

Sexual dimorphism, which is widespread in tanaids, is commonly exemplified by the enlargement of chelipeds of males (Sieg, 1983). This is observed *in K. schubartii*. Whether both types of males of *K. schubartii* can reproduce is a controversial issue. Leite & Leite (1997) suggested that both male types are reproductively active. However, based on the findings of the present investigation, it might be hypothesized that only Type II males would be able to reproduce. For instance, Type II males were mostly observed in spring and summer (main reproductive seasons). Supporting evidence for the copulatory function of males with enlarged chelipeds is found in other tanaid species. Copulatory males of *Tanais cavolinii* are characterized by enlarged chelipeds (Modlin & Harris, 1989). In *Hargeria rapax*, only males with elongated chelipeds reproduce (Kneib, 1992). In *Leptochelia savignyi* males have two developmental stages; both of them have enlarged chelipeds and reproduce (Masunari, 1983). Males of *Leptochelia dubia* have enlarged chelipeds, which are related to fighting behaviour prior to mating (i.e. competition between males for mating) (Highsmith, 1983). According to Johnson & Attramadal (1982), enlarged chelipeds could be used to grip female's chela during copulation. However, even in summer the population Type I males is abundant (~70% of males catch), and it might be suggested as indicative that they have some kind of reproductive activity. Moreover, based on histological analysis Hamers & Franke (2000) suggested that all male stages of *Tanais dulongii* might be potentially copulatory, in spite of cheliped morphology. Only laboratory studies will provide a definite answer to this question.

Based on the growth curve estimated, the average size of the onset of maturity of females (L50=6.6 mm TL) is attained in about two months after release from the marsupium. It means that there is high investment in individual growth prior to reproduction, which is consistent with ecological theory for short-lived animals (Brey & Gage, 1997). For instance, a high investment in somatic growth earlier in life enables a female to maximize its reproductive potential later in life by increasing the possible number of mancas that can be held in the marsupium.

No significant relationship was observed between brood size and TL of females. This is a contradictory finding as a significant relationship is commonly observed in peracaridans (Johnson et al., 2001). Departures from linearity in this relationship were suggested to be a result of a reduced production of mancas in both the first brood—in spite of the size of the female—and by the largest (and ageing) females (Moore, 1981). However, it must be said that there is little theoretical support, on evolutionary grounds, for a reduced fecundity at first breeding, but a reduced fecundity of ageing females is consistent with assumptions of costs of reproduction (Calow, 1979). Alternatively, the non-significant relationship might be explained by an unsynchronized development of offspring within the marsupium, as eggs, embryos, and mancas were often observed in the same brood. Because these developmental stages differ in size, a significant relationship between TL of females and brood size would be unlikely to be obtained. This is an interesting finding because it is unusual to find different developmental stages in one marsupium. The occurrence of eggs in marsupia with embryos and mancas might represent the presence of unfertilized eggs, which were not cleaned out from the marsupium. However, it is not known whether females of *K. schubartii* are able to remove unfertilized eggs, and the biological significance of a unsynchronized development is not understood.

Briefly, this investigation demonstrated that *K. schubartii* presents multiple, and fast-growing, cohorts in a year, and that the maximum longevity attained by an individual might be one year. Males present sexual dimorphism characterized by distinct levels of allometry of the chelipeds. Females can bear distinct development stages in the same brood, and a non-significant relationship between brood size and TL is observed.

D.B. Fonseca would like to thank Mr Wagner Vieira for his help in the field and laboratory work. The National Council for Scientific and Technological Development (CNPq, Brazil) supported this work.

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Submitted 20 November 2002. Accepted 29 July 2003.