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Population dynamics of *Callichirus major* (Say, 1818) (Crustacea, Thalassinidea) on a beach in northeastern Brazil

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Abstract

We describe the structure, reproductive cycle, fecundity, growth, and mortality of a harvested population of the ghost shrimp *Callichirus major*. Samples were collected at monthly intervals from September 1999 to October 2000 on an urban sandy beach (08°11′S 34°55′W) in northeastern Brazil. During this period the sex ratio did not differ significantly from 1:1 (0.98 M: 1 F). Minimum and maximum sizes of the Dorsal Oval were 2.59 and 12.19 mm for males and 4.46 and 12.62 mm for females, respectively. Ovigerous females were found throughout the period, except between August and September 2000. Maximum lifespan was estimated as 3.3 and 3.4 years for females and males, respectively. This northeastern population differed from others previously studied in southern and southeastern Brazil, in regard to sex ratio, maximum attained size, maturation size, period and duration of the reproductive cycle, and fecundity. We interpret these regional differences as evidence for overfishing at the study site, and suggest that large-scale management plans for callianassid populations should use regional population parameters.
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Keywords: Callichirus major; population dynamics; reproductive cycle; growth; lifespan; tropical environment

1. Introduction

Burrowing shrimps belonging to the infraorder Thalassinidea are important animals of the soft-bottom marine benthic community. Their bioturbation activity can influence overall community structure (Ott et al., 1976; Posey, 1986; Murphy and Kremer, 1992; Wynberg and Branch, 1994) by modifying chemical (Aller et al., 1983; Waslenchuk et al., 1983; Ziebis et al., 1996; Bird et al., 2000) and sedimentological properties (Suchanek, 1983; Suchanek and Colin, 1986). Their complex systems of galleries and shafts create, modify, and maintain a mosaic of habitats for other organisms (Berkenbusch and Rowden, 2003).

The ghost shrimp *Callichirus major* (Family Callianassidae) is a cryptic, solitary burrowing shrimp that inhabits deep burrows on sandy beaches, generally below mean water level (Frankenberg et al., 1967; Rodrigues and Shimizu, 1997). Its distribution ranges from North Carolina (about 35°N) through the Gulf of Mexico to southern Brazil (about 27°S) (Manning and Felder, 1986; Dworschak, 2000).

Along the Brazilian coast, *Callichirus major* is commonly harvested (Borzone and Souza, 1996) and has become economically important as a source of live bait for anglers. The natural abundance of these shrimps has contributed to uncontrolled exploitation in many parts of the world (Hailstone and Stephenson, 1961; Wynberg and Branch, 1994; Contessa and Bird, 2004; Skilleter et al., 2005). However, in Brazil, the scale of this practice may lead to overexploitation (Borzone and Souza, 1996). In this paper we describe the size structure, reproductive cycle, fecundity, growth, and mortality in a population of the burrowing shrimp *C. major*, and discuss the impact of harvesting on callianassid populations.

2. Materials and methods

The study area is located at Piedade Beach (8°11′18″S and 34°55′06″W), a highly urbanized area on the northeastern

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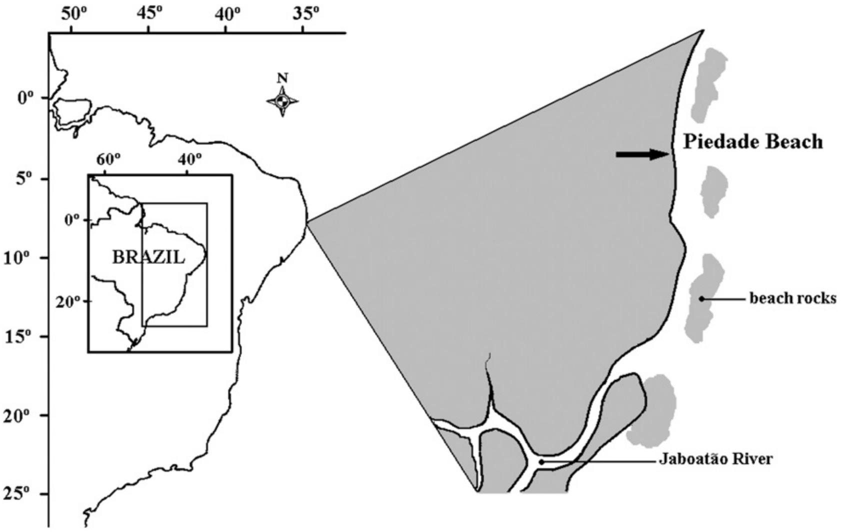

Fig. 1. Location of the study site on Piedade Beach on the northeastern coast of Brazil, at approximately 8°11′18″S and 34°55′07″W (arrow).

coast of Brazil. In this area, dunes have been eliminated by urban development near the shoreline (Duncan et al., 2003), and the coastline is being strongly modified by erosive processes. The sampling site receives terrigenous inputs from the Jaboatão River (Fig. 1). During the study period, water temperature varied between 26 and 31 °C, and was higher in summer (31 °C in February and 30 °C in April 2000) and lower in winter (26 °C in May and July 2000). Water salinity varied between 31 and 38.

Samples were taken monthly during low tide (0.0–0.2 m) between September 1999 and October 2000. *Callichirus major* burrows were found 22 m seaward from the mean high water level of spring tides. Burrow densities increased toward the sublittoral, varying from 0 to 20 per square meter, with the highest mean density being 6.07 per square meter (Botter-Carvalho et al., 2002). To quantify this stratification, the intertidal area was divided into three contiguous strata (A, B, C), each 13 m wide, parallel to the water line. Using a "yabby-pump" (Hailstone and Stephenson, 1961), approximately 100 animals were captured per month; typically about 15 would be captured from stratum A (upper midlittoral), 30 from stratum B (middle midlittoral) and 60 from stratum C (lower midlittoral).

Biometric measurements were taken using a digital caliper (nearest 0.01 mm) or a micrometric eyepiece, following Biffar's (1971) morphometric standards. The Dorsal Oval (DO) measure was used as a standard proxy for overall size, because of the fragility of the exoskeleton (Rodrigues and Shimizu, 1997).

Sex was determined by inspection of the first pair of pleopods, the presence of eggs, and sexual dimorphism of the chelipeds. Variations in the sex ratio (males/total number) were tested using a Chi Square test (χ^2).

The reproductive period was determined by the presence of at least 10% of adult egg-bearing females (ratio of ovigerous females) (Hill, 1977; Pezzuto, 1998). The percentage of ovigerous females by length class was calculated using the total number of females.

The index of ovarian development was estimated as a ratio between ovarian width (OW) and DO (Felder and Lovett, 1989). The stages of embryonic development were classified by the presence of eyed embryos, according to Rodrigues (1976) and Dworschak (1988): stages 1 to 4 (uneyed embryos) and stages 5 to 9 (eyed embryos). Only females carrying uneyed embryos were used to estimate fecundity, in order to reduce errors due to loss of embryos during incubation (Hill, 1977). Egg masses were mechanically removed from pleopods and counted. Linear and exponential regressions were applied to all sets of data points of biometrical relations, in order to find the best fit (the highest coefficient of determination).

The growth parameters were estimated from the DO size frequency distribution using the ELEFAN I routine, included in the FISAT software package (FAO-ICLARM Stock Assessment Tools) (Gayanilo and Pauly, 1997), through the von Bertalanffy Model with seasonal oscillations, as modified by Somers (1988):

$$L_t = L\infty \left\{1 - \mathrm{e}^{[-k((t - t_o) - (Ck/2\pi)(\sin 2\pi(t - t_s) - \sin 2\pi(t_o - t_s)))]}\right\} \tag{1}$$

Where: L_t = dorsal oval length at age t; $L\infty$ = asymptotic length; K = growth rate; t_o = theoretical age at zero length; C = a constant that indicates the amplitude of the seasonal growth oscillations of the growth curve; t_s = beginning of the sinusoid growth oscillation relative to $t = 0$. The "winter point" ($WP = t_s + 0.5$) is the time of the year when the growth rate is lowest.

The DO size frequency distribution for males and females was calculated for 1-mm length intervals. Growth parameters were tentatively estimated by Powell-Wetherall and Bhattacharya methods, but values obtained with these routines were not satisfactory. Instead we used the ELEFAN I routine, with seed values for $L\infty$ and K estimated using the maximum observed size and the growth rates obtained by Shimizu (1997) and Souza et al. (1998). A value for t_o was estimated using the relationship proposed by Moreau (1987):

$$t_o = 1/K \ln[(L\infty - L_h)/L\infty] \quad (2)$$

where L_h = hatching length (Moreau, 1987). The value adopted for L_h was 4.0 mm, corresponding to the smallest total length of post-larvae observed by Rodrigues (1976).

Estimates for maximum individual age within the population were made using the formula by Taylor (1958). The maximum longevity was calculated from 95% of the asymptotic length, where t_{max} = maximum longevity estimate. Therefore, the longevity for *Callichirus major* was calculated as:

$$t_{max} = (2.996/K) + t_o \quad (3)$$

Growth performances of shrimp populations were compared using the growth performance index (Φ') (Munro and Pauly, 1983). Total mortality (Z) was estimated for males and females using length-converted catch curves (Pauly, 1987).

3. Results

3.1. Population structure

A total of 1427 shrimp (707 males and 720 females with 157 ovigerous females) were captured from September 1999 to October 2000 (Fig. 2). The smallest animal collected was a male with 2.59 mm DO, in January 2000; the largest was a female with 12.62 mm DO, in April 2000. However, most individuals were in size classes larger than 5 mm.

The overall sex ratio was 0.98:1 (male to female), not significantly different from 1:1 ($\chi^2 = 0.1184$; $p > 0.05$). Considering adults and juveniles (males <6.0 mm DO and females <7.0 mm DO) separately, the population was male-biased among juveniles 1.16:1 ($\chi^2 = 15.06$; $p < 0.05$), but skewed toward females among sexually mature adults 0.83:1 ($\chi^2 = 9.51$; $p < 0.05$). Seasonal variations in the sex ratio were apparent for females from September 1999 to February 2000, and for males from March to September 2000. The sex ratio bias was only significant for females in January 2000 (lowest

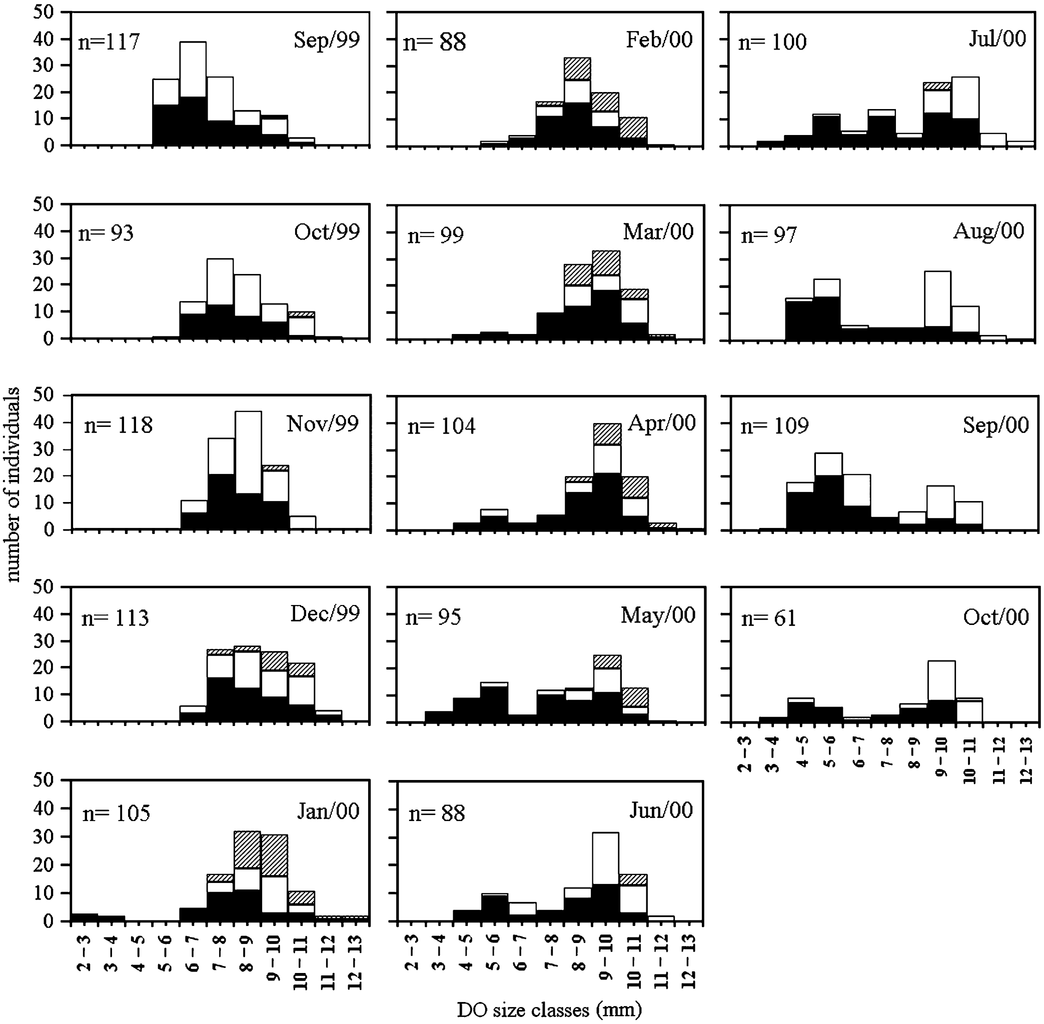

Fig. 2. *Callichirus major*. Dorsal Oval (DO) size frequency distributions for males (black bars), non-ovigerous females (white bars), and ovigerous females (dashed bars) (n = sample size).

mean ratio 0.58:1; $\chi^2 = 7.3962$, $p < 0.05$), and for males in May 2000 (highest ratio 1.71:1; $\chi^2 = 6.578$, $p < 0.05$).

Males concentrated significantly in the smaller size classes (>4, 5 and 7 mm DO) ($\chi^2 = 33.98$, 28.67 and 37.35, $p < 0.001$). Females were more abundant in the larger size classes (9, 10, 11 mm DO) ($\chi^2 = 32.53$, 52.63 and 7.35, $p < 0.001$). Ovigerous females followed the same pattern. No statistically significant differences in sex ratio were observed within the size classes 6.0–7.0, 8.0–9.0, and 12.0–13.0 mm ($\chi^2 = 0.93$, 2.30, and 2.66, $p > 0.05$).

3.2. Reproduction

Ovigerous females ($n = 157$) were found throughout the study period, except during August and September 2000. Their frequency increased to maximum values between December 1999 and May 2000 (Fig. 3). The smallest ovigerous female had 7.21 mm DO, and the largest 12.62 mm DO. However, the highest percentages (34.4% and 30.5%) were in the 9–10 and 10–11 mm size classes.

Females bearing uneyed, orange embryos predominated only during April 2000 (52.4%) at the reproductive peak (December 1999 to May 2000). Eyed, grey embryos predominated during the other months, with the highest percentage in January (63%) (Fig. 3). The number of uneyed embryos was used for calculating the relation between the number of eggs and female size (DO), and ranged between 670 (7.74 mm DO) and 3530 (10.45 mm DO). The number of eggs correlated with animal size (exponential and linear models, $R^2 = 0.4651$, $R^2 = 0.4608$, respectively) (Table 1).

Orange and swollen ovarian masses were found on adult females (>0.70 mm) during the reproductive peak. The mean OW/DO ratio also indicated the occurrence of a more advanced developmental stage during the reproductive peak. However, females with developed ovaries (OW/DO >0.70) occurred during the entire study period (Fig. 4).

3.3. Growth and mortality

Growth rates (K), performance index (Φ'), and asymptotic length ($L\infty$) were greater for females, whereas males showed slightly higher longevity ($t_{\max}$). The period of lowest growth rate occurred in March for females ($WP = 0.245$), and in July for males ($WP = 0.606$). The other parameters (C and t_o) were similar for both sexes (Table 2). Ages converted from the size range varied between 98 days (3.26 months) and 2.26 years for males, and between 158 days (5.28 months) and 2.05 years for females.

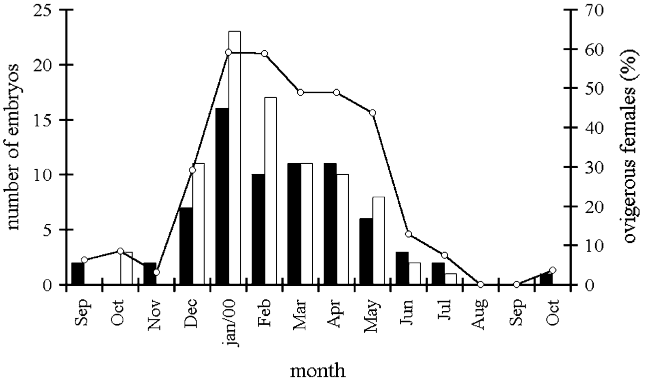

Fig. 3. *Callichirus major*. Temporal variation of the percentage of ovigerous females (line) and occurrence of females bearing uneyed (stages 1–4) (black bars) and eyed embryos (stages 5–9) (white bars). September 1999 to October 2000.

Table 1
Callichirus major ovigerous females. Exponential and linear regressions between DO length (mm) and number of uneyed embryos (En). (N = sample size; r = Pearson coefficient correlation)

Model	Regressions	N[a]	r[b]
Linear	$\text{En} = 459.45\text{DO} - 2507$	42	0.679
Exponential	$\text{En} = 7.9991\text{DO}^{2.4008}$	42	0.682

[a] Sample size.
[b] Pearson coefficient of correlation.

Total mortality rates estimated for females and males were 3.08 yr^{-1} ($r = -0.893$, CI ± 1.55) and 3.92 yr^{-1} ($r = -0.977$, CI ± 0.99), respectively.

4. Discussion

4.1. Sex ratio

The sex ratio within the population varied across size categories. Juvenile males were more prevalent. Such asymmetry has not been observed frequently in other thalassinideans (Dworschak, 1988; Hanekom and Baird, 1992; Dumbauld et al., 1996; Shimizu, 1997). However, in adults the prevalence of females is a general rule (Tunberg, 1986; Dworschak, 1988; Hanekom and Baird, 1992; Dumbauld et al., 1996; Rodrigues and Shimizu, 1997; Shimizu, 1997).

Capturing individuals using a pump may impose an undesirable sampling selectivity, favoring the capture of females. This could occur if the ovigerous females move to the upper part of the galleries to spawn or to improve the ventilation of eggs (Nates and Felder, 1999). Such an hypothesis could explain the prevalence of females of *Callichirus major* during

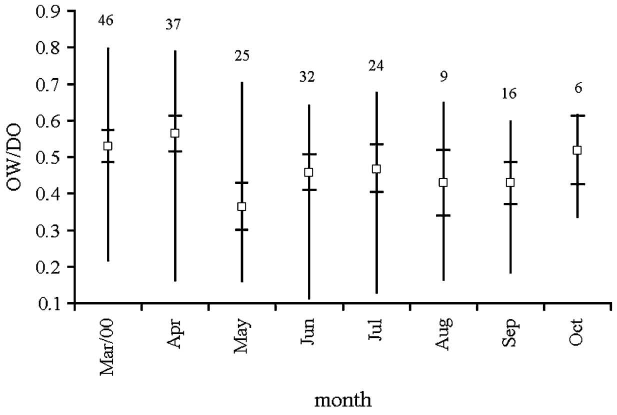

Fig. 4. *Callichirus major*. Temporal variation of the index of ovarian development (OW/DO – Ovary Width/Dorsal Oval Length). March to October 2000. Vertical lines define ranges; Squares indicate means; Error bars define 95% confidence limits; numbers indicate sample size.

Table 2
Growth curve parameters estimated for *Callichirus major*

	$L\infty$[a] (mm)	K[b] (year)	C[c]	WP[d]	Rn[e]	T_o[f] (year)	t_{max}[g] (year)
Males	14.3	0.86	0.96	0.606	0.353	−0.04	3.44
Females	15.08	0.9	0.94	0.245	0.471	−0.04	3.29

[a] Asymptotic length, that is the mean length of a given population would reach if they where to grow indefinitely.

[b] Rate of dimension time^{-1} at which $L\infty$ approached.

[c] A constant that indicates the amplitude of the seasonal growth oscillations of the growth curve.

[d] Is the time of the year when growth rate is slowest.

[e] Goodness to fit index.

[f] Theoretical age at zero length if the population had always grown according to the equation.

[g] Longevity or oldest age calculated in the sample.

January 2000, when the highest percentage (59.1%) of ovigerous females was observed. This is supported by the observations of Rowden and Jones (1994), that *Callianassa subterranea* females were captured more frequently because they occupied higher positions within the burrow. Also, field observations indicate that males, when removed from galleries, can move faster and more vigorously than females and may be able to escape more easily.

The dominance of females in the adult population may also be a response to the agonistic and territorial behavior of males. Aggressive behavior occurs in many thalassinidean shrimps (Buchanan, 1963; Tunberg, 1986; Felder and Lovett, 1989; Tamaki et al., 1997; Shimoda et al., 2005), including *Callichirus major* (Rodrigues and Shimizu, 1997), and this often leads to the death or escape of adult males (Felder and Lovett, 1989; Dumbauld et al., 1996).

Differences in the ability to escape were not observed for juveniles. The lower sampling effort (pumping/gallery/captured individual) required to capture juveniles suggests a shallower depth and/or volume of their galleries. The results obtained by Witbaard and Duineveld (1989) support this hypothesis. They suggested that the vertical distribution of *Callianassa subterranea* is a function of size, with the smaller individuals inhabiting the uppermost centimeters, and the larger ones digging deeper galleries. Thus, it is safer to estimate the sex ratio in callianassids based on immature individuals of the population. In summary, therefore, the population of *Callichirus major* at Piedade Beach was primarily male-biased.

4.2. Reproduction

Callichirus major has a well-defined reproductive period. The reproductive peak (December 1999 to May 2000) coincided with the period of higher sublittoral temperatures (Table 3). Souza et al. (1998), studying *C. major* on the southern Brazilian coast, also found ovigerous females only during the three warmest months of the year. Similarly, a study of a southeastern Brazilian population of *C. major* only found ovigerous females during 5 months of the year, with a December peak (Shimizu, 1997). On the other hand, Rodrigues and Shimizu (1997) and Nates and Felder (1999) described a continuous reproductive cycle in *C. major* and *Lepidophthalmus sinuensis*, respectively. Rodrigues and Shimizu (1997) stated that continuous reproduction might be uncommon, and suggested that it may have resulted from the steady supply of organic matter originating from domestic seawage.

The index of ovarian development (OW/DO) obtained (maximum mean value = 0.56) was lower than that obtained by Shimizu (1997) (maximum mean value ≅0.7). The occurrence of ovigerous females with developed ovaries (maximum value OW/DO ≅0.71) during the entire study period suggests the possibility of a second posture for the same female during the reproductive period. Nates and Felder (1999) suggested that in temperate areas, reproductive investment is higher, however over a shorter period of time.

The duration of thalassinidean embryonic development is influenced by temperature, as described by Hill (1977) and Tamaki et al. (1996). During the reproductive period (December to May), an unexpected prevalence of females carrying eyed embryos (stages 5–9) was observed in the first three months. The expected pattern would be the occurrence of alternating peaks of uneyed and eyed embryos (Fig. 4). This prevalence can be related to the shorter duration of stages 1–4 compared to stages 5–9 (Rodrigues, 1976), to the extended reproductive peak with the possibility of a second posture per female, and to the sampling intervals, which were probably longer than the total embryonic development time, which is 32 days at temperatures about 23 °C (Rodrigues, 1976).

The end of the reproductive peak is confirmed by: (1) accentuated decrease in the number of ovigerous females (Fig. 3); and (2) decrease in the number of eyed embryos (Fig. 3) between May and June, with the concurrent increase of males in the population.

Sizes at sexual maturation reported for *Callichirus major* from the southern and southeastern Brazilian coasts (Rodrigues, 1985; Shimizu, 1997; Souza et al., 1998) are higher than those estimated for the Piedade Beach population (Table 3). The anticipation of sexual maturation, and thus smaller sizes, may occur as a consequence of higher temperatures, as suggested for several groups, such as fishes (Morgan and Colbourne, 1999), lobsters (Fonseca-Larios and Briones-Fourzan, 1998), and other thalassinideans (Hill, 1977) (Table 3).

A direct relationship between the number of eggs and the size of females has been reported for *Upogebia africana* (Hill, 1977; Hanekom and Erasmus, 1989), *Upogebia pusilla* (Dworschak, 1988), and *Callianassa kraussi* (Forbes, 1977), but not for *Calocaris macandreae* (Buchanan, 1963). Thessalou-Legaki and Kiortsis (1997) noted that about 55% of the variation in the number of eggs in *Callianassa tyrrhena* from the Mediterranean Sea is explained by individual size. Only 46% is explained by this parameter for *Callichirus major* at Piedade Beach.

The lower fecundity compared to other populations of the same species can be related to the observed smaller individual sizes (Table 3), or to the occurrence of more than one posture in each reproductive cycle (Tamaki et al., 1996) as stated

Table 3
Reproductive aspects of some thalassinidean species in different latitudes. The dashed line separates Northern and Southern Hemisphere localities

Species	Locality	Smallest ovigerous (mm)	Eggs number	Reproductive period	Water temperature (°C)	Reference
Upogebia deltaura	North Sea (58°14′N)	15.0 CL[a]	4767	May–Aug	0.8–19.1	Tunberg (1986)
Calocaris macandreae	North Sea (55°N)	11.6 CL	80–175	Apr–Jul	–	Buchanan (1963)
Callianassa subterranea	North Sea (54°35′N)	7.0 CL	–	Apr–Jul/Sep–Oct	–	Rowden and Jones (1994)
Callianassa subterranea	North Sea (53°42′N)	7.0 CL	–	Feb–Jul	–	Witbaard and Duineveld (1989)
Neotrypaea californiensis	Eastern Pacific (46°24′N)	11.0 CL	200–14,000	Apr–Aug	–	Dumbauld et al. (1996)
Upogebia pugettensis	Eastern Pacific (46°24′N)	26.0 CL	200–14,000	Oct–Mar	–	Dumbauld et al. (1996)
Upogebia pusilla	Adriatic Sea (45°N)	9–10 CL	400–12,000	Mar–Sep	0–28	Dworschak (1988)
Callianassa japonica	Western Pacific (32°31′N)	17.9 TL[b]	962	Jun–Oct	12.7–27.8	Tamaki et al. (1996)
Lepidophthalmus louisianensis	Western Atlantic (30°N)	10.7 CL	–	Jun–Aug	12–39	Felder and Lovett (1989)
Upogebia pusilla	Aegean Sea (40°52′N)	11.5 CL	–	Apr–Aug	4.3–24.5	Kevrekidis et al. (1997)
Callianassa major[c]	Western Atlantic (35°N)	–	8170	–	–	Pohl (1946)
Sergio trilobata	Western Atlantic (27.87°N)	48.0 TL	62–412	Apr–Oct/Mar–Aug	–	Corsetti and Strasser (2003)
Lepidophthalmus sinuensis	Western Atlantic (9°17′N)	7.04 CL	138–958	Continuous (Feb–Jun peak)	30–35	Nates and Felder (1999)
Callichirus major	Western Atlantic (8°11′S)	7.2 DO; 10.2 CL	670–3530	Continuous (Dec–May peak)	26–31	Present study
Callichirus major	Western Atlantic (23°49′S)	10.3 DO[d]	–	Aug–Dec	20–27	Shimizu (1997)
Callichirus major	Western Atlantic (25°55′S)	11.3 CL	600–6600	Nov–Jan	15–29	Souza et al. (1998)
Sergio mirim[e]	Western Atlantic (32°13′S)	17.4 CL	301–6586	Sep–Jan	12–27	Pezzuto (1998)
Callianassa kraussi	Western Indian (33°52′S)	7.0 CL	40–193	May–Aug/Nov–Jan	–	Forbes (1977)
Upogebia africana	Western Indian (34°S)	10.0 CL	926–1715	–	15–24	Hill (1977)
Upogebia africana	Western Indian (34°S)	12–12.8 CL	1304–4819	Dec–Mar/Jul–Oct	13–28	Hanekom and Erasmus (1989)

[a] Carapace length.
[b] Total length.
[c] Now *Callichirus major.*
[d] Dorsal oval length.
[e] Now *Neocallichirus mirim.*

above. Water temperature can also affect the fecundity of *Callichirus major* populations. Pohl (1946) found a maximum value of 8170 eggs for a population from North Carolina, Souza et al. (1998) reported up to 6600 eggs in a southern Brazil population, and at Piedade Beach the highest value attained was only 3530 eggs.

4.3. Growth and mortality

Small differences in growth performance (Φ') and growth rates (K) have been measured in Brazilian callianassids (Table 4). At Piedade Beach, a decrease in female and male growth (*WP*) occurred in March and July, respectively. The reduction in female growth rate coincided with the reproductive peak (December to May), in agreement with the results of Pezzuto (1998) and Tamaki et al. (1997). For males, the decrease in growth rate was probably related to the lower temperatures during the winter months (lower values occurring in May and July 2000).

The estimated asymptotic length ($L\infty$) for the Piedade population was smaller than that estimated elsewhere on the Brazilian coast. Furthermore, the largest sizes found for males and females corresponded to 85% and 83%, respectively, of the estimated $L\infty$. This suggests that the maximum size reached by individuals is well below their full growth potential. Other studies have obtained percentages of 92% and 98% for *Callichirus major* (Shimizu, 1997; Souza et al., 1998) and 96% and 98% for *Neocallichirus mirim* (Pezzuto, 1998). The absence of older individuals in a population may indicate overexploitation (Sparre and Venema, 1997).

Dworschak (1988) related the smaller sizes of *Upogebia pusilla* to factors such as high salinities, food limitation, or a high incidence of parasitism. However, in the Piedade population, parasitism and competition for food did not seem to be limiting factors for growth. No individuals affected by parasites were found, and densities were not high (maximum mean density = 6.07 holes m^{-2}) (Botter-Carvalho et al., 2002).

The maximum estimated longevity for *Callichirus major* in northeastern Brazil (3.4 and 3.3 years for males and females, respectively) is close to the values suggested for other

Table 4
Parameters of the Von Bertalanffy model ($L\infty$, K) and growth performance index (Φ') obtained for callianassids studied on the Brazilian coast

Locality	Species	Sex	$L\infty$[a] (mm)	K[b] (year)	Φ'[c]	Reference
32°13′S–52°1′W	*Sergio mirim*[d]	m[e]	29.40	0.71	2.79	Pezzuto (1998)
		f[f]	31.27	0.71	2.84	
25°20′–25°55′S 48°10′–48°35′W	*Callichirus major*	m	15.00	0.9	2.31[g]	Souza et al. (1998)
		f	16.00	0.8	2.31[g]	
23°49′S–45°26′W	*Callichirus major*	m	15.37	0.90	2.32[g]	Shimizu (1997)
		f	15.30	0.83	2.28[g]	
08°11′S–34°55′W	*Callichirus major*	m	14.30	0.86	2.24	Present study
		f	15.08	0.90	2.31	

[a] Asymptotic length, that is the mean length of a given population would reach if they where to grow indefinitely.

[b] Rate of dimension time^{-1} at which $L\infty$ approached.

[c] A length based of Growth Performance Index.

[d] Now *Neocallichirus mirim*.

[e] Males.

[f] Females.

[g] Data calculated from author's values.

Brazilian populations: 3 years (Souza et al., 1998) and 4 years (Shimizu, 1997). However, in the present study, the estimated ages calculated from the largest sizes sampled in the population indicate an actual longevity of 2.05 years for females and 2.26 years for males.

The total mortality of *Callichirus major* at Piedade Beach was high ($Z = 3.92$ for males and $Z = 3.08$ for females). Similar values were obtained by Souza et al. (1998) for another harvested population of the same species ($Z = 2.75$ and $Z = 3.84$). Pezzuto (1998) estimated values of 1.53 and 1.24 for males and females, respectively, in a southern Brazilian population of *Neocallichirus mirim* that was not suffering exploitation.

On average, about 30 fishermen per day were observed during sampling sessions at Piedade. Fishermen selectively captured adult specimens, looking for the largest burrow openings and discarding the smallest individuals. Thus the predatory effect is more significant for adult mortality, and the coincidence of the reproductive period of *Callichirus major* with the summer months may enhance the impact of fishing on the shrimp population. Similar results were obtained by Borzone and Souza (1996) for a southeastern Brazilian sandy beach, where bait fishing increased in summer.

Souza and Borzone (2003) evaluated the impact of the recreational bait fishery along a southern Brazilian sandy beach, and estimated that the annual fishing harvest removed nearly 10% of the total stock of *Callichirus major*. Recent investigations on the effects of exploiting the callianassid *Trypaea australiensis* have produced conflicting results, due to different scales of sampling design (Contessa and Bird, 2004; Skilleter et al., 2005). However, both studies agree about the significant local impact of harvesting on ghost shrimp densities.

5. Conclusions

The following features of the *Callichirus major* population at Piedade Beach suggest overexploitation: (1) maximum attained individual sizes lower than the potential estimates for the population; (2) reproductive and recruitment size precocity; (3) short lifespan; (4) continuous reproduction (capability for a second hatching); and (5) high mortality. A similar conclusion was reached by Morgan and Colbourne (1999), who suggested that an increase in adult mortality could promote maturation at a younger age and smaller size. Our findings also support the view of McPhee and Skilleter (2002) that there is a potential for stocks of burrowing shrimps to be over-harvested, and there is a need to assess and monitor harvested populations, in order to gauge whether harvesting levels are sustainable.

The observed regional differences among *Callichirus major* populations are significant. Therefore, large-scale management plans should be developed with caution. Efforts towards conservation of endangered callianassid populations and their habitat restoration need to be supported by regionally based population features.

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