



Aspects of the reproductive biology of the freshwater/brackish amphipod *Quadrivisio lutzi* (Crustacea, Amphipoda) from an unstable coastal lagoon of southeastern Brazil

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ABSTRACT

The amphipod *Quadrivisio lutzi* (Shoemaker, 1933) (Maeridae) inhabits the coastal lagoons of southeastern Brazil, which are highly unstable environments. Drastic reduction in the abundance and distribution of this amphipod on these lagoons has been observed. The constant recovery of its populations suggests that this species may show a reproductive strategy that helps it to persist on these environments. Therefore, our aim was to study the reproductive biology of this species in Carapebus lagoon and to answer the question if its reproductive strategy contributes to a rapid population recovery. The size-range at sexual maturity was determined by the relative growth of the gnathopods and by the number of articles in antennal flagella. Brood size, egg diameter, size at first maturity and other relative reproductive parameters were obtained, which were compared to other species using a multivariate Principal Component Analysis (PCA). Females reach maturity at smaller size-range (2.9–3.9 mm body length (BL) than males (4.9–5.9 mm BL). Mean egg diameter was small (0.35 ± 0.08 mm) and fecundity was high (20.2 ± 9.2 eggs/female; maximum 48 eggs). The relative reproductive parameters observed in *Q. lutzi* suggest it as iteroparous species. The PCA situated *Q. lutzi* within the species of high reproductive potential, characterized by small female size at first maturity, small egg diameter, large brood size and iteroparity, which have been largely considered adaptations that allow rapid recovery of population sizes. Therefore, we concluded that the reproductive strategy of this species contributes to its survival in the highly unstable Carapebus lagoon at southeastern Brazil.

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SUBMITTED 11 November 2015

ACCEPTED 14 March 2016

PUBLISHED 19 April 2016

DOI 10.1590/2358-2936e2016003

KEYWORDS

Maeridae, unstable environment, reproductive strategy, brood size, egg diameter.

INTRODUCTION

The amphipod *Quadrivisio lutzi* (Shoemaker, 1933) (Maeridae) inhabits coastal lagoons in the southeast of Brazil (Leite *et al.*, 1980; Henriques-de-Oliveira *et al.*, 2007; Weber *et al.*, 2013), which are environments characterised by high humic acid content (see Farjalla *et al.*, 2002; 2009). This species has colonised freshwater environments (Lee and Bell, 1999) and is an important component of the trophic chain of these aquatic ecosystems, primarily as a decomposer of bottom vegetal debris but also as a consumer of animal organic litter.

The coastal lagoons of southeastern Brazil represent a diverse group of ecosystems with respect to physicochemical conditions (Petruccio, 1998; Enrich-Prast *et al.*, 2004). Most of them are highly unstable environments, with high variation in pluvial input or influxes of marine water upon the (natural or anthropogenic) disruption of the sand barriers that isolate the lagoons from the sea (Esteves, 1998; Frota and Caramashi, 1998; Rocha *et al.*, 2004). These lagoons are adjacent to the Campos Marine Basin, an off-shore oil production area with high traffic of petroleum vessels. Some of the lagoons are also subject to contamination with anthropogenic waste and/or domestic sewage (Henriques-de-Oliveira *et al.*, 2007; Esteves, 2011).

We have observed sharp declines or losses of amphipod *Q. lutzi* populations in the coastal lagoons of southeastern Brazil due to the strong changes in environmental factors (e.g., salinity and temperature). Therefore, the abundance of this species varies considerably over time and over the different lagoons. Nonetheless, this species still persists in these environments, suggesting that it may show strategies that allow it a rapid recolonization or re-establishment of population sizes when conditions return to be optimal.

Amphipods show direct development (Lincoln, 1979) and as all crustaceans they reach sexual maturity at the pubertal molt (Hartnoll, 1978; 1982). At this stage, the relative growth of some structures changes drastically, involving the development of secondary sexual characters (sexual dimorphism) (Huxley and Teissier, 1936), which allow determining when juveniles become sexually mature. Female amphipods cannot store spermatids. Therefore, during the pubertal molt, the oocytes are transferred from the oviduct to

the marsupial pouch, where the eggs are then fertilised by the males and subsequently incubated (Borowsky, 1990). The marsupial pouch is formed by the extension of the internal bases (oostegites, epipodites) of the thorax appendages (Lincoln, 1979).

Reproductive strategies of species living in unstable and unpredictable environments may be crucial to survival. Therefore, our aim was to study some aspects of the reproductive biology of *Q. lutzi* and to determine if the reproductive strategy of this species may contribute to survival and persistence in the unstable environment of the Carapebus coastal lagoon. With an estimated area of 6.5 km² and a watershed area of 126 km², Carapebus is the largest coastal lagoon of the Parque Nacional da Restinga do Jurubatiba, located at the north of Rio de Janeiro State, Brazil (Panosso *et al.*, 1998).

MATERIALS AND METHODS

Sampling

One hundred and fifty four specimens (81 females, 61 males and 12 with undefined sex) of *Quadrivisio lutzi* were collected on 4 November 2013 at shallow waters of Carapebus lagoon (22°15'9.4"S 41°35'30.2"W). They were found at the bottom of the lagoon under vegetal debris or within the roots of macrophytes, at depths of 0.10–1.2 m, near the sand barrier that separates the lagoon from the sea at 26°C and salinity of 0.3 ppt. Amphipods were collected by hand by removing carefully the roots or vegetal debris, which were immediately poured on a plastic container. Lagoon water was added to the top of the container and then transported live to the laboratory. In the laboratory they were transferred to small flasks and fixed in absolute ethanol for the morphometric and reproductive analysis.

Body size and reference parameter

The specimens were classified by sex (male, female or undifferentiated) using the size of the second gnathopods and by the presence of eggs or oostegites in females. The body length (BL) of 154 specimens was measured with their natural curvature under stereomicroscope over a rule of 0.5 mm precision and grouped on 1 mm size classes for the construction of a frequency histogram. Individuals were measured from the rostrum to the end of the third segment

of the urosome (Fig. 1). Those few individuals that showed an unusually extended or contracted position were not included in the analysis. The head length (HL) was chosen as the reference parameter for the study of the relative growth and it was measured under stereomicroscope by using a micrometer of 0.025 mm precision (Fig. 2). The head length was obtained from a total of 139 specimens (66 females, 61 males and 12 undefined sex). The head or cephalic length is widely used as adequate reference parameter instead of body length in amphipods (Fenwick, 1984; Leite and Wakabara, 1989; Cunha *et al.* 2000; Leite and Güth, 2003; Lopes and Masunari, 2004; Wellborn and Cothran, 2007; Prato *et al.*, 2009). The body length was related to the reference parameter by a regression function.

Allometric growth

The length (PG2L) and the width (PG2W) of the propodus of the second gnathopods (Fig. 3) were measured in 136 specimens (61 males, 66 females and 9 of undefined sex) with the same accuracy and instrument used for HL. The number of articles of the antennal flagellum of the first and second pair was recorded from 79 specimens (30 males, 37 females and 12 of undefined sex). All parameters were plotted against the reference parameter (HL) to evaluate the relative growth. The size-range of the onset of sexual maturity was obtained by the identification of the change in the relative growth (inflexion or discontinuity) on the scatterplot, inferring BL from the regression function with HL. Observed signs of maturity in both sexes



Figure 1. Body length (BL) with the natural curvature of the body, measured from point A (rostrum) to point B (end of the third segment of the urosome) in *Quadrivisio lutzi*.

helped to confirm the size-range of the onset of sexual maturity obtained from the scatterplot. Comparisons of regression lines of immature and mature phases were done by the Univariate Test of Significance with the over-parameterized model, Type III decomposition and 50 iterations.

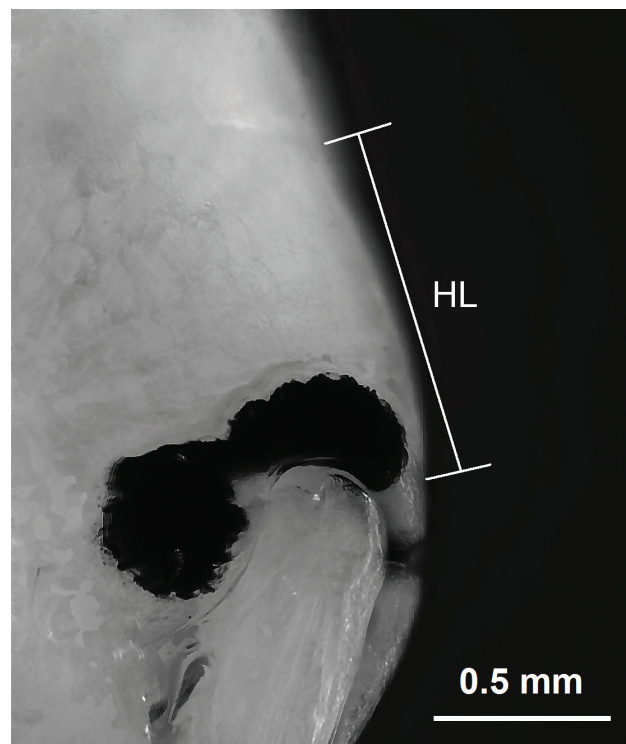


Figure 2. Head length (HL) used as a reference parameter in *Quadrivisio lutzi*.

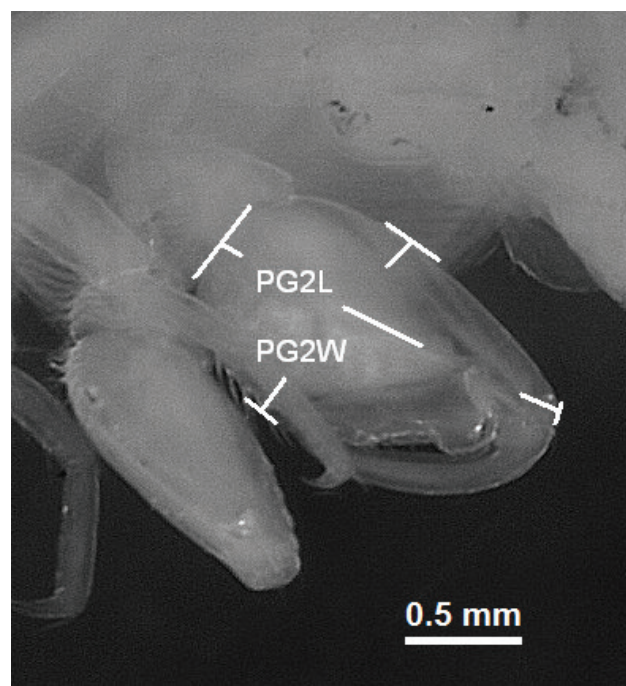


Figure 3. Length (PG2L) and width (PG2W) of the propodus of the second gnathopods in *Quadrivisio lutzi*.

Reproductive parameters

The index HMFBLr (half-range of mature female body length ratio) described by Sainte-Marie (1991), $HMFBLr = (BL_{max} - BL_{med}) / BL_{med}$, was calculated for *Q. lutzi*, where BL_{max} corresponds to the maximum size of females and BL_{med} to the mean size of mature females. This index represents the mean size range at which females can reproduce, where large values indicate higher reproductive chances during lifespan.

Brood size (BS) was obtained by removing and counting the eggs from the marsupial pouch of 50 females. Brood size was examined as a function of BL by a linear regression. The brood size/body length ratio (BS/BL) was calculated using the means of both parameters obtained from mature females. For comparisons, were selected species from the literature with female mean sizes within 3.5 to 8.0 mm BL (see Supplementary material).

Five eggs/female of 35 ovigerous females have their larger diameter measured. For comparisons with other species, the mean egg diameter obtained was expressed as a percentage of the mean size of mature females (EggD-%FS), which was also calculated for those species to which *Q. lutzi* was compared (see supplementary material).

The reproductive parameters of HMFBLr, BS/BL and EggD-%FS were used as variables to compare the reproductive potential of *Q. lutzi* with 89 species from 31 amphipod families obtained from the literature compiled by Nelson (1980), Sainte-Marie (1991), Cardoso and Veloso (2001) and Appadoo and Myers (2004). Comparisons were also performed by obtaining the two main factors of these variables by a multivariate Principal Component Analysis (PCA), which allowed the distribution of the species on the 2D-plane formed by the two main factors. For this analysis were used only those species from which was available the information of the three parameters. The STATISTICA, v. 7 package (Statsoft Inc.) was used for all statistics analysis.

RESULTS

Males (N = 61) were larger than females, reaching sizes up to 11 mm BL with a mean size of 7.2 ± 2.2 mm BL and a median of 7.5 mm BL. Females (N = 81) had a mean size of 5.7 ± 1.8 mm BL, a median size of 6.0 mm BL and a maximum size of 10 mm BL. The specimens

with undefined sex (N = 12) showed a mean size of 2.1 ± 0.8 mm BL (Fig. 4). Therefore, specimens with undetermined sex were mostly under 3 mm BL. The correlation between BL and HL was high ($r = 0.901$), well characterized by a significant linear regression ($y = 0.010 + 9.702 x$; where x and y represent HL and BL, respectively) (Fig. 5). Males (N = 61) showed a mean of 0.743 ± 0.193 mm HL, females (N = 66) showed a mean of 0.561 ± 0.167 mm HL and those with undefined sex (N = 12) showed a mean head of 0.256 ± 0.115 mm HL. In accordance to the regression that relates both parameters, the body length with the natural curvature was close to ten times the head length.

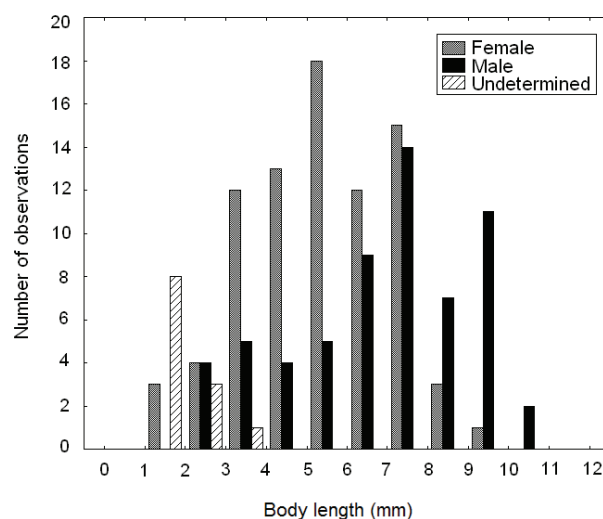


Figure 4. Body-size frequency distribution obtained from a total of 154 specimens (81 females; 61 males and 12 of undefined sex) of *Quadrivisio lutzi*.

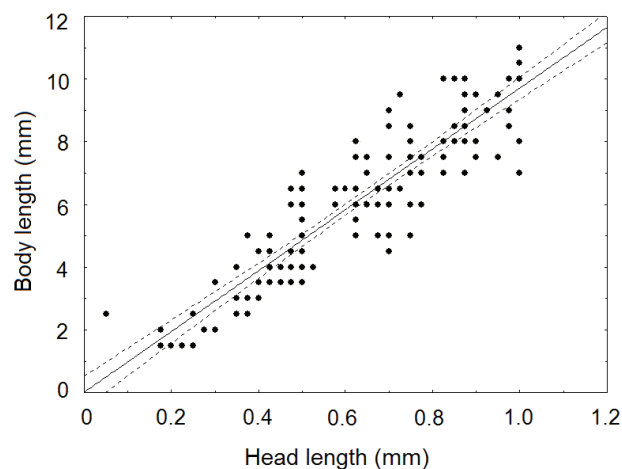


Figure 5. Regression line showing the positive relationship between the body length (BL) and the head length (HL) in 139 specimens (66 females, 61 males and 12 undefined sex) of *Quadrivisio lutzi*, where BL is close to ten times HL.

Relative growth, maturity and sexual dimorphism

Changes in the relative growth of the propodus of the second gnathopod and in the number of flagellum articles were evident in both sexes, at 0.3 mm HL (2.9 – 3.5 mm BL) in females (Fig. 6) and at 0.5 mm HL (4.9 – 5.9 mm BL) in males (Fig. 7). The means and their standard deviations of all the parameters used for these analyses are shown in Tab. 1. Mature females showed an increase in the relative growth of the number of flagellum articles for both antennal pairs, while males showed a decrease of these parameters in the mature phase (Figs. 6, 7; Tab. 2). Females showed a slight increase of the relative growth of the propodus length of the second gnathopod after maturity (Fig. 6; Tab. 2). All slopes of regression lines were significantly different between immature and mature phases (Fig. 7; Tab. 2) and only the number of articles of the second antenna in males showed a significant change of position after reaching the mature phase.

The means of the parameters, their standard errors and the 95% confidence limits of mature specimens are given in Tab. 3. Maturity was assigned for all females over 3 mm BL and all males over 5 mm BL, in accordance to the results of the relative growth of the parameters. Mean values of the second gnathopods dimensions and the number of antennal articles were significantly different between mature males and females, confirming sexual dimorphism with males showing larger second gnathopods and higher number of antennal flagella than females (Tab. 3).

Reproductive parameters

The half-range of mature female body length ratio was high (HMFBLr = 0.754). Mean brood size was 20.2 ± 9.2 eggs/female with a maximum value of 48 eggs observed in a female of 10 mm BL. Female brood size was positively correlated with BL ($y = 13.19 + 5.14x$; $p < 0.0001$; $r = 0.718$) (Fig. 8). The mean ratio

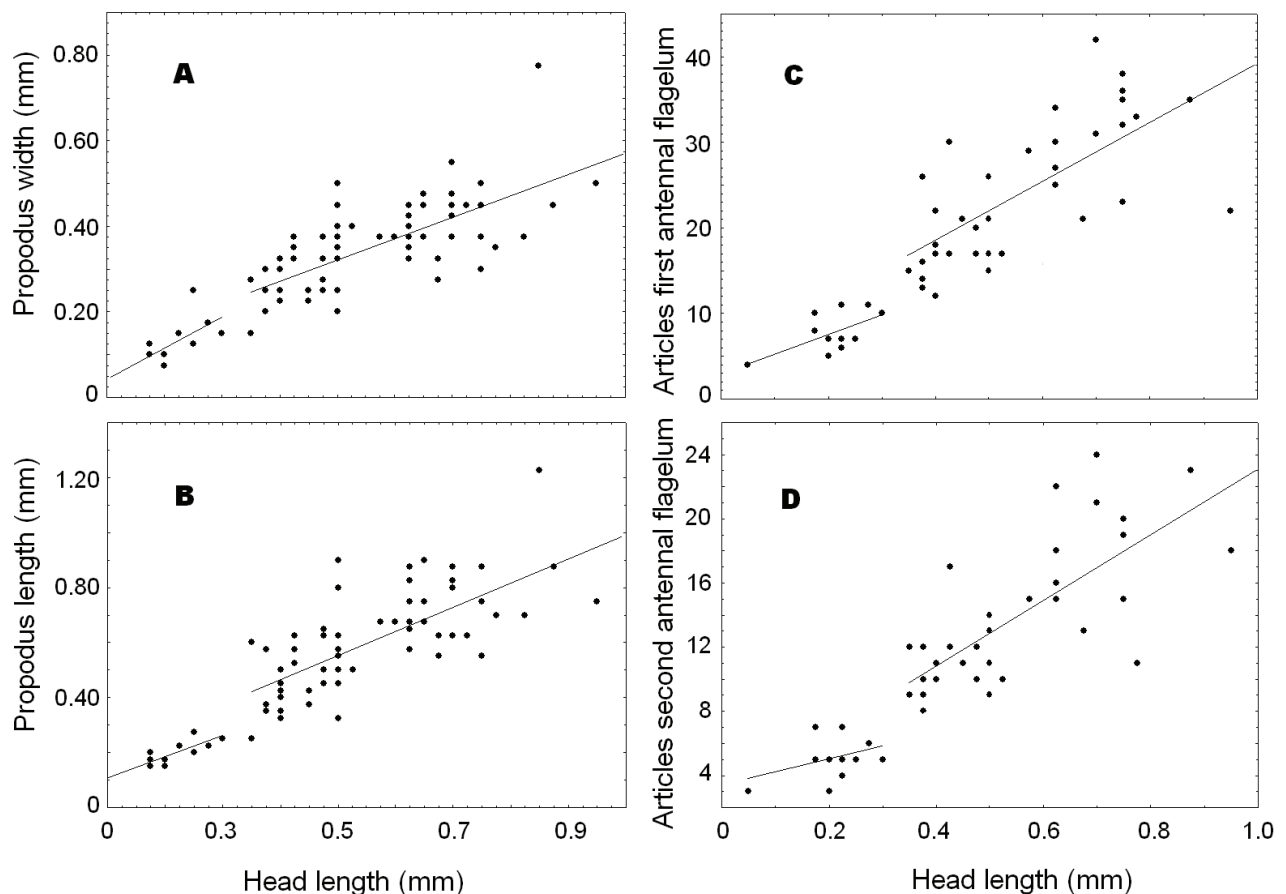


Figure 6. Female relative growth of the width (A) and length (B) of the propodus of the second gnathopods; and the number of articles in the first (C) and second (D) pair of antennal flagella. Discontinuity of the regression lines represents the size-range at which maturity is reached in females of *Quadrivisio lutzi*. Gnathopods were measured from 75 specimens (66 females and 9 of undefined sex) and flagella articles were counted from 49 specimens (37 females and 12 of undefined sex).

Table 1. Means, standard deviations and number of specimens by sex of *Quadrivisio lutzi*, which were used to study the allometric growth of the width (PG2W) and length (PG2L) of the propodus of the second pair of gnathopods and of the first (1A) and second (A2) pair of antennal flagella.

Parameter	Mean ± SD (mm) by sex (N)			Total
	Females	Males	Undefined	
PG2W	0.357 ± 0.113 (66)	0.636 ± 0.206 (61)	0.175 ± 0.091 (9)	0.470 ± 0.224 (136)
PG2L	0.616 ± 0.205 (66)	1.157 ± 0.401 (61)	0.267 ± 0.116 (9)	0.835 ± 0.430 (136)
A1	23.2 ± 8.8 (37)	27.0 ± 9.4 (30)	9.8 ± 5.0 (12)	22.6 ± 10.3 (79)
A2	13.6 ± 5.0 (37)	15.6 ± 5.1 (30)	6.4 ± 3.0 (12)	13.3 ± 5.6 (79)

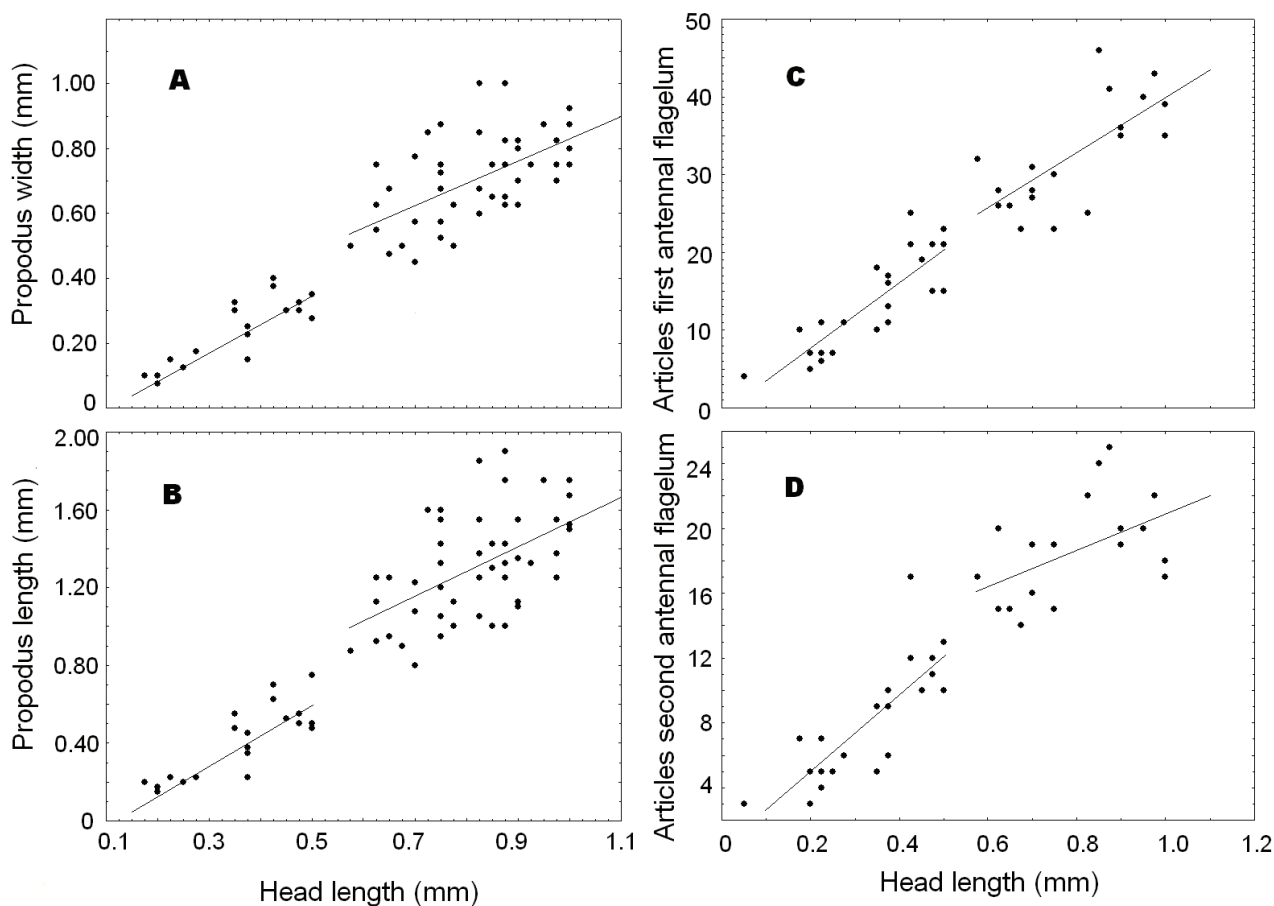


Figure 7. Male relative growth of the width (A) and length (B) of the propodus of the second gnathopods; and the number of articles in the first (C) and second (D) pair of antennal flagella. Discontinuity of the regression lines represents the size-range at which maturity is reached in males of *Quadrivisio lutzi*. Gnathopods were measured from 70 specimens (61 males and 9 of undefined sex) and flagella articles were counted from 42 specimens (30 males and 12 of undefined sex).

BS/BL for ovigerous females was 3.04 ± 1.13 . For comparisons with other species, this parameter was calculated from the means of brood size and body size of mature females, as was calculated for the other species, given a value of 3.54 for *Q. lutzi*. Egg diameter showed a mean value of 0.35 ± 0.08 mm and was not correlated with HL ($y = 0.329 + 0.036 x$; $p = 0.722$; r

$= 0.062$) neither with BL, and corresponds to 6.1% of the mean length of mature females. In order to compare this reproductive parameter with other species, it was also calculated for those species obtained from the literature. The mean values of the relative reproductive parameter, obtained for the species to which *Q. lutzi* was compared, are shown in Tab. 4.

Table 2. Regression lines of the relative growth (allometric equation) of the width (PG2W) and length (PG2L) of the propodus of the second pair of gnathopods; and the number of articles of first and second pair of antennal flagella in the amphipod *Quadrivisio lutzi*. Significance of the allometric equation ($p < 0.05$); correlation coefficient (r) of the two parameters. Univariate test of significance for the comparison of two regression lines (immature and mature phases); significance at $p < 0.05$. Regression for each phase was established by graphical observation, where males over 5 mm BL and females over 3 mm BL were considered mature.

Parameter (y)	Sex	Phase	HL (x)			Univariate Test of Significance	
			Allometric equation	p	r	Slopes	Intercepts
PG2W	Females	Immature	$y = -0.014 + 0.691 x$	0.068	0.598	F(2) = 32.98	NS
		Mature	$y = 0.085 + 0.487 x$	< 0.001	0.697	p < 0.00000	$p < 0.43237$
	Males	Immature	$y = -0.037 + 0.836 x$	< 0.001	0.836	F(2) = 20.82	NS
		Mature	$y = 0.193 + 0.639 x$	< 0.001	0.560	p < 0.00000	$p < 0.07791$
PG2L	Females	Immature	$y = 0.048 + 0.696 x$	0.013	0.749	F(2) = 40.47	NS
		Mature	$y = 0.104 + 0.915 x$	< 0.001	0.730	p < 0.00000	$p < 0.79123$
	Males	Immature	$y = -0.086 + 1.387 x$	< 0.001	0.810	F(2) = 17.86	NS
		Mature	$y = 0.263 + 1.276 x$	< 0.001	0.543	p < 0.00000	$p < 0.19430$
Articles 1st Antenna	Females	Immature	$y = 3.429 + 21.352 x$	0.044	0.589	F(2) = 21.82	NS
		Mature	$y = 4.895 + 34.329 x$	< 0.001	0.704	p < 0.00000	$p < 0.81172$
	Males	Immature	$y = -0.593 + 42.012 x$	< 0.001	0.848	F(2) = 29.46	NS
		Mature	$y = 3.903 + 35.930 x$	< 0.001	0.708	p < 0.00000	$p < 0.48249$
Articles 2nd Antenna	Females	Immature	$y = 3.816 + 6.548 x$	0.352	0.295	F(2) = 28.16	NS
		Mature	$y = 2.666 + 20.529 x$	< 0.001	0.755	p < 0.00000	$p < 0.72099$
	Males	Immature	$y = 0.218 + 23.921 x$	< 0.001	0.818	F(2) = 19.74	F(1) = 6.55
		Mature	$y = 9.701 + 11.227 x$	0.032	0.494	p < 0.00000	p < 0.01458

Table 3. Means, standard error (SE) and confidence limits of the morphological parameters studied in mature specimens of *Quadrivisio lutzi*, considering mature those females with sizes over 3 mm BL and those males over 5 mm BL. The effect of sex was evaluated for each parameter by a one-way ANOVA, confirming sexual dimorphism in mature amphipods for all parameters studied.

Parameter	Sex	N	Mean (mm)	SE (mm)	CI (mm) (-95% to +95%)	ANOVA results Effect of sex
PG2W	F	59	0.378	0.015	0.349 – 0.407	F = 246.5; $p < 0.000$
	M	48	0.723	0.016	0.691 – 0.756	
PG2L	F	59	0.656	0.029	0.599 – 0.713	F = 241.4; $p < 0.000$
	M	48	1.321	0.032	1.258 – 1.384	
A1	F	31	25.5	1.4	22.8 – 28.2	F = 10.1; $p = 0.0026$
	M	18	32.6	1.8	29.0 – 36.1	
A2	F	31	14.7	0.7	13.2 – 16.2	F = 10.9; $p = 0.0018$
	M	18	18.7	1.0	16.8 – 20.7	

Table 4. Number of species (N) to which *Quadrivisio lutzi* was compared; their mean, standard deviation (SD) and 95% confidence limits (CL) of the reproductive parameters.

Reproductive Parameter	N	Mean	SD	-95% CL	+95% CL	<i>Q. lutzi</i>
HMFBLr	84	0.286	0.152	0.253	0.319	0.754
BS/BL	89	2.5	1.6	2.1	2.8	3.5
EggD-%FS	44	7.9	2.7	7.1	8.8	6.1

The Principal Component Analysis performed over 39 species (supplementary material) using the three reproductive parameters, generated three factors as shown in Tab. 5. The first and third factors were explained mainly by the relative values of brood size and egg diameter and the second factor, explained mainly by the values of HMFBLr. The correlation of

these variables with the factors is shown in Tab. 6. The eigenvalues of correlation matrix and the percentage of the explained variance (Tab. 7) showed that the first two factors explained more than 81% of the total variance. Therefore, the position of *Q. lutzi* in relation to the three reproductive variables (HMFBLr, BS/BL and EggD-%FS) was visualized over the 2D-plane formed

Table 5. Eigenvectors of correlation matrix obtained from the PCA using the reproductive parameters as variables for 39 amphipod species listed in supplementary material, from which the three parameters were obtained.

Variable	Factor 1	Factor 2	Factor 3
HMFBLr	-0.381778	0.938581	0.048414
BS/BL	-0.669517	-0.206908	-0.713397
EggD-%FS	0.659564	0.276144	-0.699085

Table 6. Factor-variable correlation obtained from the PCA using the reproductive parameters as variables and 39 amphipod species listed in supplementary material, from which the three parameters were obtained.

Variable	Factor 1	Factor 2	Factor 3
HMFBLr	-0.418165	0.907640	0.036447
BS/BL	-0.819469	-0.200087	-0.537063
EggD-%FS	0.807285	0.267041	-0.526288

Table 7. Eigenvalues of correlation matrix and explained variance obtained from the PCA using the reproductive parameters as variables and 39 amphipod species listed in supplementary material, from which the three parameters were obtained.

Factors	Eigenvalue	% of total variance	Cumulative eigenvalue	Cumulative % of variance
1	1.498101	49.94	1.498101	49.94
2	0.935155	31.17	2.433256	81.11
3	0.566744	18.89	3.000000	100.00

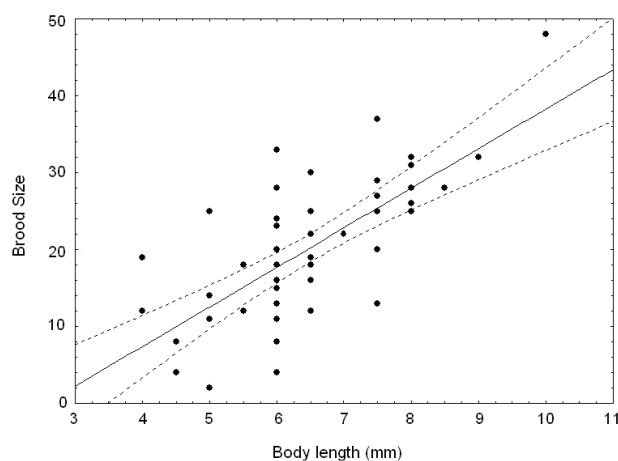


Figure 8. Regression line showing the positive relationship between brood size and body length in the amphipod *Quadrivisio lutzi*.

by the two main PCA factors (Fig. 9), in comparison with other 38 amphipod species within the range of mean female size of 3.5 to 8.0 mm BL. This 2D-plane shows HMFRLr and BS/BL growing over Factor 1 (in the left quadrant) in the opposite direction of Egg-%FS (in the right quadrant). Over the second factor, HMFRLr increases over the left upper quadrant. The amphipod *Q. lutzi* was located by the PCA on the upper left quadrant.

DISCUSSION

Sexual dimorphism and size-range of the onset of sexual maturity

Changes in the relative growth of the propodus of

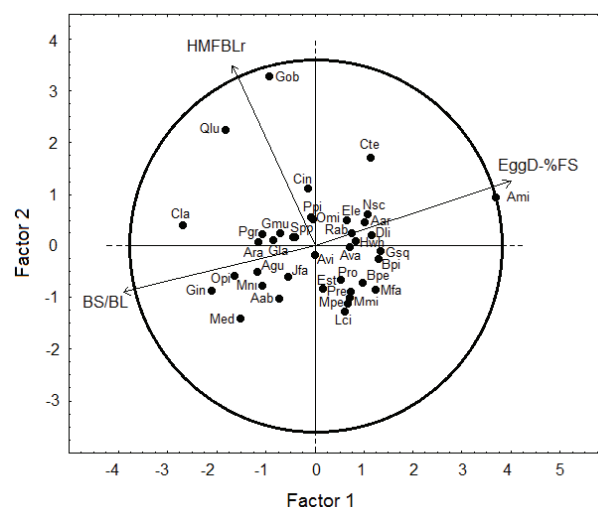


Figure 9. Position of *Quadrivisio lutzi* relative to other 38 amphipod species, over the 2D-plane formed by the main two PCA factors obtained from the three reproductive variables. Vectors are represented by fine line arrows. (Aab) *Ampelisca abdita*, (Aar) *A. araucana*, (Ava) *A. vadorum*, (Gsq) *Gitanopsis squamosa*, (Ara) *Ampithoe ramondi*, (Agu) *Atylus guttatus*, (Avi) *Amphiporeia virginiana*, (Bpe) *Bathyporeia pelagica*, (Bpi) *B. pilosa*, (Cla) *Calliopius laeviusculus*, (Mpe) *Metaleptamphopus pectinatus*, (Cte) *Chelura terebrans*, (Cin) *Corophium insidiosum*, (Gla) *Gammarus lawrencianus*, (Gmu) *G. mucronatus*, (Gob) *G. obtusatus*, (Est) *G. (=Equinogammarus) stoerenis*, (Nsc) *Neohaustorius schmitzi*, (Ami) *Acanthohaustorius millsii*, (Ppi) *P. pietschmani*, (Lci) *Lepidepcreum cingulatum*, (Jfa) *Jasa falcata*, (Hwh) *Hippomedon whero*, (Mfa) *Metambasia faeroensis*, (Omi) *Orchomenella minuta*, (Opi) *O. pingus*, (Ele) *Elasmopus laevis*, (Mni) *Melita nitida*, (Med) *Monoculodes edwardsi*, (Dli) *Diogodias littoralis*, (Pro) *Paraharpinia rotundifrons*, (Rab) *Rhepoxynius abronius*, (Gin) *Gammaropsis inaequistylis*, (Pre) *Photis reinhardi*, (Pgr) *Prostebbingia gracilis*, (Mmi) *Metopelloides micropalpa*, (Qlu) *Quadrivisio lutzi*; (Spp) corresponds to (Pba) *Parhyalella barenensis* and (Gpa) *Gammarus palustris*.

the gnathopods and in the number of articles in antennal flagella have been previously studied in other amphipods to relate them either with growth phases, sexual dimorphism or size at maturity (Leite and Wakabara, 1989; Moore and Wong, 1996; Lopes and Masunari, 2004; Tsoi and Chu, 2005). Sexual dimorphism in *Q. lutzi* was observed in body length, in the dimensions of the second gnathopods and in the number of articles of the antennal flagella. Males larger than females with larger second gnathopods have been observed in most gammaridean amphipod species (Barnard, 1975; Sainte-Marie, 1991; Moore and Wong, 1996; Wellborn and Cothran, 2007). Females of *Q. lutzi* reach maturity at smaller sizes than males, probably because of their smaller mean body length than the males. Comparing *Q. lutzi* with 15 species with mature female mean size within the range of 3.5 to 8.0 mm BL, four species showed first maturity (FM) at the same or lower size than *Q. lutzi*. *Melita appendiculata* (Say, 1818) (Melitidae, marine) showed similar size at FM than *Q. lutzi*, but it shows lower mean female size (3.8 mm LB). *Elasmopus laevis* Smith, 1873 (Melitidae, marine, FM = 2.8 mm LB) and *Lembos websteri* Bate, 1857 (Aoridae, marine, FM = 2.5 mm LB) have smaller FM and body size (4.3 and 4.7 mm LB, respectively) than *Q. lutzi*. Only *Ampithoe longimana* Smith, 1873 (Ampithoidae, marine) showed much lower FM (2.4 mm LB) than *Q. lutzi* with similar mean mature female size (5.8 mm LB). Therefore, we can consider *Q. lutzi* within the groups of species with small size at first maturity. Small size at first maturity has been related with larger brood size (Nelson, 1980). Cunha *et al.* (2000) and Appadoo and Myers (2004) suggested that iteroparous species can be inferred when the minimum size of ovigerous females is less than half the size of the largest female, implying several subsequent moults, enabling consecutive broods.

Reproductive parameters

HMFBLr

The half-range of mature female body length ratio in *Q. lutzi* was 0.754, higher than the mean observed for 84 species corresponding to 31 families and much higher than the upper 95% confidence limits of the mean (see Tab. 4). Out of 84 species, only two species showed higher value of HMFBLr than *Q. lutzi*: *Echinogammarus obtusatus* (Dahl, 1938) (0.875) and *Gammarus tigrinus*

Sexton, 1939 (0.785). Therefore, *Q. lutzi* is within the few species with highest values of HMFBLr. High values of HMFBLr are characteristics of iteroparous species (Sainte-Marie, 1991). Iteroparous females can copulate again very soon after spawning, reducing their time without broods (Krishnan and John, 1974), having therefore high reproductive potential. Field observations during collections of *Q. lutzi* carried out since 2013 for obtaining live amphipods for maintenance in the laboratory or bioassays, demonstrated that ovigerous females represented $96.3 \pm 9.1\%$ of mature females and can be found all year through (personal observation). This information, added to the high value of HMFBLr is further evidence of iteroparity in *Q. lutzi*.

Brood size

The positive linear relationship between brood size and body length in *Q. lutzi* is a common feature in gammaridean species (Steele and Steele, 1970; Nelson, 1980; Highsmith and Coyle, 1991; Sainte-Marie, 1991; Cardoso and Veloso, 2001; Tsoi and Chu, 2005). The mean BS/BL in *Q. lutzi* was 3.5, obtained from the mean values of brood size and body size. The comparison with 89 species corresponding to 31 different families (supplementary material) showed that *Q. lutzi* is over the mean values obtained for these species and over the upper 95% confidence limits. When comparisons were done with the mean values of 31 families, *Q. lutzi* showed a value over the mean of 25 of those families, including Gammaridae; showed similar value to Crangonyctidae and Urohaustoriidae; and lower value than four families, represented by few species (Atylidae, 4.70, n = 1; Chiltoniidae, mean = 6.7, n = 2; Ischyroceridae, mean = 4.8, n = 3; and Photidae, mean = 4.1, n = 2), indicating that at least these few species showed higher values than *Q. lutzi*.

Egg diameter

Egg diameter was consistent with values found by Stephensen's (1933) for *Q. lutzi* from Aruba. No correlation was found between egg diameter and head length, neither with body length within the species. Mean egg diameter in *Q. lutzi* (0.35 ± 0.08 mm) was homogeneous in size. Homogeneity in egg diameter has been explained by simultaneous fertilisation and by eggs at the same stage of development (Leite and

Wakabara, 1989). In order to compare, using the egg diameter as the percentage of mean body size of mature females (EggD-%FS), was observed out of 44 species corresponding to 20 different families that the EggD-%FS of *Q. lutzi* is lower than the mean of all species; and under the low 95% confidence limit of the mean. When comparisons were done with 20 different families, *Q. lutzi* showed lower value of EggD-%FS than most families and showed values close to the mean values showed by Gammaridae (6.0, $n = 5$) and by Ampithoidae (6.1, $n = 3$). Only three families showed EggD-%FS values lower than 6.0, which were mainly represented by one species: Oedicerotidae (4.7, $n = 1$); Pontogeneiidae (5.6, $n = 1$) and Calliopiidae (5.2, $n = 2$). Small egg diameter has been suggested to be an adaptation in species that mature at small sizes, allowing individuals to produce numerous subsequent offspring, increasing population size rapidly (Steele and Steele, 1970; Cardoso and Veloso, 2001). The potential advantages of small egg size in a highly risky environment have been summarised by Van Dolah and Bird (1980) as follows: increased chances of successful release under high adult mortality probability; increased number of eggs that females can carry per brood; shorter incubation time, allowing more broods over a reproductive season; decreased time to maturity, increasing therefore population growth rate; and finally smaller reproductive females, which are less subject to selection than are large adults.

Reproductive strategy

The PCA 2D-plane obtained from the two main factors (Fig. 9) allowed the distribution of species in function of their reproductive strategy, determined by the three reproductive parameters chosen (HMFBLr, BS/BL and EggD-%FS). On the right quadrants over the first factor of Fig. 9 are situated all the species with large eggs and low mean brood sizes; on the left quadrants over the same factor, are situated those species with small eggs and large brood sizes, where those species situated far from the null value of the first factor showed the highest values of brood size and smallest egg diameters. On the upper quadrants over the second factor are situated those species with large HMFBLr, and in the lower quadrants over this factor, those with low values of HMFBLr. Although *Q. lutzi* is not the species with the largest brood size, it is situated on the upper left

quadrant, where are the species with combined high reproductive potential (large brood size, small egg diameter and high HMFBLr), while those species situated on the lower right quadrant are those with the lowest reproductive potential.

Species with high reproductive potential (small embryo size, early female maturity, large brood size and iteroparity) are more common at low latitudes (e.g., the tropics), where warmer temperatures and food are continuous all year-long (Morino, 1978; Nelson, 1980; Sainte-Marie, 1991; Steele and Steele, 1991; Cunha *et al.*, 2000; Appadoo and Myers, 2004).

Gammaridean species are largely littoral amphipods that live in high-risky environments, such as exposure to low tides, osmotic stress and temperature shock. The reproductive strategy of these amphipods may be an adaptation to these highly unstable environments, in which strong population depletion or extinction events are frequent and where population recovery is largely reliant on adaptive mechanisms that allow a rapid increase in population size and therefore, population recovery.

The degree of instability and uncertainty of environments predicts different reproductive strategies (Fenwick, 1984; Sainte-Marie, 1991). R-selection predicts that organisms experiencing wide fluctuations in population density, high density-independent mortality or repeated colonisation tend to evolve a combination of earlier maturity, larger broods, higher reproductive effort (total broods over the female's lifespan) and shorter lifespan relative to those experiencing stable population density or are subject to density-dependent mortality (MacArthur and Wilson, 1967; Pianka, 1970).

It has been observed sharp declines or losses of the amphipod *Q. lutzi* populations in some of the coastal lagoons of southeastern Brazil due to strong changes in salinity. For example, at Carapebus lagoon collection site, salinity was stable in 0.3–0.6 ppt until the end of 2013, where amphipods were abundant. After the breakdown of the sand barrier that separates the lagoon from the sea on 23 December 2013, salinity raised and amphipods were not found. Since then salinity has been changing and in March 2014, salinity was 13.4 ppt and again no amphipods were found at the collection site. In October 2014, salinity was in 4.0 ppt and few amphipods were found; and in November 2014, at

salinities of 8.3 ppt, amphipods were abundant again (TBM and LIW, pers. obs.).

The reproductive parameters observed in *Q. lutzi* at the coastal lagoon of Carapebus (small embryo size, early female at maturity, large brood size and iteroparity) may be considered adaptations of increased reproductive potential for rapid population recovery. These reproductive parameters allow the amphipod a rapid re-establishment of population size when conditions return to be optimal for the amphipod, contributing so to the survival in the highly unstable environment of Carapebus lagoon. Whether the reproductive patterns observed in *Q. lutzi* represents an evolutionary adaptation of the species to the unstable environments of the coastal lagoons of the southeast coast of Brazil or whether represents physiological adaptations to local unstable conditions still remains to be answered.

ACKNOWLEDGEMENTS

We are very grateful to FAPERJ for the IC grant given to TM; to CNPq-PELD-Sítio-5 for research financial support; and to João Marcelo S. de Souza, for technical support during sampling. We are also very grateful to anonymous reviewers for their valuable comments, criticisms and suggestions to the manuscript. All field and laboratory work was supported by the ICMBIO Licence number 26145.

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