A test of large-scale reproductive migration in females of the amphidromous shrimp *Macrobrachium acanthurus* (Caridea : Palaemonidae) from south-eastern Brazil

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Abstract. *Macrobrachium acanthurus* inhabits estuaries and rivers in the western Atlantic. It is not clear whether females migrate towards estuaries to hatch larvae, as reported for other congeneric shrimps. We tested whether females of *M. acanthurus* exhibit reproductive migrations. The population dynamics of this shrimp was studied in the Ribeira de Iguape River, Brazil. Four sites that differ in position with respect to the coast were sampled monthly during 2007. In *M. acanthurus*, reproduction was seasonal and reproductive intensity did not vary among study sites. Females brooding early and late embryos were found at all study sites during the reproductive season. No disappearance of reproductive females was observed at the study site located furthest away (∼150 km) from the coast. Thus, reproductive females of *M. acanthurus* do not exhibit reproductive migrations towards estuaries to hatch larvae. Maturity in females was reached at smaller body sizes during the austral summer and spring compared with winter and autumn. Growth rate and body size was sex-specific; males grew slower but attained larger average and final body sizes than females. This information needs to be considered in assessing stocks and establishing sustainable management plans for *M. acanthurus* in Brazil.

Additional keywords: freshwater prawn, growth, maturity, reproduction, sex ratio.

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Introduction

Shrimps from the infraorder Caridea use a diverse range of habitats and exhibit considerable diversity in terms of life cycles (Bauer 2004; De Grave *et al.* 2009). Many caridean shrimps are symbiotic with sessile marine invertebrates, others inhabit deep-sea chemoautotrophic environments, a few have conquered semiterrestrial mangrove forests, and a relatively large number of species have colonised freshwater environments (Bauer 2004; De Grave *et al.* 2009). Most freshwater shrimps pertain to three different monophyletic groups (i.e. the families Atyidae and Xiphocarididae, and the genus *Macrobrachium* in the family Palaemonidae: see Bauer 2004, 2011) and the life cycle of these shrimps differs widely. In some species, the transition from the marine ancestral environment to the freshwater realm is complete; the entire life cycle takes place in freshwater and parental females brood a few large embryos that hatch either as a crawling juvenile or at an advanced larval stage (e.g. *M. ferreirai*: Magalhães and Walker 1988; *Dugastella*

valentina: Cuesta *et al.* 2006). In other species, parental females brood numerous and small embryos that hatch at an early larval (Zoea) stage, the larval period is extended, and larvae do require marine or estuarine conditions to complete development. In some of these species with indirect development, each individual in the population exhibits amphidromous behaviour: larvae released in rivers drift downstream to marine or estuarine habitats and then, after settlement and metamorphosis, post-larvae migrate back to the freshwater environment (Bauer and Delahoussaye 2008; Bauer 2011). This amphidromous life cycle is also shared by a considerable number of freshwater fishes and mollusks (McDowall 2007).

The genus *Macrobrachium*, with 243 described species, has a worldwide tropical and subtropical distribution (De Grave and Fransen 2011). Some shrimps in this genus are rather small, attaining a total body length of no more than a few centimetres (e.g. *M. jelskii*) while other species attain large body sizes (>30 cm total length) (Holthuis 1980; Jayachandran

2001). Some species exhibit abbreviated larval development (*M. ferreirae*) while others have extended larval periods and exhibit an amphidromous life cycle (*M. ohione*) (Magalhães and Walker 1988; Bauer and Delahoussaye 2008).

In this study, we were interested in examining the reproductive biology of the shrimp *M. acanthurus*, a common inhabitant of the western Atlantic (Holthuis 1980; Bond-Buckup and Buckup 1989; Melo 2003). *M. acanthurus* can be found in estuaries and in rivers up to ~300 km inland and individuals inhabit rocks, underneath death trees, and among aquatic vegetation (Coelho 1963). *M. acanthurus* exhibits indirect development and females hatch carnivorous planktonic larvae that take 30–40 days to metamorphose (Valenti 1985). In south-eastern Brazil, *M. acanthurus* reproduces year-round, but with the greatest intensity during the austral summer (Valenti *et al.* 1986). Males and females attain a maximum body length of 138 mm and 108 mm, respectively (Valenti *et al.* 1987). Given its large body size, *M. acanthurus* is exploited by artisanal fisheries in Central and South America, including Brazil (New *et al.* 2000).

Several details concerning the life history of *M. acanthurus* are not known. For instance, it is not clear whether females migrate towards estuaries to hatch larvae, as is reported to occur in other congeners (Mohamed and Rao 1971; Lee and Fielder 1979; Read 1985; Bauer and Delahoussaye 2008; John 2009; Rome *et al.* 2009; Olivier and Bauer 2011), or whether females hatch larvae anywhere along the river. Choudhury (1971) demonstrated that larvae of this species have the ability to live in freshwater for ~1 week after hatching. This suggests the absence of reproductive migrations in *M. acanthurus*. In contrast, other authors have suggested that females do migrate towards estuaries during each reproductive season (Hughes and Richard 1973; Chávez-Alarcón and Chávez 1976).

In this study, we tested whether or not parental females of *M. acanthurus* exhibit reproductive migrations – from fully freshwater environments to estuaries for larval hatching. For this purpose, we described the population dynamics of this species at a single basin (i.e. Ribeira de Iguape) but at different study sites located far away or close to the coast. If females do not exhibit reproductive migrations, we expected females brooding early- and late-stage embryos to be consistently present at different study sites along the river both far away (e.g. 150 km from the estuary) and close to the coast during the same reproductive season. Also, we determined site-specific population parameters such as sex ratio, size at first maturity, sex-specific growth rate, and maximum body size, and we compared the parameters above among localities to reveal further details about the life history of this economically valuable shrimp.

Materials and methods

Study site

The Ribeira de Iguape basin (23°45′S, 46°45′W to 25°30′S, 50°W), covering an area of ~25 000 km², is one of the largest basins in south-eastern Brazil (Fig. 1). Following Köppen's climate classification, most of the Ribeira de Iguape basin has a climate type Af, characterised by rainy tropical weather, the absence of a dry season during the year, and an average precipitation of >60 mm during the driest months of the year (Rolim *et al.* 2007). In the upper portion of the Ribeira de Iguape River, currents are comparatively strong while in the lower portion of the river, near the estuary, water runs slowly, the river meanders, and swamps, marshes and other areas that surround the river potentially flood during the rainy season (Camargo *et al.* 1972).

Collection of M. acanthurus

Individuals of *M. acanthurus* were collected once per month, from January to December 2007, at four different sites in the Ribeira de Iguape River. Sampling sites were selected to

Fig. 1.   Study site showing Vale do Ribeira and the different sampling sites (Eldorado, Sete Barras, Registro and Iguape) along the Ribeira de Iguape River.

characterise the reproductive biology of this shrimp along the length of the river. Iguape was located the closest to the mouth of the river (72 km from the mouth), and Registro (114 km), Sete Barras (138 km) and Eldorado (155 km) were progressively located more inland (Fig. 1).

At each study site, shrimps were sampled using a combination of minnow traps and kick nets. A total of 12 minnow traps (1 m length, 30 cm diameter, and 8 mm mesh pore) were baited with small pieces of banana and/or cow bones, placed either among the vegetation near the margin of the river ($n = 6$ traps) or at the bottom of the river ($n = 6$ traps), and retrieved after 24 h. In addition, two people with a single kick-net (0.5 m^2, 5 mm mesh pore) sampled the margin of the river (against the current) during a total of 20 min specifically focusing on semisubmerged vegetation known to harbour *M. acanthurus*. Thus, we consistently used a total of 12 replicates (sampling units) per month and per study site throughout the entire sampling period. The rationale for using different sampling methodologies and for sampling different microhabitats at each study site was to capture all ontogenetic stages (recruits, juveniles, and adults), sexes, and body sizes of *M. acanthurus* in their natural proportions. Thus, we produced a representative picture of the shrimp population structure and sex ratio at each study site throughout the year.

Immediately after collection, shrimps were placed in plastic bags within an ice chest and transported alive to the Laboratory of Crustacean Biology and Cultivation (LABCRUST), UNESP-Registro, Registro, where shrimps were frozen until they were measured and sexed (see below). In total, we collected 20 159 shrimps ($n = 11\,987$, 2878, 2746, and 2548 specimens in Iguape, Registro, Eldorado, and Sete Barras, respectively) during the entire study period. Logistic and time constraints did not permit measuring and sexing each collected individual in such a large sample. Thus, we followed the criterion of Wenner *et al.* (1991) (also employed in Baeza *et al.* 2010) to obtain a representative sample from each study site and sampling date. We measured and sexed all individuals in samples comprising 80 or fewer shrimps. In samples containing 80–160 shrimps, we measured 80 haphazardly selected specimens. Lastly, we measured and sexed 50% or 25% of all shrimps in samples comprising 160–320 individuals or more than 321 individuals, respectively. In total, 10 914 shrimps (54.14% of the total capture) were sexed and measured during this study.

The carapace length (CL) of each selected shrimp >10.0 mm CL was measured with a caliper (to the nearest 0.1 mm) as the distance between the orbital angle and the posterior margin of the carapace. Specimens <10.0 mm CL were measured to the nearest 0.025 mm under the stereomicroscope using a graduated ocular micrometer. Shrimps were classified as males or females according to the presence or absence, respectively, of appendix masculina on the second pleopods and gonopores on the coxae of the fifth pereopods. Lastly, each female was classified according to the presence or absence (brooding or non-brooding, respectively) of embryos and the developmental stage of the embryos (early, intermediate, and late) beneath the abdomen: early-stage embryos are those that have been spawned recently and have no eyes and a uniformly distributed yolk; intermediate-stage embryos have visible but not well developed eyes; late-stage embryos have little yolk, well developed eyes, chromatophores, and appendages.

Population dynamics of M. acanthurus

Previous studies on the population dynamics of other shrimp species have shown differences in growth parameters between the sexes (e.g. Andrade and Pérez 2004, 2007). Therefore, during this study, we calculated growth parameters separately for males and females of *M. acanthurus*. Also, we aimed to study age and growth schedules of *M. acanthurus* separately for each study site (see Results). Lastly, we also conducted an analysis that included shrimps collected from all study sites to provide a general picture of the life-history schedule of *M. acanthurus* across the entire basin.

For each study site and for all study sites grouped together, the age and growth of *M. acanthurus* were determined using length–frequency distributions (LFDs) (Andrade and Pérez 2004, 2007; Baeza *et al.* 2010). We reconstructed monthly LFDs using 3-mm-CL size intervals, as this scale proved useful for the detection of modes during preliminary data analyses. Next, growth parameters were fitted to our data using the von Bertalanffy growth curve without seasonality (Sparre and Venema 1997):

$$L_t = L_\infty \left(1 - e^{-K(t-t_0)}\right)$$

where L_t is the average length estimated at age t, L_∞ is the asymptotic maximum length, K is a curvature parameter defining how quickly L_∞ is achieved and t_0 is the theoretical age at which shrimps would have zero length. This von Bertalanffy model is a useful expression of growth in shrimps (Silliman 1969; Parrack 1979; García and Le Reste 1987) although crustaceans exhibit a discontinuous growth pattern. We estimated the different growth parameters using the software LFDA5 (Kirkwood *et al.* 2001). This software uses Rn as a measure of goodness of fit for estimated growth parameters. Rn ranges between 0 and 1 and values closer to unity indicate better goodness of fit.

For each sex, expected longevity was estimated using the values obtained above for the different growth parameters. We assumed a minimal number of years necessary for individuals of each sex to reach L_∞ (Pauly 1991),

$$\lambda = \frac{3}{K} + t_0$$

A proxy of the instantaneous rate of natural mortality M for each sex was estimated using Alagaraja's equation described by Sparre and Venema (1995) as:

$$M = -\frac{\ln(0.01)}{\lambda}$$

where λ corresponds to longevity of *M. acanthurus* calculated as the time needed by a cohort to reach maximum average length (estimated by the von Bertalanffy growth equation). Natural mortality was estimated by determining when 99% of a cohort disappears from the population.

Lastly, we were interested in measuring variability in size at first maturity and sex ratio in *M. acanthurus* throughout the sampling period at the different study sites. Sex ratio was calculated as the number of males divided by the total number

Table 1. Body size of male and female *Macrobrachium acanthurus* captured and measured during the sampling period at Ribeira de Iguape River, São Paulo, Brazil

	Males	Non-ovigerous females	Ovigerous females	Total
Carapace length (mm)				
N	5012	4333	1569	10914
Minimum	3.6	2.5	9.7	2.5
Maximum	41.0	27.0	28.6	41.0
Mean ± s.d.	14.8 ± 8.8	8.6 ± 5.3	18.1 ± 2.5	12.8 ± 7.8
Total body length (mm)				
N	4489	2901	1535	8925
Minimum	11.0	10.4	27.6	10.4
Maximum	98.8	70.5	71.7	98.8
Mean ± s.d.	42.7 ± 19.9	30.2 ± 14.2	49.8 ± 5.8	39.8 ± 17.9

of individuals [males plus females] in the population. For each sampling date and site, the observed proportion of males to females was tested for deviations from a 1 : 1 sex ratio using a binomial test (Wilson and Hardy 2002). In females, size at first maturity (L_{50}) was estimated as the CL at which the probability of brooding embryos was 0.5 using logistic regression (Wilson and Hardy 2002). The analysis of size at first maturity was conducted on a per season rather than a monthly basis given the low frequency of females brooding embryos during most months (see Results).

Results

Considering all study sites and months, shrimps varied in body size between 2.5 and 41 mm CL with an average (±s.d.) of 12.8 (±7.8) mm CL (Table 1). A Kolmogorov–Smirnov test demonstrated significant differences in size–frequency distribution between the two sexes ($P < 0.05$). The median size (50-percentile) was 11 mm CL in males and ~8 mm CL in females. All percentiles were higher for males when compared with those for female shrimps (Fig. 2).

Males and females, both large and small, were found during most of the year at all study sites (Fig. 3).

The population-wise von Bertalanffy equations estimated for males and females were

$$L_t = 75.7 \cdot (1 - \exp^{-0.49 \cdot (t+0.11)})$$

and

$$L_t = 71.4 \cdot (1 - \exp^{-0.42 \cdot (t+0.77)}),$$

respectively. Natural mortality was slightly greater in males (0.77 year^{-1}) than in females (0.72 year^{-1}). In turn, longevity was slightly shorter in males (6 years) than in females (6.4 years) (Table 2).

Small shrimps (<9.0 mm CL) were intermittently found at all study sites (Fig. 3). However, they were more frequently observed at Iguape from April to August compared with the remaining study sites and months. Thus, recruitment in
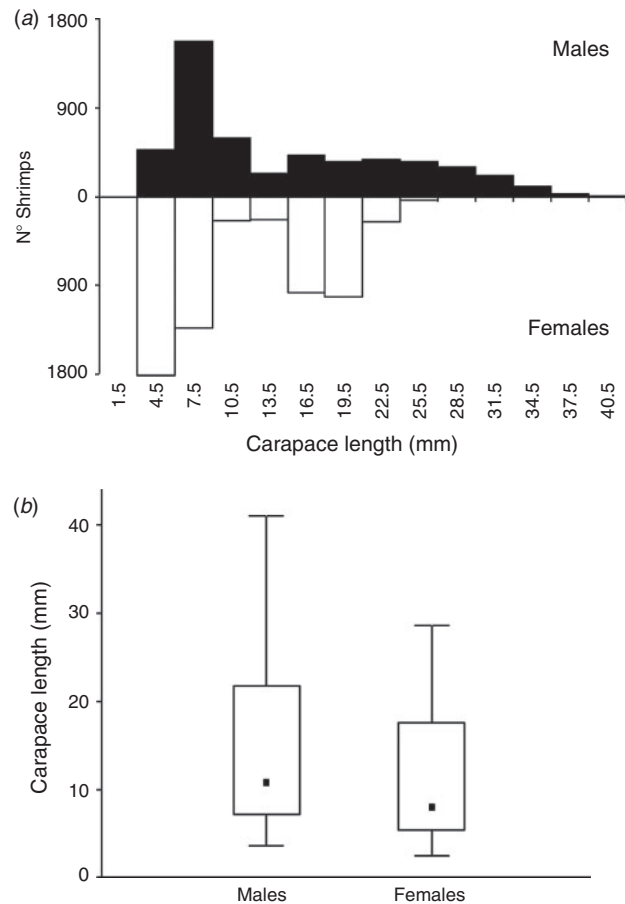

Fig. 2. (*a*) Size frequency distribution for the entire sample of male and female shrimps collected during 2007. (*b*) Box-plot showing the median body size (central point) of male and female shrimps collected during the entire study period. White boxes represent 50% of the observed data, and whiskers show 25% of the observed data.

M. acanthurus occurs throughout the river continuum, but is more intense in Iguape during the autumn and winter period.

The greatest differences in population dynamics of *M. acanthurus* occurred between Eldorado and Iguape, located the furthest from, and closest to, the coast, respectively (Table 2). In Iguape, the population was dominated by small male and female shrimps during the entire year (Fig. 3). The relative abundance of shrimps with intermediate and large body sizes increased only during October and December. By contrast, Eldorado was characterised by the presence of intermediate and large shrimps during most of the year. However, during the spring and summer months (September–December), small recruits were not found at this site (Fig. 3). The largest shrimps in our samples were collected at Eldorado. At Sete Barras and Registro, size–frequency distributions were more similar to those observed at Eldorado and Iguape, respectively. In Sete Barras, shrimps from all body size classes were present during most of the year but small shrimps were absent during October, November, and May. In Registro, the population was dominated by small male and female shrimps during the entire year but adults were common from October to April.
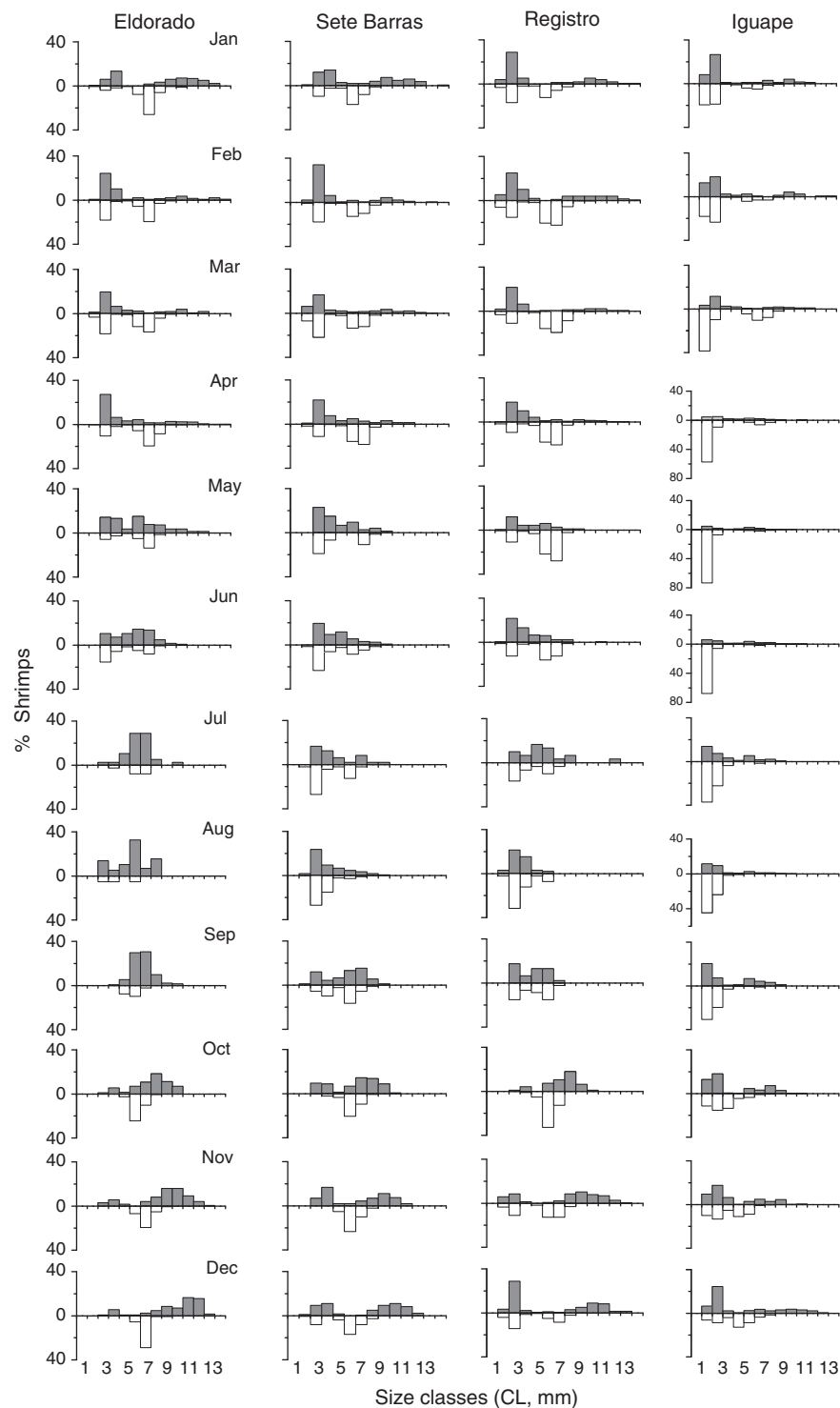
Fig. 3. Size frequency distribution of *Macrobrachium acanthurus* during 2007 in Eldorado, Sete Barras, Registro and Iguape in the Ribeira de Iguape River. Grey and white bars above and below the abscissa represent male and female shrimps, respectively.

The percentage of brooding females varied considerably during the study period at all study sites (Fig. 4). Brooding females dominated the population (>50%) from January to March but their relative abundance decreased substantially from April to June at all study sites. No brooding females were found during July and August at all study sites. Starting in September, the percentage of brooding females increased to dominate the population during October and December. Interestingly, from

Table 2. Summary of growth parameter estimates for male and female *Macrobrachium acanthurus* sampled at different study sites along the Ribeira de Iguape River, São Paulo, Brazil

L_∞, asymptotic carapace length; K, growth rate; t_0, age at zero length; T_{max}, longevity (years); M, natural mortality (annual). For Sete Barras and Eldorado, the dataset did not show convergence

	L_∞ (mm)	K (year^{-1})	t_0 (years)	T_{max}	M
All Localities					
Males	75.7	0.49	−0.10	6.0	0.77
Females	71.4	0.42	−0.77	6.4	0.72
Iguape					
Males	64.7	0.80	–	–	
Females	37.1	1.00	–	–	
Registro					
Males	33.5	0.10	–	–	
Females	23.9	0.50	–	–	

January to May, the percentage of brooding females at Iguape and Registro was low compared with that observed at Sete Barras and Eldorado during the same period. Nonetheless, this relatively low percentage of brooding females is explained by the relatively high abundance of small juvenile females at these two sites during the same months. Thus, *M. acanthurus* reproduces seasonally throughout the studied river portion and there is no indication of females moving towards the mouth of the river during the most intense reproductive period.

Size at first maturity varied between 12.0 mm CL (95% confidence intervals [CI] = 11.2–12.7 mm CL) at Iguape and 23.3 mm CL (CI = 20.1–n.a. mm CL) at Eldorado (Table 3). Size at first maturity was invariably attained at smaller body sizes during the summer and spring seasons than during the winter and autumn seasons at all study sites (Fig. 5).

Sex ratios varied between 0.14 (May, at Iguape) and 0.85 (August, at Eldorado) during the study period. Equal sex ratios were observed during most of the year at Sete Barras and Registro. At Eldorado, located the farthest away from the coast, sex ratio was skewed towards males during most of the year (Fig. 6). In turn, at Iguape, located the closest to the coast, sex ratio was skewed towards females during most of the year (Fig. 6).

Discussion

In the shrimp *M. acanthurus*, reproduction at the Ribeira de Iguape River is seasonal, peaking during the warmer months of the year, decreasing during spring and autumn, and almost completely ceasing during the coldest months of the year (July–September). Furthermore, seasonal reproductive activity did not vary much among study sites. Importantly, females carrying embryos in all stages of development were found at all study sites. Also, females of all body sizes were found year around at all study sites. Although, the sex ratio was biased in favour of females from March to September at Iguape, no evident disappearance of large reproductive females (brooding early and late embryos) was observed at this and other study sites located 10–100s of kilometres away from the coast that could have indicated a massive large-scale female reproductive migration. Altogether, the information above indicates that reproductive females of the amphidromous

shrimp *M. acanthurus* do not migrate considerable distances (i.e. hundreds of kilometres) down river to hatch larvae during the reproductive season.

That females of *M. acanthurus* hatch larvae kilometres away from the coast might imply, at first glance, considerable osmoregulatory stress and decreased survivorship for the larvae as they are expected to spend relatively long periods in fresh water before they reach the estuary. Nonetheless, laboratory experiments have shown that the early larval stages of *M. acanthurus* can and do survive in fresh water for up to 5–8 days and that the first zoea larva is lecitothropic (Choudhury 1971). Recent studies have also demonstrated that other diadromous species of *Macrobrachium* are transient hyper–hypo-osmoregulators (with isosmotic points at salinities ∼17–21) and that the early larval stages are those with the greatest osmoregulatory ability (Charmantier and Anger 2011). The above suggests that early larvae of *M. acanthurus* (and other congeneric species) are 'well equiped' from a physiological perspective to spend relatively long periods experiencing fully freshwater conditions during transportation to estuaries with proper conditions (more stable and higher salt concentrations) to complete development. Importantly, in the laboratory, larval development of *M. acanthurus* is successfully accomplished in salinities of 15–20 ppt (Choudhury 1971). In turn, *in vitro* larvae experiencing salinities above 33 and below 5 ppt, respectively, usually die within 10 days' exposure (Choudhury 1971). The above suggests that estuarine conditions represent an obligatory requisite for successful development in *M. acanthurus*.

Importantly, the greatest reproductive activity of *M. acanthurus* (November–March) coincides with the wet season at the studied latitude, characterised by strong river runoff and currents. Indeed, average water currents during the wet season at the Ribeira de Iguape River vary between 3.5 km h^{-1} and 4.2 km h^{-1} (measurements taken during spring and summer of the years 2004, 2005, 2011, and 2012 at Eldorado, Sete Barras, and Registro: information available at Departamento de Águas e Energia Elétrica do estado de São Paulo [www.daee.sp.gov.br]). Taking into account the average water currents above and the distance between Eldorado and the coast, larvae hatched at this study site located the farthest away from the coast (∼150 km) need ∼37 h for passive transportation to the estuary. Certainly, this period of passive larval transportation is much shorter than the longest period reported for larvae to survive when exposed to fully freshwater conditions (up to 5–8 days: Choudhury 1971). Overall, river conditions during the main reproductive season do facilitate larval transport in *M. acanthurus* and larvae are fully equipped to resist riverine conditions during passive transportation towards the estuary at the Ribeira de Iguape River.

The reproductive behaviour herein reported for *M. acanthurus* differs from that observed in several other congeneric species. Parental females migrate towards river mouths and/or estuaries to hatch larvae in *M. idella* (Mohamed and Rao 1971), *M. australiense* (Lee and Fielder 1979), *M. petersi* (Read 1985), *M. rosenbergii* (John 2009) and *M. ohione* (Bauer and Delahoussaye 2008; Rome *et al.* 2009; Olivier and Bauer 2011). On the other hand, the reproductive behaviour herein reported for *M. acanthurus* is similar to that observed in several other congeneric species. Females
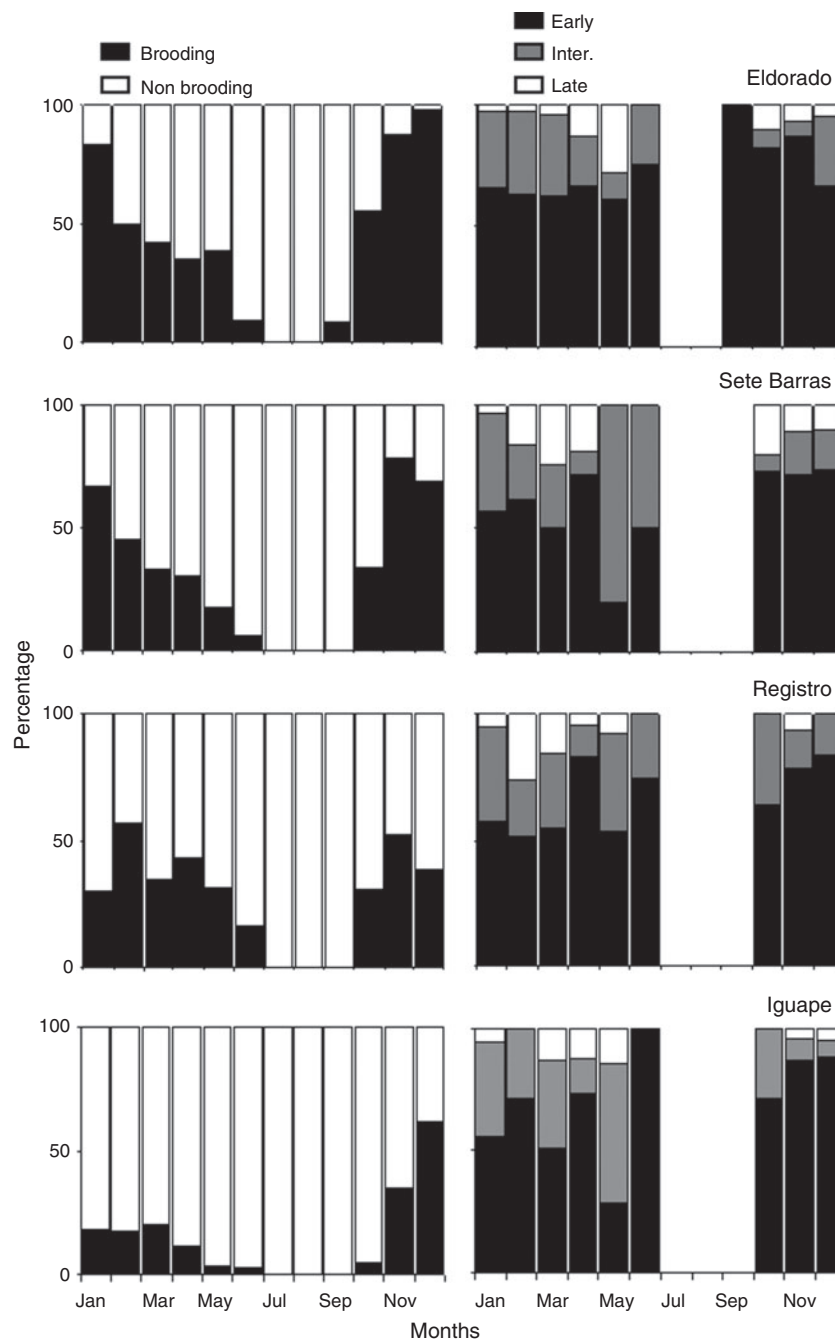
Fig. 4. Frequency of occurrence of brooding females of *Macrobrachium acanthurus* during 2007 in Eldorado, Sete Barras, Registro and Iguape in the Ribeira de Iguape River.

exhibit no obvious migrations and newly hatched zoea I larvae drift down river aided by water currents in *M. malcolmsonii* (Rao 1986; Prasad and Kanaujia 2006), *M. gangeticum* (Rao 1986; Prasad and Kanaujia 2006), *M. nobilii* (Balasundaram and Pandian 1982), *M. carcinus* (March *et al.* 1998), *M. crenulatum* (March *et al.* 1998), *M. faustinum* (March *et al.* 1998), *M. heterochirus* (March *et al.* 1998), and *M. lanchesteri* (Phone *et al.* 2005). This life-history variability suggests that *Macrobrachium* shrimps can be used as a model system to understand

those conditions driving amphidromy in organisms that have colonised freshwater environments.

This study suggests that *M. acanthurus* grows quickly. Females attain 23 and 37 mm CL two and 12 months after larval settlement, respectively. Also, males attain a smaller body size than females: 12 and 32 mm CL, two and 12 months after larval settlement, respectively. Previous studies have reported rapid growth rates in other species of *Macrobrachium* (Kanaujia *et al.* 1997; Romero and Silva 2008; Alhassan and Armah 2011)

(see review in Table 4). Also, sex-specific growth rates, as shown here for *M. acanthurus*, have been reported before in other crustaceans (e.g. penaeid shrimps: Andrade and Pérez 2004; caridean shrimps: Sánchez-Palacios *et al.* 2008). Our

Table 3. Size at the onset of first maturity (estimate ± confidence limits [CL]) in *Macrobrachium acanthurus* during spring, summer, autumn and winter 2007 in Eldorado, Sete Barras, Registro and Iguape

	Size at first maturity		
	Estimate	Lower CL	Upper CL
Eldorado			
Spring	16.9	16.2	17.5
Summer	14.1	12.8	15.1
Autumn	18.6	17.8	19.5
Winter	23.3	20.1	na
Sete Barras			
Spring	16.3	14.7	17.7
Summer	13.4	12.5	14.2
Autumn	17.7	16.8	18.7
Winter	22.4	19.8	40.2
Registro			
Spring	16.9	16.1	17.6
Summer	14.9	14.0	15.8
Autumn	19.5	18.4	21.0
Winter	21.0	19.3	26.9
Iguape			
Spring	15.3	14.5	16.2
Summer	12.0	11.2	12.8
Autumn	18.4	17.6	19.2
Winter	19.5	17.8	21.9

results agree, but only partially, with those of Choudhury (1970) who reported an initial body size of 6.5 mm total body length (TL) and 27 mm TL for juveniles 40 days and two months after metamorphosis, respectively (data obtained from laboratory-reared specimens after larval development). Using previously published equations that relate CL to TL ($CL = 0.533 \times TL$ and $CL = 0.5043 \times TL$ in males and females, respectively: Albertoni *et al.* 2002), our results fit well with those previously reported by Choudhury (1970) for males but not for females. An overestimation of the t_0 parameter, herein reported to be 0.77 in females versus 0.11 in males, might explain differences in initial body size between our study and that of Choudhury (1970). Such initial body size is expected to be similar in males and females. Studies examining differences in initial body size (i.e. at metamorphosis) between the two sexes are needed to reveal whether or not differences in growth rate between the two sexes are natural or due to parameter overestimation.

In *M. acanthurus*, males grow more slowly than females but attain larger average and final body sizes. This pattern of sexual dimorphism (males > females) agrees with previous observations on the same species (see Table 4 and references therein). Nonetheless, the maximum body sizes herein reported for males and females are larger than those reported before for the same species. For instance, Valenti *et al.* (1987) reported maximum body sizes of 138 mm TL (or 69.5 mm CL calculated using the equation that relates CL to TL: Albertoni *et al.* 2002) and 108 mm TL (or 57.6 mm CL) in males and females, respectively. The reasons for dissimilarities between our results and those of Valenti *et al.* (1987) remain to be addressed. Sexual dimorphism is also known in several other species of *Macrobrachium* (e.g. *M. rosenbergii*: Sampaio and Valenti 1996; *M. olfersi*: Mossolin and Bueno 2003; *M. iheringi*: Fransozo *et al.* 2004).
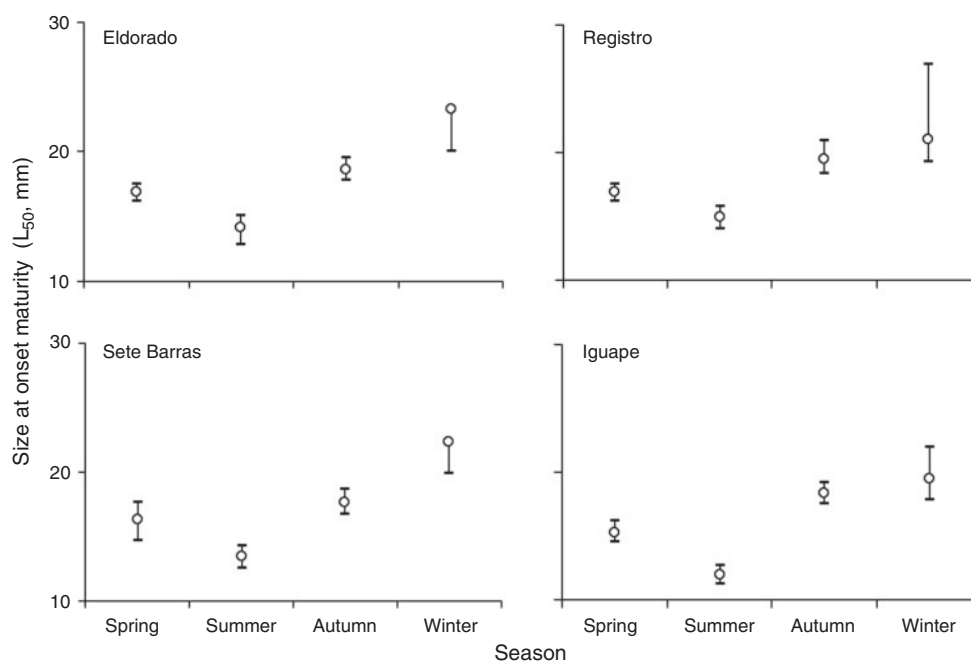

Fig. 5. Size at the onset of first maturity (estimate ± confidence intervals) in *Macrobrachium acanthurus* during summer, spring, autumn, and winter 2007 in Eldorado, Sete Barras, Registro and Iguape.
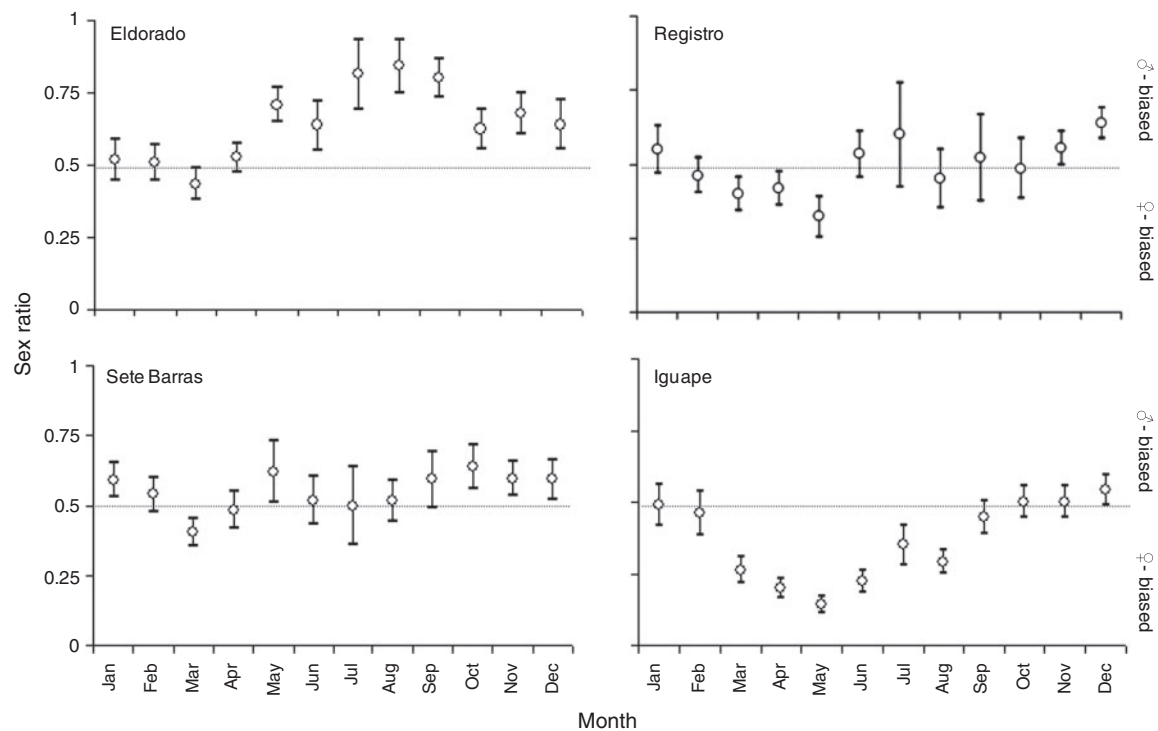
Fig. 6. Sex ratio (mean ± standard error) from January to December 2007 in Eldorado, Sete Barras, Registro and Iguape.

Table 4. Summary of growth parameter estimates in different species of *Macrobrachium*

$L\infty$ CL, asymptotic carapace length (mm); $L\infty$ TL, asymptotic total body length (mm); K, growth rate (year^{-1}); Φ', growth performance index ($\Phi' = \log(K) + 2\log(L\infty)$); M, natural mortality; T_{max}, longevity

Species	Sex	$L\infty$ CL	$L\infty$ TL	K	M	T_{max}	Φ'	Locality	Reference
M. acanthurus	Male	75.7		0.49	0.77	6.0	3.45	Ribeira de Iguape River, São Paulo, Brazil	Present study
	Female	71.4		0.42	0.72	6.4	3.33		
	Male		138	0.197			2.66	Ribeira de Iguape River, São Paulo, Brazil	Valenti *et al.* 1987
	Female		108	0.200			3.37		
	Total		212	0.24			4.03	Rio Palizada, Campeche, Mexico	Román-Contreras and Campos-Lince 1993
M. amazonicum	Total		102.5					Ceará, Brazil	Guest 1979
	Total		105.1	0.68	0.92		3.87	Belém, PA, Brazil	Silva *et al.* 2007
	Male		123.7	1.36			4.32		
	Female		140.3	0.67			4.12		
M. equidens	Total		107.1	1.25	2.69	2.5	2.16	Cross River estuary, Nigeria	Nwosu 2008
M. intermedium	Male					1.5		New South Wales, Australia	Gray 1991
M. macrobrachion	Total		129	1.79	3.36	1.7	2.48	Cross River estuary, Nigeria	Enin 1995
	Male		141.3	1.21	2.44	2.5	4.38	Cross River estuary, Nigeria	Nwosu *et al.* 2007
	Female		117.5	1.60	3.09	2	4.34		
M. minhoacanus	Total		176			3		Oaxaca, Mexico	Romero and Silva 2008
M. rosenbergii	Male		420	0.98	1.57		5.24	Vembanad Lake, India	Harikrishnan and Kurup 1997
	Female		308	1.10	1.71		5.02		
M. völlenhovenii	Total	54	164	3.19	3.61	0.94	2.93	Lobe River, Kribi, Cameroon	Gabche and Hockey 1995
	Total		180[A]	0.91	1.97	3	4.46	Côte d'Ivoire, West Africa	Etim and Sankare 1998
	Total		236.5	1.14	2.14	2.10	2.80	Asu River, south-east Nigeria	Okogwu *et al.* 2010
	Total		142	1.0	2.20	3	2.3	Dawhenya Impoundment, Ghana	Alhassan and Armah 2011
	Male		213.6	1.24	2.21	2.42	2.75	Cross River estuary, Nigeria	Nwosu and Wolfi 2006
	Female		198.3	1.25	2.27	2.40	2.69		

[A]Length from the base of the eye stalk to the tip of the telson.

Our results in *M. acanthurus* support the notion that classical sexual dimorphism (males > females) is more common than reverse sexual dimorphism (e.g. females > males in *M. ohione*: Bauer and Caskey 2006) within the genus. In *M. acanthurus*, sexual dimorphism might be explained by a 'large male advantage'. Large body size might increase male mating opportunities if monopolisation of receptive females occurs via overt aggression, as reported before in other congeneric shrimps (e.g. *M. rosenbergii*: Sampaio and Valenti 1996). Experiments examining male mating tactics in the presence and absence of receptive females might help reveal the conditions that explain sexual dimorphism in *M. acanthurus*.

Based on logistic regression, size at first sexual maturity (CL_{50}) in females of *M. acanthurus* varied between 12.0 and 23.3 mm CL among sites throughout the study period. Importantly, visual examination of the data indicated no major differences in size at first maturity among study sites. However, size at first maturity was invariably attained at smaller body sizes during summer and spring than during winter and autumn at all study sites. Studies on seasonal variation in size at first maturity are rare among crustaceans, including freshwater shrimps. However, shifts in size at first maturity in fish are commonly reported (Beacham 1983; Gerritsen *et al.* 2003; Armstrong *et al.* 2004). Among shrimps, Oh *et al.* (1999) compared size at first maturity in *Crangon crangon* over four years and observed no major differences in this parameter through time. On the other hand, in agreement with our results in *M. acanthurus*, size at first maturity is reported to decrease during warm months and when reproduction is intense in other shrimps (e.g. *Parhippolyte misticia*: Onaga *et al.* 2012). Laboratory experiments have demonstrated that temperature and photoperiod affect the timing of size at (female) maturity in protandric simultaneous hermaphroditic shrimps (Bauer 2002). In *M. acanthurus*, a decrease in size at first maturity during the main breeding season (when environmental conditions are optimal for reproduction) might be adaptive if early-maturing females produce more broods than late-maturing females. Additional experimental studies are needed to understand abiotic and biotic conditions driving the timing of size at first sexual maturity in *M. acanthurus*.

We have reviewed previous studies reporting size at first sexual maturity in *M. acanthurus* along the Brazilian coast and found that our estimates (12.0–23.3 mm CL) are considerably larger to those reported by Anger and Moreira (1998) (6.9 mm CL) for *M. acanthurus* inhabiting São Sebastião, northern coast of São Paulo State. *A posteriori*, we believe that our values are overestimated due to the relatively large number of adult females not brooding embryos observed at each study site throughout the year. Indeed, the body size of the smallest female carrying eggs observed during this study was 9.7 mm CL. This value is similar to that reported by Anger and Moreira (1998). Overall, uncertainty in size at maturity might have important implications for fisheries stock assessment (J. Anderson and J. A. Baeza, unpubl. data). We argue in favour of studies constructing an age-structured model to evaluate the effect of uncertainty in size at maturity on population assessments of *M. acanthurus*.

In *M. acanthurus*, sex ratio varied considerably (between 0.14 and 0.85) among study sites throughout the study period.

Equal sex ratios were observed during most of the year in Sete Barras and Registro. At Eldorado, located the farthest away from the coast, the population was dominated by males during most of the year. In turn, at Iguape, located the closest to the coast, sex ratios were skewed towards females during most of the year. The differences in sex ratio among localities are puzzling. For gonochoric (separate sexes) species such as *M. acanthurus*, sex allocation theory predicts equal sex ratios as parents should produce an equal number of male and female offspring because of frequency-dependent selection against the more common sex in the population (Fisher 1930). However, female or male skewed population-wise sex ratios have been reported before in other shrimps (Alon and Stancyk 1982; Bauer and Abdalla 2001; Fransozo *et al.* 2004; Mejía-Ortíz and Alvarez 2010) and major causes for imbalances in sex ratio among marine invertebrates include sex-specific growth and/ or mortality rates (Wenner 1972), sex-dependant migration (Wenner 1972; Costa *et al.* 2010), sex-dependant mating behaviours (Willson and Pianka 1963; Castilho *et al.* 2008), and/or sampling error (Bolaños *et al.* 2012). Sex-dependant migration does not appear to occur in the studied river. Also, we have taken precautions during this study to avoid any sampling error that might result in sex ratio biases. However, we cannot discard sex-specific growth rates, mortality rates, and/or mating behaviours driving biased sex ratios in some but not in other localities.

Here we have shown that reproduction is seasonal in the amphidromous shrimp *M. acanthurus* and that females do not migrate down river towards the estuary to hatch larvae. Indeed, we have shown that parental females of *M. acanthurus* liberate offspring throughout the river, even when inhabiting sites located hundreds of kilometres from the coast. Also, population-level reproductive parameters, including size at first maturity and sex ratio, vary considerably at moderate spatial scales throughout the year. The information generated in this study needs to be considered in assessing stocks and establishing sustainable management plans for *M. acanthurus* in south-eastern Brazil.

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