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ORIGINAL ARTICLE

Larval export strategy as an indication of ontogenetic migrations towards open sea of the fiddler crab *Leptuca leptodactyla* (Rathbun, in Rankin, 1898) (Crustacea, Ocypodidae) from Guaratuba Bay, southern Brazil

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ABSTRACT

The influence of salinity on the survival of the larvae of *Leptuca leptodactyla* (Rathbun, in Rankin, 1898) from zoea (Z) to megalopa (M) stage was analyzed in order to deduce the larval dispersal strategy of the species. Larvae were obtained from 10 ovigerous females captured in the mangrove of Guaratuba Bay, southern Brazil. Five salinity treatments were conducted from 0 to 35 PSU (S0, S5, S15, S25 and S35). The larvae were individually raised in plastic cell culture plates, totaling 120 experimental units per treatment, kept under natural photoperiod (12:12 h) and constant water temperature (26.3 ± 0.82°C), and fed with microalgae, rotifers and *Artemia* nauplii. While all larvae died at S0, S5 and S15, complete larval development until the M stage was only observed at S25 and S35. The highest survival rate was recorded at S35 (18 M from 120 newly-hatched Z, survivorship 15%) and the lowest at S25 (2 M, 1.66%). No significant difference in the total duration was observed between S25 (28.5 ± 0.70 days) and S35 (23.61 ± 3.05 days). The life cycle of *L. leptodactyla* is based on a larval exportation strategy as they need to perform ontogenetic migrations to the coastal area.

KEYWORDS

Larval dispersal, larval survival, salinity treatment.

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Introduction

Most brachyuran crabs have a biphasic life cycle, consisting of a variable number of planktonic stages that precedes their benthic existence (Anger, 2001; 2006). The larval development in the plankton may last from several days to weeks, or even months, according to the species (Morgan, 1995; Anger, 2001; 2006).

During ontogenesis, larvae are exposed to an array of ecological variables. Physical and chemical variables such as temperature, salinity, dissolved oxygen, food availability, light, turbidity, pollutants, pH, distance from hatching sites, tidal cycle, speed and direction of marine currents, will influence their chances of survival, development, dispersal and recruitment. In addition, biotic variables such as predation and competition are also significant in this regard (Levinton, 1982; Sastry, 1983; Morgan, 1990; 1995; Epifanio and Garvine, 2001; Anger, 2001; 2003; 2006; Fernandes *et al.*, 2002; Queiroga and Blanton, 2005; Simith and Diele, 2008).

Fully marine species are adapted to relatively stable environmental conditions and usually do not tolerate wide oscillations in physicochemical variables. However, the species that evolved in coastal areas, estuaries and other transient habitats are constantly exposed to sudden changes in temperature and salinity, among other abiotic variables. Therefore, physiological and behavioral adaptations to environmental variability are particularly pronounced in these organisms (Anger, 2001).

Salinity is considered the most important abiotic variable for these larvae, especially for estuarine species, since it usually oscillates in response to tides and continental freshwater inlets. The newly hatched larvae may suffer stress due to salinity variation with significant impact on survival, development, growth, morphology, molting cycle, feeding activity, metabolism, and even its biochemical composition (Anger *et al.*, 1998; Anger, 2001; 2003; Giménez and Anger 2001; Torres *et al.*, 2002; 2008; Silva *et al.*, 2012). The salinity tolerance of larval decapods depends largely on the capability to actively regulate the internal concentration, in contrast to adult decapods that reduce the permeability of their integument by acquiring a thick and heavy cuticle (Anger, 2001).

Coastal decapods may present distinct evolutionary strategies to cope with the prevailing salinity of a given estuarine habitat. Less tolerant larvae may be forced to migrate to coastal marine areas, such as the continental shelf, or even the open seas, where the environment is more stable, with higher salt concentrations. On the other hand, larvae of certain species evolved the ability to withstand oligohaline waters, and they can be retained within the same estuary where the adult population lives (Sandifer, 1975; Strathmann, 1982; Morgan, 1995; Wooldridge and Loubser, 1996; Anger, 2001; Luppi *et al.*, 2003).

Most estuarine species export their larvae to adjacent marine areas while only a few retain their larvae within the parental habitat (Anger, 2001; Paula *et al.*, 2004). Among the brachyuran species that show larval retention mechanisms are *Rhithropanopeus harrisii* (Gould, 1841) (Cronin, 1982), *Neohelice granulata* (Dana, 1851) (Cervellini, 2001) and *Minuca mordax* (Smith, 1870) (Martins, 2014).

The ability of larvae to tolerate different salinity levels is an indicator of the type of dispersion strategy adopted by the species: larvae exportation or larvae retention (Strathmann, 1982; Anger *et al.*, 2008). Larvae of *Minuca vocator* (Herbst, 1804) cultivated in salinities of 0, 5, 10, 15, 20, 25 and 30 PSU, showed 100% mortality in salinities below 5 PSU. This mortality indicates that *M. vocator* has a dispersion strategy of exporting its larvae to higher salinity coastal waters through ebb tide currents, returning to estuarine area as megalopa for recruitment (Simith *et al.*, 2012).

Although the average salinity content in areas with adult populations of *Leptuca leptodactyla* (Rathbun, in Rankin, 1898) is known, no information is available about the suitable salinity for larval development in pelagic environments. The present work aims to analyze the tolerance of the larvae of *L. leptodactyla* when cultivated in different salinities, for purposes of inferring its larval dispersal strategy.

Leptuca leptodactyla is a fiddler crab with a wide geographic distribution in the Western Atlantic Ocean coast, occurring from Florida (USA) to the southern Brazilian state of Santa Catarina, including Gulf of

Mexico, Antilles and Venezuela (Laurenzano *et al.*, 2016). As most fiddler crabs, *L. leptodactyla* is a semi-terrestrial species. It is usually found in the estuarine intertidal zone that is flooded by waters with salinities higher than 18 PSU (mean = 21.3 ± 2.9 PSU, see review in Thurman *et al.*, 2013). Its populations live outside of mangrove forest but on sandy tidal flats that are contiguous to it, often partially covered by cordgrass *Spartina alterniflora* (Masunari, 2006). Due to the occurrence of adult populations in saltier areas of Guaratuba Bay, we hypothesized that *L. leptodactyla* larvae are exported to the open sea environment.

Material and Methods

Collection of ovigerous females

The zoea larvae were obtained from 23 ovigerous females of *L. leptodactyla* that were collected in the vicinity of the mangrove area of Barra do Saí, Hydrographic Basin of Guaratuba, southern Brazil (26°00'25"S 48°36'25"N), during the low tide on 10 January 2017. Burrows in the occurrence site of the population were explored with the aid of a garden shovel, and only females bearing a dark grayish colored egg mass were manually captured, as this color indicates proximity of egg hatching (personal observation).

These females were transported in plastic containers to the Center for Marine Aquaculture and Repopulation (CAMAR) of Federal University of Paraná (UFPR), a marine aquaculture laboratory situated at Leste Beach, municipality of Pontal do Paraná, southern Brazil. The bottom of the containers had 5 cm depth of water from the collection site, lined with sandy-muddy substrate and with added mangrove leaves.

CAMAR has access to large amounts of 32–34 PSU water of oceanic quality by the use of its pumping station situated close to the shore. Before utilization in experiments, this collected water is filtered to 25 µm, disinfected with 5 ppm of sodium hypochlorite for 24 hours and neutralized with sodium thiosulfate.

The females were washed with filtered seawater for residue removal and transferred to a plastic tank (64 cm × 31 cm) until egg hatching. The tank was constantly maintained with 10 cm depth of clean marine water and under constant aeration, at room temperature of 26.5°C ± 0.87 and a natural photoperiod of 12:12 hours. Pieces of small PVC pipe were added to serve as shelters, as well as a partially submerged thick plastic mesh net to serve as a "dry substrate" to allow the crabs to leave the water if they wish. The females were maintained under constant surveillance until egg hatching, without any food.

Experimental design

The treatments consisted of five different salinities: 0 PSU (S0); 5 PSU (S5); 15 PSU (S15); 25 PSU (S25) and 35 PSU (S35). The first four treatments simulated the salinities frequently observed in estuarine systems and the last one, the oceanic condition. All experiments were exclusively performed with artificial sea water; natural sea water was only used for maintenance of ovigerous females.

The artificial sea water was prepared with refined artificial sea salt without iodine (Blue Treasure®) dissolved in distilled water, in the proportion of the desired salinity, with the aid of a precision scale and thereafter checked with an optical refractometer (Veegee, Model STX-3).

Of the 23 ovigerous females collected, only ten synchronously released larvae on 11 January 2017; only these larvae were taken for the experiments.

The newly hatched larvae were attracted with a spotlight, pipetted from the hatching tank to a one liter glass beaker containing artificial seawater with salinity 35. Prior to the transference to experimental polyethylene container units, the larvae were acclimated to the forthcoming treatment salinities. In the S35 vessel, the transference was direct, as it had the same salinity as the hatching water. In the remaining treatments (S0, S5, S15 and S25), they were gradually acclimated to lower salinity following Foskett (1977), Charmantier and Charmantier-Daures (1991) and Simith *et al.* (2014).

After acclimatization the larvae were attracted again with a light source and transferred to experimental units contained in 24-well acrylic plates. The internal diameter of each well measured 16.25 mm with a total volume of 3.5 ml. The wells were filled with 3.0 ml of

water with the salinity concentration set for each of the five respective treatments; 120 larvae per treatment for a total of 600 experiment units.

The larvae were maintained individually in each well for more precise monitoring of the developmental stages and collection of exuvia (Fig. 1). Only active larvae were chosen for the experiments in order to ensure a healthy initial condition.

Experimental units were maintained in a room under controlled photoperiod (12:12h) and temperature (air = 26.5 ± 0.87°C and water = 26.3 ± 0.82°C). From the ZI to ZIII stage, larvae of all treatments were daily fed with three species of microalgae *Chaetoceros calcitrans* (300,000 cells.ml^{-1}) *Tetraselmis suecica* (50,000 cells.ml^{-1}) and *Thalassiosira weissflogii* (300,000 cells.ml^{-1}) and with the rotifer *Brachionus plicatilis* Müller, 1786 (10 individuals.ml^{-1}).

From ZIII until M stage, the former food was supplemented with newly-hatched *Artemia* nauplii (0.6 individuals.ml^{-1}), according to the protocol used in larviculture of other fiddler-crab species (Rieger, 1996; 1997; 1998; 1999; Simith *et al.*, 2014). The *Artemia* nauplii were obtained by decapsulation and incubation following standard methods (Leger and Sorgeloos, 1992; Barbieri and Ostrensky, 2001). *Artemia* Leach, 1819 was provided only at the nauplius stage, when it is still small but rich in yolk reserves.

To avoid interference from solutions containing food-organisms to the experiment units, feeding was carried out as follows: rotifer and *Artemia* solutions were filtered with a 100 µm mesh sieve and washed with the same salinity as the destination units. Microalgae solutions were diluted with deionized water until reaching as close as possible to the salinity of the respective treatment.

The water of the larval units was 100% renewed daily by transferring the larva to a new vessel containing clean water and fresh food, with the aid of a pipette. The dead larvae were counted, fixed and preserved in 75% alcohol with glycerin, daily. Exuviae from all culture units were observed under a stereomicroscope (Fig. 1) in order to recognize the larval stage.

The experiment was concluded when no live zoeas were found in the experimental treatments either because they reached megalopa stage or had died.

Figure 1. *Leptuca leptodactyla*. Inspection of the presence of exuviae and counting of dead larvae under stereomicroscope. Each well contained one larva.

Data analysis

Data from salinity experiments were analyzed by Log-Rank test (Ayres *et al.*, 2005). As data about the duration of larval development did not present a normal distribution (Kolmogorov-Smirnov test $p > 0.05$), they were analyzed with a Kruskall-Wallis Anova and Tukey *post hoc* test. All analyses were performed using BioEstat 5.0 software (Ayres *et al.*, 2007).

Results

Effect of salinity on larval survival and metamorphosis

The salinity concentration influenced the survival rates of zoea larvae ($p < 0.001$). Comparisons between tested concentrations showed significant differences, except in treatments S0 and S5 (Tab. 1).

Table 1. *Leptuca leptodactyla*. Log-Rank test result applied to detect differences in larval survival among the five salinity treatments. S0: 0 PSU; S5: 5 PSU; S15: 15 PSU; S25: 25 PSU and S35: 35 PSU. * statistically not significant

Treatment	x^2	p
S0 x S5	1.2953	0.2551*
S0 x S15	581.5093	< 0.0001
S0 x S25	896.9855	< 0.0001
S0 x S35	1032.8663	< 0.0001
S5 x S15	584.4586	< 0.0001
S5 x S25	904.4010	< 0.0001
S5 x S35	1042.1087	< 0.0001
S15 x S25	313.2062	< 0.0001
S15 x S35	582.1080	< 0.0001
S25 x S35	104.1864	< 0.0001

Ontogenetic larval development of *L. leptodactyla* was composed of five or six stages of zoea (Z) and one of megalopa (M). The complete development to metamorphosis was only observed in treatment S25 (2 M obtained from 120 newly hatched Z, or 1.66% of survivorship) and at S35 (18 M, or 15%). In the remaining treatments (S0, S5 and S15), all larvae died as Z at various stages (Figs. 2, 3).

In the treatments from S0 to S15, the survival time tended to be directly proportional to the salinity concentration. In S0, all larvae died within 24 hours as ZI, without suffering ecdysis to next stage. In S5, they survived for 48 hours, with the highest mortality rate recorded in the first 24 hours (117 deaths of 120 Z). The remaining three larvae survived for up to 48 hours, but they also did not undergo molting. In S15, the larvae survived for 22 days and underwent molting until the ZIII stage (Figs. 2, 3).

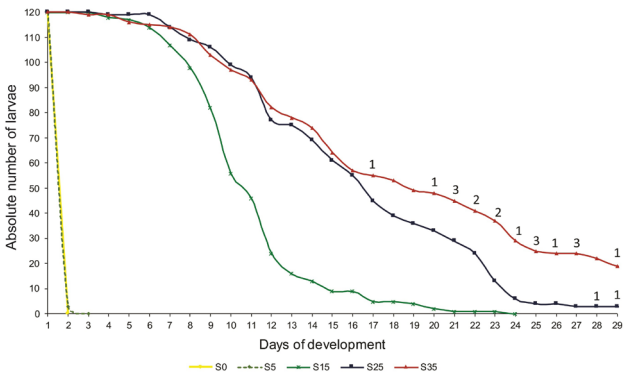

Figure 2. *Leptuca leptodactyla*. Survival curves (in absolute number) of the larvae during the five salinity treatments. S0: 0 PSU; S5: 5 PSU; S15: 15 PSU; S25: 25 PSU and S35: 35 PSU. The numbers above the survival curves of S25 and S35 indicate the number of zoea that underwent ecdysis to megalopa stage.

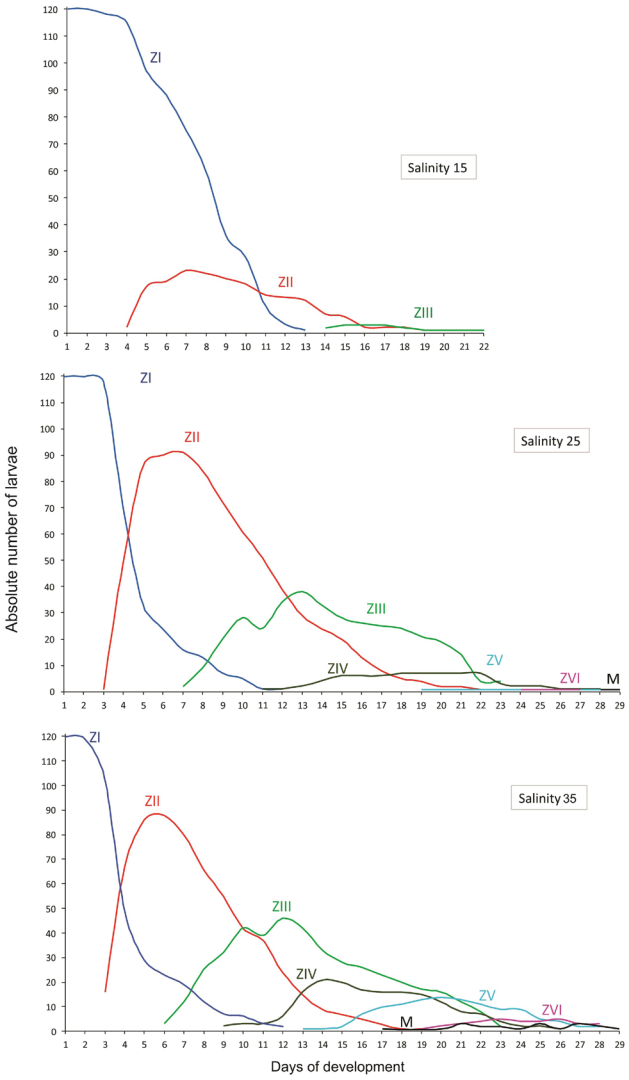

Figure 3. *Leptuca leptodactyla*. Survival curves (in absolute number) and duration of the zoea stages (in days) of the larvae submitted to treatments S15, S25 and S35.

Duration of larval development

Larvae that were raised at S15 required a significantly longer period to reach the ZII and ZIII stages in comparison to S25 and S35 (Tab. 2). However, all larvae died before reaching ZIV at S15. From ZIV until M, no significant differences were observed between S25 and S35.

Furthermore, the ZIII stage first appeared on the 6th day after the beginning of the experiment at S35, on the 7th day at S25 and only on the 14th day at S15 (Fig. 3). All the remaining stages were only observed at S25 and S35, whose ecdysis occurred almost synchronously. In these last two treatments, 27 larvae reached stage ZV, two at S25 and 25 at S35 (Tab. 2).

Although M larvae were raised from both ZV and ZVI, only five from a total of 20 M (one at S25 and four at S35) originated from a ZVI stage (Tab. 2).

There was a significant difference (Kruskall-Wallis; H = 4; 3707; d.f. = 1; $p < 0.05$; Tukey = 4.8889; Q = 3.1232; $p < 0.05$) in the total duration of complete ontogenetic larval development, from ZI to M, between S25 and S35 (Tab. 3). Only two M larvae were obtained at S25 after an average of 28.5 ± 0.70 days, while at S35, 18 M larvae emerged between the 17th and 29th day, averaging 23.61 ± 3.05 days (Figs. 2, 3).

Table 2. *Leptuca leptodactyla*. Daily individual monitoring of development of all larvae that attained megalopa stage or at least zoea V and zoea VI in the experiments. The first two lines refer to S25 and the remaining to S35.

	Days of culture																											
Larvae	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
1	I	I	I	I	II	II	II	II	II	II	II	III	III	III	III	III	III	IV	IV	IV	IV	IV	V	V	V	V	V	V	M
2	I	I	I	II	II	II	II	III	III	III	III	III	IV	IV	IV	IV	IV	IV	V	V	V	V	V	VI	VI	VI	VI	M	
1	I	I	I	II	II	II	II	II	III	III	III	III	III	IV	IV	IV	IV	IV	IV	IV	IV	IV	V	V	V	V	V	V	M
2	I	I	I	I	II	II	II	II	II	II	II	III	III	III	III	III	IV	IV	IV	IV	V	V	V	V	V	V	M		
3	I	I	I	II	II	II	II	III	III	III	III	III	IV	IV	IV	IV	IV	IV	IV	IV	V	V	V	V	V	M			
4	I	I	II	II	II	II	III	III	III	III	III	III	III	IV	IV	IV	IV	IV	V	V	V	V	V	V	M				
5	I	I	I	II	II	II	II	II	III	III	III	III	III	III	IV	IV	IV	IV	IV	V	V	V	V	V	M				
6	I	I	I	II	II	II	II	II	II	II	III	III	III	III	III	IV	IV	IV	IV	V	V	V	V	V	M				
7	I	I	I	II	II	II	II	III	III	III	III	III	IV	IV	IV	IV	V	V	V	V	V	V	M						
8	I	I	II	II	II	II	II	III	III	III	III	III	IV	IV	IV	IV	V	V	V	V	V	M							
9	I	I	I	II	II	II	II	III	III	III	III	III	IV	IV	IV	IV	V	V	V	V	V	M							
10	I	I	II	II	II	II	III	III	III	III	III	IV	IV	IV	IV	V	V	V	V	V	M								
11	I	I	I	II	II	II	II	III	III	III	III	III	IV	IV	IV	V	V	V	V	V	M								
12	I	I	I	II	II	II	II	III	III	III	III	III	IV	IV	IV	V	V	V	V	V	M								
13	I	I	II	II	II	III	III	III	III	IV	IV	IV	IV	IV	V	V	V	V	V	M									
14	I	I	II	II	II	III	III	III	IV	IV	IV	IV	V	V	V	V	M												
15	I	I	I	II	II	II	II	II	III	III	III	III	III	IV	IV	IV	IV	IV	V	V	V	V	VI	VI	VI	VI	M		
16	I	I	I	II	II	II	II	II	III	III	III	III	IV	IV	IV	IV	IV	V	V	V	V	VI	VI	VI	VI	VI	M		
17	I	I	I	II	II	II	II	III	III	III	III	III	IV	IV	IV	V	V	V	V	VI	VI	VI	VI	M					
18	I	I	I	I	II	II	II	II	III	III	III	III	IV	IV	IV	V	V	V	VI	VI	VI	VI	M						
19	I	I	I	II	II	II	II	II	II	II	II	III	III	III	III	III	IV	IV	IV	IV	V	V	V	V	V	VI	VI	VI	VI
20	I	I	I	I	I	II	II	II	II	II	II	III	III	III	III	III	IV	IV	IV	IV	IV	V	V	V	V	V	VI	VI	
21	I	I	I	I	II	II	III	III	III	III	III	III	IV	IV	IV	IV	IV	IV	V	V	V	V	VI	VI	VI	VI	VI	VI	
22	I	I	II	II	II	II	III	III	III	III	III	IV	IV	IV	IV	IV	V	V	V	V	VI	VI	VI	VI	VI	VI			
23	I	I	I	II	II	II	II	II	II	II	III	III	III	III	IV	IV	IV	IV	IV	IV	IV	IV	IV	IV	IV	V	V	V	
24	I	I	I	II	II	II	II	II	II	II	II	III	III	III	III	IV	IV	IV	IV	IV	IV	IV	V	V					
25	I	I	II	II	II	II	II	III	III	III	III	III	III	IV	IV	IV	IV	IV	IV	V	V	V							

Table 3. *Leptuca leptodactyla*. Mean and Standard Deviation (SD) of the duration (in days) of the larval stages at the treatments S15, S25 and S35. No ZI larvae underwent to next stage at S0 or S5.

Treatment		Zoea I	Zoea II	Zoea III	Zoea IV	Zoea V	Zoea VI
S15	Mean	4.34	8.33	–	–	–	–
	SD	0.88	1.15	–	–	–	–
S25	Mean	3.60	6.01	5.77	5.5	5.5	4
	SD	0.82	1.69	1.48	0.70	0.70	0
S35	Mean	3.18	5.80	5.43	5.04	4.81	4.25
	SD	0.82	2.04	2.06	1.94	0.79	0.5

Discussion

Effect of salinity on larval survival and metamorphosis

In Guaratuba Bay (southern Brazil), the mean salinity oscillates from 0.33±1.15 PSU (inner part of the bay) to 23.63±4.25 PSU (near the mouth of the bay) during low tides (Masunari, 2006). Therefore, in this estuary the salinity hardly reaches the optimum value (=35 PSU) for survival of *L. leptodactyla* larvae, although adult populations of this species are usually distributed in polyhaline tidal flats near the mouth of the bay. At most, this optimum salinity could be observed for a short time during the invasion of coastal waters into the bay at high tide. Therefore, there is a clear indication that these larvae have to be exported to the coastal area, where they can find suitable and stable salinity conditions.

The exportation of larvae to oceanic waters is generally perceived as an escape from stressful salinities or high densities of estuarine predators, and to avoid massive larval mortality within the estuarine waters. For Simith *et al.* (2012; 2014), the physiological characteristics of the larvae seem to be an evolutionary adaptation of estuarine reproducing species, where unstable conditions of salinity prevail, especially for those adult populations living in hard environmental conditions.

The primary importance of the larval exportation strategy is to achieve higher degrees of gene flow among distant habitats. As the larvae travel via coastal currents, genetic exchange among populations of different estuaries is facilitated (Paula, 1989; Morgan, 1990; 1995; Charmantier *et al.*, 2002). Species with this strategy would constitute metapopulations connected by a string of larval flow. As these populations adapt to their local environmental conditions, it is possible that specific evolutionary modifications would arise.

A retention strategy for larvae is also based upon behavioral responses to numerous physical parameters such as gravity, light, pressure, salinity and current speed. In contrast to an export strategy, the retention strategy has mechanisms preventing involuntary export from the parent estuary and these are connected to endogenous rhythms of larval release, behavioral responses of larvae and tidal and diurnal changes in the horizontal or vertical distribution. This strategy is performed by a relatively low number of taxa, suggesting that its evolutionary attainment is limited by phylogenetic constraints (see revision in Anger, 2001).

These divergent dispersion strategies (exportation or retention of larvae) can be partially related to the local occurrence of the respective adult populations, due to the passive transportation of their larvae (see Anger, 2001 for revision). In this context, it is probable that adult populations of *M. mordax* that colonize the inner oligohaline areas (salinities zero to 8 PSU) of Guaratuba Bay (Masunari, 2006) release larvae that are passively transported to the central mesohaline area that has about 20 PSU salinity (Martins, 2014), while those of *L. leptodactyla* that inhabit polyhaline areas – salinities from 20.40 ± 5.10 PSU to 23.63 ± 4.25 PSU, according to Masunari (2006) release larvae to coastal areas that have about 35 PSU.

Another explanation for diversified dispersion strategies may be related to salinity variation in the adult habitat. Brodie *et al.* (2007) verified that larvae of *Minuca minax* (Le Conte, 1855) obtained from ovigerous females living in a freshwater area survived longer (4–5 days) in zero salinity than those obtained from populations occurring in brackish water (2–3 days). These authors suggest that this could be related to the prevailing salinity during the embryonic period. Hence, the low tolerance of the larvae of certain species to freshwater would restrict the distribution of the adult populations in polyhaline waters.

In other Brazilian estuaries, the oligo- and mesohaline adult fiddler crabs such as *Minuca rapax* (Smith, 1870) that tolerate a wide range of salinity (1.0–42.1 PSU) (Thurman *et al.*, 2013), can produce larvae that also have an optimal salinity in a wide range (30–35 PSU) (Tab. 4). Similarly, the oligo- and mesohaline *M. vocator* that lives in areas with 0.9–36.3 PSU (Thurman *et al.*, 2013) also has a wide range of optimal salinity for its larvae, although at lower values (15–30 PSU) (Simith *et al.*, 2012) (Tab. 4). As *L. leptodactyla* larvae reach the megalopa stage at maximum frequency only at salinity 35, it can be inferred that it is imperative that they migrate to ocean waters to complete the larval cycle.

The larvae of other estuarine or semi-terrestrial brachyuran crabs have highly variable optimal salinities (15–35 PSU), but only *Parasesarma*

Table 4. Optimal salinity for larval development of the semi-terrestrial brachyuran crabs.

Fiddler crab species	Optimal salinity	Locality (country)	Reference
Minuca vocator	15-30	Mangrove of Caeté River (Brazil)	Simith *et al.* (2012)
Minuca mordax	20	Guaratuba Bay (Brazil)	Martins (2014)
Minuca minax	20-30	Delaware Bay (USA)	Epifanio *et al.* (1988)
Minuca pugnax	30	Delaware Bay (USA)	Epifanio *et al.* (1988)
Minuca rapax	30-35	Mangrove of Caeté River (Brazil)	Simith *et al.* (2014)
Uca tangeri	32	Cádiz Bay (Spain)	Spivak and Cuesta (2009)
Leptuca leptodactyla	35	Guaratuba Bay Basin (Brazil)	Present study
Other brachyuran crabs	**Optimal salinity**	**Locality (country)**	**Reference**
Armases miersii	15-25	Discovery Bay (Jamaica)	Anger (1996)
Helice leachi	20	Taiho River, Okinawa (Japan)	Mia and Shokita (2002)
Cardisoma guanhumi	20-25	Mangrove of Ceará River, Ceará (Brazil)	Abrunhosa *et al.* (2000)
Armases sangustipes	20-30	Mel Island, Paraná (Brazil)	Anger *et al.* (1990)
Aratus pisonii	25	National Park Morrocoy and Tacarigua Lagoon (Venezuela)	Díaz and Bevilacqua (1986)
Cardisoma armatum	25	Aquarium store, Munique (Germany)	Cuesta and Anger (2005)
Neohelice granulata	25	Mar Chiquita (Argentina)	Anger *et al.* (2008)
Sesarma brockii	25	Mangrove of Pitchavaram (India)	Kannupandi *et al.* (2000)
Ucides cordatus	25	São Mateus, Espírito Santo (Brazil)	Silva (2002)
Aratus pisonii	25-35	Paranaguá Bay, Paraná (Brazil)	Marochi *et al.* (2017)
Armases rubripes	30	Punta Carretas, Montevideo (Uruguai)	Luppi *et al.* (2003)
Ucides cordatus	30	Mangrove of Caeté River, Pará (Brazil)	Simith and Diele (2008)
Parasesarma catenatum	35	Estuary of Transkei, Mgazana (África)	Paula *et al.* (2003)

catenatum (Ortmann, 1897) seems to have an exportation strategy (Paula *et al.*, 2003), due to its optimal salinity being restricted to oceanic water (35 PSU). Most of the remaining species have larvae with a wide range of salinity tolerance (Tab. 4).

A low tolerance to freshwater and oligohaline water is observed in larvae originating both from species whose adults live in polyhaline waters (such as *L. leptodactyla*) or oligohaline ones (such as *M. mordax*). The ZI larvae of the first species survived at S0 and S5 for 24 hours and 48 hours respectively, without molting to the next stage (present study), and for larvae of *M. mordax* these salinities are lethal (Martins, 2014). Other fiddler crabs also show similar responses to oligohaline water (low tolerance) for example, *M. rapax* reported by Simith *et al.* (2014), *M. minax* by Brodie *et al.* (2007), and *M. vocator* by Simith *et al.* (2012). This behavior indicates a low level of adaptation to zero or low salinities for fiddler crab larvae.

After the larvae reach the last stage of development (megalopa) in the mesohaline or polyhaline waters, they have to come back to the limnic or estuarine environments in order to ensure the renewal of the parental populations (Anger *et al.*, 1994; Morgan, 1995). During the present work, larvae of *L. leptodactyla* only reached the megalopa stage in salinities equal to or above 25 PSU while those of *M. mordax* did so in salinities as low as 15 PSU (Martins, 2014). This divergent salinity requirement of megalopa larvae would ensure the appropriate colonization of parental populations. Results from previous studies support this assumption, including that adults of *M. rapax* and *M. vocator* live in mean salinities of 16.7 ± 2.2 PSU and 10.7 ± 3.0 PSU, respectively (Thurman *et al.*, 2013), hatch larvae that only reach the megalopa stage in salinities of at least 25 PSU and as low as 10 PSU, respectively (Simith *et al.*, 2012; 2014).

Salinity oscillations may vary among estuaries with different climatic and hydrological characteristics. According to Simith *et al.* (2014), the type of larval dispersal (exportation or retention) may be dissimilar, even within the same species, in the case of geographically isolated populations. Therefore, these authors suggest that this factor should be extensively investigated in fiddler crab populations occurring in numerous estuaries located along the Brazilian Atlantic coast.

Effect of different salinities on the duration of larval development and number of larval stages

The present study confirmed that salinity constitutes not only a limiting factor for larvae survival, but also influences the duration and number of larval stages of *L. leptodactyla*. Zoea larvae reached megalopa in a shorter time at S35 than at S25. Similar results were also observed in *M. rapax* (Simith *et al.*, 2014) and in *Afruca tangeri* (Eydoux, 1835) (as *Uca tangeri*, Spivak and Cuesta, 2009).

The slower development pace may be related to increased excretion rate (Johns, 1981; Kannupandi *et al.*, 1997) or to the osmotic stress caused by unfavorable salinity during development. This may have an affect on food absorption (alteration in the eating behavior and metabolism) that, in turn, directly influences the growth rate of larvae (Anger, 2001; 2003). On the other hand, according to Ismael *et al.* (1997), the reduction in larval development duration observed in more favorable conditions is likely due to a decrease in the intermolt period.

Gonçalves *et al.* (1995) state that a shorter larval development time allows species to have a greater chance to reach maturity earlier, which is important for their survival. In addition, an abbreviated larval development could reduce the risk of predation and physical stress in the pelagic environment (Morgan, 1995). On the other hand, the reduction in development time does not necessarily represent a competitive advantage, since it may limit larval dispersion in natural environments (Anger *et al.*, 1990).

Another effect of less-than-favorable salinities during larval development is the emergence of supranumery stages. From ten fiddler crab species occurring along the Brazilian coast (Bezerra, 2012) only six were successfully raised in the laboratory until reaching the megalopa stage: *Leptuca thayeri* (Rathbun, 1900) (Anger *et al.*, 1990), *L. uruguayensis* (Nobili, 1901) (Rieger, 1996), *M. mordax* (cf. Rieger, 1997), *M. burgersi* (Holthuis, 1967) (Rieger, 1998), *M. vocator* (Rieger, 1999), and *L. leptodactyla* (present study). The first four species showed five stages of zoea and one of megalopa, while the last two had only four zoea stages. Although of rare occurrence, supranumerary stage (6th stage) of zoea can be observed in some species when cultivated in the laboratory.

This prolongation of larval development duration through a 6th stage of zoea before the megalopa represents a possible alternative pathway, which occurs under unfavorable food or environmental conditions (Montú *et al.*, 1990; Anger, 2001). In fact, Silva *et al.* (2012) verified that the emergence of a 6th stage was associated with poor feeding conditions during cultivation of the larvae of *Ucides cordatus* (Linnaeus, 1763). Additionally, most successful metamorphosis occurred directly from zoea V to megalopa, and most zoea VI died without molting to megalopa in this species.

On the other hand, other authors found supranumery larval stages in some species of fiddler crabs, even when the larvae were cultivated under favorable conditions (Anger *et al.*, 1990; Rieger, 1996; 1997; 1998). Negreiros-Fransozo *et al.* (2009) suggest that the extension of zoea larval development may be a strategy to wait for more favorable tidal regimes for megalopa settlement.

Costlow and Bookhout (1968) have previously observed that the number of larval stages of certain crustaceans is not constant and can be influenced by diet and other factors, not only in the laboratory but also in nature.

The evolutionary meaning of greater or lesser numbers of larval stages in the development of decapod crustaceans is inconsistent among authors. Sandifer and Smith (1979), studying Palaemonidae, stated that, in addition to abiotic variables, the tendency of a given larva to pass through a number of larval stages may be hereditary. According to the authors, variations in the number and duration of each planktonic larval stage can affect the dispersion of the species and the survival of the parental genotypes. On the other hand, Waterman and Chace (1960) point out the evolutionary tendency to both extend the embryonic period and to shorten, or totally eliminate, larval stages in many crustacean groups. Based on this hypothesis, Rieger (1999) infers that fiddler crabs are undergoing an evolutionary process towards reducing the number of zoea stages. This pattern may be a favorable trait for larval survival, since their planktonic life is quite critical for them, while incubation on the female pleopods provides

protection during embryonic development (Rieger, 1997). However, it is quite difficult to consider that the closely related Brazilian fiddler crabs, including *L. leptodactyla*, could have a distinct evolutionary pattern, based only on the number of zoea stages.

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